IV.—*On the Mechanism of Aquatic Respiration and on the Structure of the Organs of Breathing in Invertebrate Animals.*

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[With two Plates.]

[Continued from vol. xiii. p. 312.]

Mollusca.

The Annulose and Arthropodal series conduct by a separate path across that wide space which divides the Echinodermal from the Vertebrate animal. The Molluscan subkingdom traverses the same distance by a divergent route which begins at the Bryozoon and terminates at the Cephalopod. These grand invertebrate chains of beings unite mutually below at the Echinoderm and Bryozoon, and superiorly at the basilar link of the vertebrated series. The zootomist, having studied serially the articulate families, is constrained to return to the base of the invertebrate cone, in order to seize the point of departure of that independent road along which the molluscan families attain the summit. Between these groups there exist few points of intercommunication. Reciprocal affinities nowhere attract attention. The Mollusca constitute a separate study: in varieties of form they are equalled by no other division of invertebrate animals; in number of species they exceed almost the limit of arithmetic; in diversities of structure they bewilder the anatomist; in modes of life discordantly diverse, they perplex the student of their habits. And yet a deeper insight into the plan of the molluscan organism enables the earnest thinker to seize the clue of natural union which obtains between the countless members of this variegated group.

Provided with a heart to circulate the blood, a distinct alimentary system, a nervous system, and its satellitic organs of sense, a muscle-apparatus, viscera of complex organization, and a blood-fluid fibrinized and corpusculated, they offer to the physiologist a problem by no means easy of solution.

Of this composite machinery the respiratory function is the primary moving power. Without it nothing can go on. It is momentarily important. What provisions are made to insure its full and adequate performance? The terrestrial Gasteropods excluded, all mollusks respire on the aquatic principle. They are tenants of the water. The organs of breathing in bulk and complexity of structure far surpass those dedicated to other offices. The bulk of blood, which at any given time is included within the limits of the branchial organ, is relatively considerable. Measured by the complex magnitude of the branchiæ, the inert oyster is a physiological paradox. It is hard thence to believe that muscularity and respiration are directly proportional. The force generated by the act of breathing is expended in other directions. Cephalopods and air-breathing Gasteropods apart, the branchial structures of every known mollusk are abundantly ciliated. In this anatomical particular they contrast strikingly with those of the Crustacea. Both are breathers of water. In one only are cilia provided. The question implicating the *reason* of natural things lies far too deep to be fathomed by a mechanical explanation. In both the purpose to be accomplished is the same; in both the means employed are intimately similar, and yet in one instance vibratile cilia are constituently admitted into the mechanism, in the other they are rejected. Biochemistry at a future æra will elucidate these mysteries.

The peripheric circulation in the Mollusca is lacunar rather than capillary. This capital fact was first established by Milne-Edwards* and Valenciennes †: these authors describe the blood as effused into the parenchyma of the body. It returns into the veins without the intervention of capillaries. The details upon which rest these general postulates will be afterwards stated. In the anatomical character of the peripheric passages, in the small proportion of fibrine in the blood, the circulating system and the blood of the Mollusca resemble obviously the chylaqueous fluid and its containing system.

In all mollusks, separate, specially constructed organs are consecrated to the function of breathing. Even the Brachiopoda are not exceptional to this rule; they are pallio-branchiate. The universal presence of complexly formed and profusely multiplied respiratory organs attests the extreme value of the office which they are designed to fulfill.

The ultimate vessels of the branchiæ in all mollusks, those of Brachiopods and Tunicates ‡ excepted, occur in the form of straight

* Obsérv. et Expér. sur la Circul. chez les Mollusques.—Comptes Rendus, 1845, xx. p. 261.

† Nouv. Obsérv. sur la constit. des appareils de la Circul. chez les Mollusques.—*Ibid.* p. 750. See also Ann. des Sc. Nat. 1845, iii. p. 289.

‡ I regret that no recent opportunity has occurred to me to test the validity of the anatomical principle expressed in the text. For the present I assume that the ultimate blood-channels in the branchiæ of the Tunicate mollusks *reticulate* (Pl. I. fig. 2 & fig. 4); that is, that the blood which moves at one moment in one direction courses at the next in another at right angles with the former, the whole being on the same plane, and the circumscribed stigmata being water-passages. This assumption conforms with the description of all observers from the time of Savigny.

parallel non-communicating tubes, of regular outline and uniform diameter in the Lamellibranchiata, of irregular contour and variable diameter in the Cephalophora. In *all*, the ultimate blood-channel constitutes one, single, independent tube from one end of its course to the other. Returning upon itself it does not lose its individuality: it nowhere inosculates: it reticulates in no single instance. *One* foundational law of structure is thus proved to preside over the disposition of the ultimate elements of the branchial organs in all the mollusks above the Tunicata. Already the thoughtful eye descries the bright, continuous thread of 'principle' linking remotely separated and disjointed varieties into the golden chain of consistent unity. Another generality no less remarkable remains to be propounded. The branchiæ of *all* Tunicate and *all* Lamellibranchiate, and a considerable majority of the Gasteropod mollusks are *penetrated* by the aërating water. The branchia is a sieve through which the water filters. This act of branchial filtration is a fundamental fact in the history of all the inferior mollusks. The area which is circumscribed by the mantle, at least in all Tunicate and Lamellibranchiate mollusks, is divided more or less completely into two distinct compartments, the one pallial and external, the other internal and visceral (Pl. I. fig. 7, *c* & *d*; Pl. II. figs. 9 & 13). The branchiæ constitute *cribriform* plicæ developed on the divisional membrane (fig. 7, *e, e, e, e*) by which these two compartments (*c, d*) are separated.

These leading propositions outlined in brief, will suffice to prepare the mind for the right conception of those interesting details which it is now proposed to consider.

The limits of these papers render it impossible to refer *in extenso* to those anatomic specialties by which the branchial organs of every species are more or less differentially characterized. Those only can be selected for study which involve a typical principle. Rules, not exceptions, it must be the aim of these investigations to define.

Tunicata.

Tunicate mollusks stand immediately above the Bryozoon. From the latter they are distinguished in the possession of a heart. The movement of the blood is due exclusively to the contractions of this central organ. The heart is systemic and tubular. In many genera it is valveless, as indicated by alternations of direction in the blood's course. No definitely parieted vessels occur on any segment of the peripheric arc of the circulatory system. To this rule the branchial forms an exception. The branchial "bars" are, however, not ordinary vessels. They are peculiarly formed. They are not analogous to those of the vertebrated animals. They are bounded by skilfully configurated cartilages, as will be afterwards explained. In the Tunicata, as in other Acephala, the blood leaving the open ends of the arteries passes into the interstices—*lacunæ*—of the parenchyma of the body; thence it is taken up by the open mouths of the venous radicles. The solids are thus literally soaked in the fluids. The former are everywhere bathed by the latter. It may be affirmed in a general sense, that the higher the serial position of the animal, the smaller the breadth of the ultimate blood-currents, and conversely. The degree of subdivision which occurs in the blood-streams represents a numeric measure of the nutritive actions. The area comprehended by the mantle is divisible in the Tunicata, as in Acephala, into two sub-areas. The one is either bounded, lined, or traversed by the branchiæ, and contains the mouth; the other embraces the viscera and includes the anal outlet. This fact is absolute. That space into which the *mouth* opens is homologous with the pallial extra-branchial or general cavity of the mantle in the Acephala. That in which the intestine terminates coincides with the intra-branchial or visceral enclosure in all bivalves. An exact conception of these primary divisions of the body in the inferior mollusk is really indispensable to the perfect understanding of those respiratory and alimentary currents of the water, the direction and relative bearing of which have perplexed anatomists from the epoch of Cuvier to the æra of Messrs. Hancock and Clark.

In the œconomy of the Tunicate and Acephalan mollusks this principle is inviolable—that nothing, neither water nor alimentary particles, is conducted to the mouth, which has passed *through the gills.* Water charged with carbonic acid is never swallowed.

The feculent pellets are never and cannot be mixed with the alimentary. The current which conveys fresh water to the branchiæ is convective also of food to the mouth. The stream which carries away the effete product of respiration bears off the feculent rejectamenta.

There are then, in truth, but *two* chief œconomic water movements in these animals—that which enters the pallial or extra-branchial space, and that which leaves the visceral and intra-branchial inclosure. This is simple and intelligible. It resembles a ray of light shining amidst a darkness which for half a century has brooded over a vexed and perplexing controversy.

It is impossible to perform one step in advance towards a more satisfactory knowledge of this subject, unless the meaning of the "siphons" (Pl. I. fig. 1, *a*, *h*) be first brought into the light of clear definition. They are commonly distinguished into the branchial and the anal. The terms in the ordinary signification would indicate the first as the orifice of ingress, and the last as that of egress. This, however, is not the acceptation in which they are used by authors of great celebrity. Mr. Rupert Jones* observes: "The position of the animal is such, that of the two orifices the branchial is always the highest; the entrance into the branchial sac being generally placed at or near the superior extremity of the body, and the œsophageal opening at the base of the branchial sac having an upward direction." This is directly opposed to the definition of M. G. P. Deshayes†, who says—"Whether connected or not, the superior siphon is always characterized as the *anal*, the inferior as the *branchial* siphon." Of course the comparative "superior" must mean that which is nearest to the hinge or dorsum; "inferior," that which is next to the venter, the antipodal point to the hinge. The branchial siphon of Mr. R. Jones is therefore correspondent with the anal of M. Deshayes.

The expression of Cuvier—"deux ouvertures séparées, l'une pour la respiration, l'autre pour les excrémens," &c.—suggests the idea that one tube, the branchial, is devoted exclusively to respiration; that is, that through the *same* tube the inspiratory and expiratory currents concerned in breathing take place.

Dr. George Johnston observes: "The water is imbibed through a branchial siphon. The effete fluid is expelled again through another or anal siphon ‡." The branchial siphon of other authors is the longest or superior, and is distinguished as that which *emits* the refuse water which has traversed the branchiæ. The branchial siphon in the sense in which it is used by Mr. Garner § is synonymous with the inhalent tube, and the anal with the exhalent. In this acceptation the terms are also used by Forbes and Hanley ||, by Alder and Hancock¶, and by Mr. Clark in his excellent controversial papers against Mr. Hancock in the 'Annals.' Dr. J. E. Gray attaches to these words a similar meaning, calling the inhalent 'the lower' siphon, and the exhalent 'the upper'**.

The "branchial" siphon of the most esteemed authors then is that tubular extension (Pl. I. fig. 7, *a*, *a'*) of the mantle by which the surrounding element is admitted into the "bran-

* See article Tunicata.—Cyclop. Anat. Phys.

† See the article Conchifera.—Cyclop. Anat. Phys.

‡ See his recent excellent work, entitled 'Introduction to Conchology,' p. 275. Van Voorst, 1850.

§ Transactions of Zoological Society, vol. ii. p. 91.

|| British Mollusca, vol. i.

¶ See their valuable papers on the Branchial Currents in *Pholas* and *Mya*, Annals and Magazine of Natural History, Oct. and Nov. 1851.

** See his original and instructive papers in recent Numbers of the 'Annals,' on "A Revision of the Arrangement of the Families of Bivalve Shells," &c.

chial vault" (Clark), "branchial chamber" (Hancock), or "pallial cavity" (Forbes and Hanley) (*d*). It is indifferently described as the "lower," "shorter," "inferior" or "ventral." It is the further of the two siphons from the hinge. Its office is "inspiratory," "inhalent," "branchial" or "prehensile."

The "anal" siphon (fig. 7, *b, b'*) is variously defined as the "upper," "superior," "dorsal," "exhalent," "excrementitial," "expiratory," "longer," &c.

That is called "inhalent" which the most conscientious and truth-loving observers declare does not inhale: that the "exhalent" to which an emissive office is strenuously denied! There are but two cavities (fig. 7, *c, d*) and only two siphons (fig. 6, *a, b*). Of the latter one communicates with one cavity, the other with the other. The boundaries of these cavities severally are conspicuously and unequivocally marked. They are as distinctly defined as the siphons with which they respectively communicate. But though clearly bounded they are not independent. Fluid introduced into the one will unquestionably pass into the other*. Neither the process by which food is brought to the mouth, nor that of respiration, could be understood before the fact was discovered of the *permeability* of the branchial lamellæ. To Dr. Sharpey should be ascribed the merit which belongs to the first discovery of this point†; to Mr. Hancock that of its full and com-

* At a subsequent stage of these inquiries, this general statement will be supported by abundant evidence.—See Acephala.

† Dr. Sharpey's description cannot be misconstrued. "On removing one of the valves, turning down the cloak, and putting moistened charcoal powder on the surface of the gills, the finer part of the powder soon disappears, having *penetrated through the interstices of the bars or vessels* into the space between the two layers of the gills. On arriving there, a part is often forced out again from under the border of the unattached layer at the base of the gill, but most of it is conveyed rapidly backwards between the two layers, and is carried out at the excretory orifice with the general current . . . The coarser particles remain outside the gill and are slowly carried to its edge, following the direction of the bars: they then advance along the edge of the gill towards the fore part of the animal. It thus appears that the water first passes in between the lobes of the mantle to the external surface of the gills; it is then *forced* into the space enclosed between their layers, from whence it is driven out at the excretory orifice, *to which the enclosed spaces of all the gills lead.* As this process continues to go on after the shell and lobe of one side are removed, it is evident that the motion of the water must be *mainly produced by the cilia of the gills.* . . . By their agency the fluid is forced into the space within the gills, and this operation taking place over the whole extent of the gills, must by its concentrated effect give rise to a powerful issuing stream at the excretory orifice, of which the entering stream seems to be a necessary result."—Art. Cilia: Cyclop. Anat. & Phys. In this most able summary, three *principles* are lucidly affirmed:—1st. That the water concerned in breathing *permeates the branchial lamellæ,* and thus traverses the partition which divides

plete demonstration. Mr. Clark*, however, embraces still the doctrine which contends for the non-communicating independence of the siphons and of the cavities of which they are the external continuations. In this respect, his conclusions are directly opposed to the results of the author's observations. That the cavities recently so clearly defined by Mr. Hancock are by structure and office distinct, will be afterwards irrefragably proved. This division of the pallial enclosure into two leading sub-areas constitutes a fundamental feature in the œconomy of the Tunicate and Lamellibranchiate mollusks. It suggests a natural process of thought by which the siphonic actions are interpreted infallibly. It will be subsequently proved, that that siphon which is said by Messrs. Alder and Hancock to give ingress to the water, is really no more branchial than that by which the fluid makes its egress. Both bear to the branchiæ the same anatomical relation. It were as correct to designate the opercular orifice in the fish as the "anal," and the mouth as the "branchial," as to apply such terms to the siphons of the Tunicata and Acephala. Such designations misinform. They express either what is not true, or what is only partially true. The "branchial" siphon is as much oral or prehensile as branchial. The "exhalent" as much anal as expiratory.

It is quite established that two distinct offices devolve upon each siphon. The one is designed to take in water for the purpose of breathing, and alimentary particles for the purposes of food; the other emits at once the products of the respiratory and digestive processes. One name as applied to either will not express the double function. Let the name therefore be drawn

the pallial from the anal chamber. 2ndly. That by this act of sieving the food, the aliment is separated from the water and impelled by ciliary action towards the free margins of the gills and along the groove formed expressly for this purpose on this margin, and finally borne in the direction of the mouth. And 3rdly. The distinctness of the inhalent from the exhalent current; while Dr. Sharpey speaks plainly upon the point that the *excurrent* is set in motion *exclusively* by the *branchial* cilia. It is extraordinary that, in asserting claims to originality upon these very points, in papers published ten years afterwards, so careful and honest a student as Mr. Hancock should have permitted this accessible and celebrated article of Dr. Sharpey to elude his literary search! I rejoice rather than lament over Mr. Hancock's "sin of omission." Confirmation, enriched by numerous valuable original details, proceeding from so truthful an observer, must prove of immense service to the cause of science; but, *palmam qui meruit*. To widen the bounds of knowledge is the highest gratification which belongs to the true man of science. This is his most valued title of nobility. To withhold from the labourer his just reward, is to perpetrate a criminal offence against science.

* On the Pholadidæ.—Ann. and Mag. Nat. Hist. Nov. 1850.

from structure rather than from office. In these papers accordingly that siphon which opens into the pallial or ventral chamber will be distinguished as the *extra-branchial* siphon; that leading from the dorsal, visceral or anal cavity, as the *intra-branchial siphon.* These distinctives express only the anatomical position of these tubes relatively to the branchial partition by which they are separated. They involve no hypotheses. They attribute no function. They cannot misguide.

In the Tunicata the *extra-branchial* siphon (Pl. I. fig. 1, *a*; 2, *a*; 3, *a*) leads into the pharyngeal cavity (*b*), which is homologous with the ventral or pallial chamber of the Acephala. It is the longer and higher of the two. All fluid which reaches the mouth (fig. 3, *b*), seated at the lower boundary of this cavity, must gain the pharyngeal chamber through the extra-branchial siphon. All alimentary substances *rejected* by the mouth, that is, those material particles *not swallowed,* are sent out again by a convulsive jerk of the cavity through the *same* siphon. It is essential to distinguish the substances thus *refused* by the mouth from the true excrementitious pellets which are *always* ejected by the *intra-branchial* siphon.

The *mode* in which the surrounding element enters the pallial space has distracted controvertists, and divided them in belief. By Mr. Hancock, representing one class of observers, it is maintained that the inhalent current is set in motion exclusively by the action of vibratile cilia seated on the lining membrane of the siphon itself. By Mr. Clark this explanation is denied. The former naturalist rests his theory upon the alleged demonstration of cilia on the *internal* surface of the inhalent siphon, the latter upon observation of the currents. The inquiries of Mr. Hancock were confined to the Lamellibranchiate mollusks. But it may be stated with confidence, that what is true of this class will apply to the case of the Tunicata. The dispute is really easy of adjustment. The adjustment here, however, fails in this sense, that the demonstration which is negative is less persuasive than that which is positive. To prove a denial is less easy than to substantiate an affirmation. The microscope leaves it beyond doubt, that the internal lining membrane of the *extra*-branchial siphon of the Tunicate is *not* provided with a vibratile epithelium. They sometimes exist on the tentacles at the base of the siphon, but most certainly not on the walls of the latter. The water which enters this siphon is assuredly therefore not drawn in by the agency of cilia within the siphon.

Further observations are required to determine the exact course of the currents excited by the cilia distributed over the branchial bars. It is not proved that the water enters the siphon in virtue of the cilia situated at the latter point. It enters at the moment of the diastole of the pharyngeal chamber. Such a movement operates suctorially upon the fluid within the sphere of its influence. Having entered the cavity, the water is whirled in a thousand *definite* directions by the branchial cilia. Every particle of material substance contained is rolled into minute pellets and borne in the direction of the mouth. If it be palatable, it is swallowed; if not, it is emitted forcibly again by the same siphon. The water which falls under the influence of the proper branchial cilia is impelled in such manner and direction, and in myriad invisible currents, that it permeates the branchial membrane (fig. 1, *b*; fig. 2, *b*) by means of the meshes circumscribed by the vascular bars. The passage of the water through these meshes does not occur in direct currents, but in streams which pass up and down the sides of the meshes several times before they finally reach the *intra-branchial* or visceral cavity—therefrom to be rejected by the intra-branchial or anal siphon, so that the aërating element by this contrivance is detained for some time in contact with the blood-channel. The egressing current saturated with carbonic acid escapes from this latter siphon in a *continuous* stream,—such a stream as an uninterruptedly acting force alone could determine. The microscope was accordingly applied to the examination of the lining of this siphon, anticipating the immediate detection of vigorous ciliary action. Ascidians, Cynthians, and Clavellinans, submitted to careful inspection, disproved the anticipation. In none, by any device, could cilia be demonstrated on the inner wall of this anal or *intra-branchial* siphon. The current, therefore, which escapes at its orifice is not set in motion by any force within the limit of the siphon itself, but rather by that which is placed at a distance—the *branchial* ciliary action. The space interposed between the branchial membrane and the mantle in Tunicates forms a part of the intra-branchial or visceral cavity. It is filled with refuse water, rendered poisonous by carbonic acid. This effete fluid enacts no further part in the organism. It is finally rejected.

In the Tunicata then the two siphons are *continuous* through the branchial stigmata. The mass of water which always more or less fully distends the body of the animal, observes only one normal or regular movement, viz. that tending from the extra-branchial siphon (fig. 1, *a*) in the direction of the intra-branchial (*h*). The *irregular* and *occasional* currents are propelled in the reverse directions. The pharyngeal cavity may muscularly contract, and now and then emit pure unrespired water, and unused alimentary substances held by this water in suspension. If such discretionary power did not exist, the indiscriminating mouth would swallow every solid substance borne mechanically into the pharyngeal chamber by the water drawn in by the extra-branchial siphon. Nature's machinery would then, indeed, wear the disgraceful impress of faultiness.

In the Ascidians the branchiæ completely line the walls of the pallial chamber. In figure the chamber varies; it is oblong in some species, oval and rectangular in others. The branchial membrane in *Ascidia, Phallusia,* &c. forms a plane unfolded sheet, adapting itself to the cavity of the mantle; in *Cynthia, Boltenia,* &c. it is longitudinally plicated (fig. 5) and disposed in deep and regular folds. The ultimate vessels (*d*) are arranged rectangularly. The circumscribed 'stigmata' (*c*) are parallelogrammic in figure. These perforations lead from the pharyngeal into the "thoracic" chamber of Milne-Edwards. Why it should be called 'thoracic' is difficult to understand. As already defined, it is really the visceral, intra-branchial or cloacal cavity. The branchial vessels in the Ascidians are arranged in two planes (fig. 4). In *Cynthia ampulla* the meshes are very irregular and almost inextricable, some of the minute vessels having apparently a spiral arrangement. In *Chelyosoma,* Eschricht figures a similar vermicular disposition of the branchial vessels. The branchial membrane of *Cynthia* presents large longitudinal vessels. They are crossed by others of equal size. Large meshes (*d*) are thus formed. Smaller vessels (*b*) lying on a different plane form by crossing smaller stigmata. In *Ascidia* and *Chelyosoma,* the angles of the meshes of the branchial membrane bear *papillæ* (*c*) more or less prominent. In *Cynthia* they do not exist. These papillose processes are hollow recesses. They are by-receptacles for the nutritive fluid. In size the branchial vessels vary in different genera. In *Cynthia* they are large, in *Ascidia* they are minute, in *Cystingia* they are indistinct. The branchial plicæ converge at the mouth whenever they exist.

By Carus and Van Beneden a *lateral* opening in the respiratory cavity has been indicated, by which the water passes directly from the branchial sac into the cloaca (fig. 1, *o*; fig. 3, *e*). This aperture corresponds with the open fissure which in many species of Acephalans exists between the attached border of the branchiæ and the base of the foot. It is a safety-valve, as will be hereafter explained.

In Clavellinidæ, Botryllidæ, in the genera *Pyrosoma, Pelonaia* and *Salpa,* such is the structure of the branchiæ, that the water readily traverses the respiratory stigmata, and passes from the extra-branchial into the intra-branchial chambers.

In all genera the branchial membrane is attached by means of threads and vessels externally to the mantle.

The branchiæ in the Clavellinidæ exist in form of a band stretching across the cavity of the mantle, and dividing the pharyngeal from the cloacal chamber. In ultimate structure the branchiæ of this genus differ from those of the Ascidians: in place of presenting on each side simple striæ furnished with vibratile cilia, as in the Salpians, they bear right and left a series of filiform appendages directed horizontally towards the ventral side of the respiratory cavity, where they are fixed on each side of the middle sulcus, and during their passage across are united together by a number of other slender vertical filaments. From this disposition of parts there results a kind of trellis-work, which fills up all the pharyngeal portion of the branchial chamber, permitting no communication between the latter and the cloaca except through the meshes of its network, which are bordered all around with vibratile cilia*.

The branchial sac of the Botryllidæ is like that of the Clavellinidæ: it is similarly organized. The branchial spiracles are variable in number. It is in general only slightly folded. The respiratory sac in *Botryllus* lies horizontally, and has only nine rows of stigmata, grouped into threes by the longitudinal folds. The angles of the branchial network are marked with *papillæ* in *Distoma* and *Diazona*.

The *branchiæ* in *Pyrosoma* line the internal tunic of the mantle. They are orally disposed. They consist of numerous vessels or channels anastomosing with each other at right angles. "Nothing is more curious," says Milne-Edwards, "than the respiratory apparatus of these animals, when the vibratile cilia with which each of the stigmata is furnished are simultaneously effecting their vorticiform movements with rapidity and perfect harmony†."

In *Salpæ* the gill is constructed of a flattened tube, stretched on a vertical plane obliquely across the central or branchial cavity of the body. It is composed of a double membrane formed by a fold of the internal tunic or mantle. It partitions the branchial chamber into two portions—the pharyngeal and cloacal.

The circulatory systems of the Ascidians resemble that of the Bryozoa. If the heart were removed, it would be a chylaqueous system. It is transitional between the Polypes and the Mollusks. Van Beneden compares the Ascidian to a digestive canal suspended in the midst of an external envelope surrounded by a fluid moving in the open spacious perintestinal space. It is only in the branchial network and tentacles that it can be said to be contained in vessels.

Mr. Gosse gives an exact description of the living circulation in *Perophora Listeri* (fig. 3). Speaking of the blood-globules, he

* See article Tunicata.—Cyclop. of Anat. and Phys.

† Annales des Sciences Naturelles, 2nd ser. tom. xii. p. 375 (1835).

observes, "They do not appear to pass into a defined system of vessels, ... but find their way through the interstices of the various organs in the various cavities of the body. . . . They proceed by jerks; some find their way into the space between the breathing surfaces, and slip in between the rows of oral rings (*stigmata*), and wind along down between the rings in irregular courses*."

In the Ascidiadæ and Clavellinidæ the centres of this system consist of two trunks, a dorsal and a ventral, the capillary system of the branchiæ being intermediate. Lister's famed observations on this subject should be consulted†. The descriptive details afterwards to be presented on the subject of the respiratory and circulatory systems of the Acephalans, will illustrate many points of interest in the structure of the corresponding systems of the Tunicata. The peripheric channels of the blood are analogous in the two classes. The ultimate structure, though not the *arrangement* of the vessels of the branchiæ, is also similar. The nutritive fluids, morphotically distinctive, are chemically identical in the two classes.

Acephala.

In the Terebratulidæ there exists no express apparatus for breathing. With the Craniadæ they are therefore placed at the inferior limit of the Lamellibranchiate series. Prof. Owen has shown that the mantle in the Brachiopods is more vascular than in those orders of bivalves in which gills exist. Dr. Carpenter‡ has lately shown that the external layer of the mantle in *Terebratula* and certain other Brachiopoda, sends out *cæcal* tubes *through* the shell. They are respiratory in office, and the exact counterpart of those membranous processes which the author of these papers has described in the Echinodermata as projecting up above the external surface of the body. The *cæcal* character of these parts establishes a community of type between the fluid system of the Brachiopods and the chylaqueous system as defined by the author. The arms are long, richly ciliated tubes. In these tubes the blood moves in a *single* channel by flux and reflux. This incident also in the history of the fluids allies these inferior mollusks with those animals in which a chylaqueous system only exists. This latter fluid never undergoes an orbital movement: it fluctuates to and fro. The ultimate respects in which the vessels in the mantle of the Brachiopods differ from

* See his interesting work, 'A Naturalist's Rambles on the Devonshire Coast,' p. 245.

† Phil. Trans. 1834.

‡ Proceedings of the Royal Society, April 6, 1854.

those of the mantle of the higher Acephala; and what differentiation of these parts was required to enable an ordinary structure to discharge a special office, has been shown by Dr. Carpenter.

The organs of breathing are well developed in all the Lamellibranchiate Acephalans. Their vascular system is elaborately multiplied. They are capable of containing a considerable amount of blood. If aquatic were not less intense than atmospheric respiration, the aggregate area of the surface exposed by the gills of mollusks in general would insure a measure of effect sufficient to raise these animals high in the scale of physiological activity. *Surface* is not the only factor to be counted in determining the dynamic value of the respiratory office. The composition of the blood demands a numeric place in the calculation. If the fluid occupying the vessels were identical in density with the exterior element, no interchange of gases could proceed. A difference in the specific densities of the gases held in solution by fluids of identical gravities would constitute a condition in virtue of which the gases would reciprocally move independently of the fluids. The less the proportion of fibrine in the blood, other things being equal, the lower is its absorptive capacity for gases. The blood of mollusks is less charged with fibrine than that of the higher Articulata. In the former the floating corpuscles are less highly organized. They are strikingly less filled with solid contents. They are smaller and yet not more numerous. The physical conditions as regards the fluids then are not favourable in the Mollusca to a high rate of respiration.

Cuvier first defined the bivalve mollusks under the title of *Acephala testacea*. By Lamarck they were constituted into a separate class under the name of *Conchifera*. M. de Blainville marshalled them under the order *Acephalophora lamellibranchiata*. The anatomical definition of Cuvier presents clearly the chief points of structure:—" Leur corps qui renferme le foie et les viscères est placé entre les deux lames du manteau; en avant, toujours entre ces lames, sont les quatre feuillets branchiaux striés regulièrement en travers par les vaisseaux; la bouche est à une extremité, l'anus à l'autre, le cœur du côté du dos; le pied, lorsqu'il existe, est attaché entre les quatre branchies*."

The *mantle* of the mollusk is a grand feature of the organism. Its horizontal lobes embrace, its *vertical* process, on which the branchiæ are evolved structurally and functionally, bisects, the whole body. The mantle at once invests and secretes the shell, and forms the very basis of the body of the animal. It is composed of muscles, nerves, fibres, and vessels. It is lined internally in all cases with vibratile epithelium. A straight line,

* Règne Animal, vol. sur les Mollusques, p. 182.

carried from the anterior to the posterior extremity of the shell in any Acephalan, divides the mantle and the body into two very distinct and dissimilar halves. On one side lie the branchiæ and extra-branchial, ventral, or oral chamber (Pl. II. fig. 13); on the other are disposed the viscera, the intra-branchial or dorsal cavity; with the latter the exhalent or intra-branchial siphon is *necessarily* and *invariably* connected; in this dorsal compartment, also, the anal orifice terminates. That cavity (*b*) which lies on the ventral (the side opposed to the hinge) or right side of the hypothetical line, whether the ventral borders of the mantle be open or closed, siphonal or asiphonal, is always and *necessarily* filled with *pure water*. In this chamber the branchiæ (Pl. I. fig. 7^2, *a, b*) whatever be their number or position, figure or size, freely float; it is here always that the oral orifice (fig. 13, *a*) opens; it is at once a reservoir of pure water for breathing and pure material for food. All varieties centre in the unity of this idea—all specific aberrations are reducible to this basilar type. Specific diversities arise more frequently from variations in the number, size, siphonal or non-siphonal character of the openings communicating with this (oral or extra-branchial) chamber (Pl. I. fig. 6, *b, b*; fig. 7, *c, d*), than from those which occur in the siphonal processes of the intra-branchial or anal cavity (fig. 13, *e*). Mr. Clark * and Dr. J. E. Gray † are the most recent and distinguished conchologists who have attempted intelligently to found a classification of the Conchifera on the basis of the varieties which occur in the pallial orifices. Dr. Gray groups the whole class under two primary designations—the *Siphonophora* and *Asiphonophora*—which are again subclassified into orders, genera, and species. In the Pholadidæ, Myadæ, Gastrochænidæ, and Solenidæ, the ventral borders of the mantle are united, and the siphonal tubes are long and more or less distinct. The mantle is also closed in the Corbulidæ and Anatinidæ, but the siphons are short. In the Tellinidæ the mantle is open, while the tubes are prolonged. An open mantle coexists with short siphons in Cardiadæ, Veneridæ, Mactridæ, and Donacidæ. An open mantle is co-present with sessile tubes in Cycladidæ, Kelliadæ, Lucinidæ, Cyprinidæ, Unionidæ, and Arcadæ. In Mytilidæ, Ostreadæ, Pectinidæ, and Anomiadæ, the whole gape of the mantle is one undistinguished capacious orifice. Guided by the rule that pure water must in some manner or other, with adequate freedom, be admitted into the oral or extra-branchial cavity, it is quite obvious that the

* Ann. and Mag. Nat. Hist., June 1851. "On the Classification of the Marine and Testaceous Mollusca."

† Ann. and Mag. Nat. Hist., May 1854.

larger the ventral or common opening of the mantle, the *less* is the necessity for the lower or extra-branchial siphon. If, on the contrary, the leaves of the mantle be fused at their borders all round, a well-developed siphon is absolutely required. This cavity must have a free and ready communication with the exterior. If this communication is not established in one mode, it must in another. A siphon is a *necessary* provision if the mantle be closed; if open, it is only supplementary. In the former case, everything fluid and solid which enters the pallial cavity must pass through the extra-branchial siphon. It can gain the chamber through no other source. In the latter, the siphon is only incidentally and occasionally used. The great bulk of water drawn into the cavity rushes in through the ventral and pedal openings. That which, alike solid and fluid, is returned *unused* from this cavity, is indiscriminately jerked out by muscular action through any of the mantual openings. If the pellet of sand be situated near the opening of the siphon of this cavity, at the moment when it receives the impulse of ejectment, it escapes through the *inhalent* or extra-branchial siphon (Pl. I. fig. 6, *b*). If, on the contrary, it be placed at the other end of the chamber, it will be driven out either through the ventral or pedal gape. The orifice and direction in which *refused jets* of water take place from this cavity are contingent upon the position which the rejected portion may have previously occupied in the cavity. Upon this important point neither Mr. Clark nor Mr. Hancock are clearly informed. Mr. Clark is correct in stating that the ingress of the water into the great mantual or extra-branchial cavity is due, not to the invisible agency of vibratile epithelium on the lining membrane of the siphon, but to the diastolic separation of the valves. Mr. Hancock is undoubtedly in error in stating that the water entering this cavity is drawn in by cilia of the *siphon*. The microscope disproves completely the assertion that the internal lining membrane of the inhalent or extra-branchial siphon is the scene of ciliated epithelium. In no single instance of the numerous siphonal species examined by the author, could cilia be discovered in this situation. If at this place cilia do *not* exist, it admits of no dispute, that the occasional inward-tending current which reaches the cavity through this siphon cannot be due to the instrumentality of cilia, at this point at least. Mr. Clark is unquestionably wrong in supposing that, because now and then the inhalent or extra-branchial siphon, and the ventral and pedal openings of the mantle *emit* a jet of water and solid pellets, this cavity is therefore independent, that the "siphons therefore do *not* communicate," and that therefore the ingress and egress of the water designed for respiration take place through the same orifices. Every one of these inferences are *non-sequiturs*. Mr. Hancock is inaccurate in affirming that *all* the water which enters this cavity from without travels *exclusively* along the inhalent or extra-branchial siphon, and never, under any circumstance, through either the ventral or pedal openings*. *All* the water which is admitted into the extra-branchial cavity is not respired; in other language, does not pass through the branchiæ into the dorsal or intra-branchial chamber (fig. 6, *f*); nor is *all* the solid substance, which it may perchance contain, seized by the mouth and swallowed. The act of the passage of the true respiratory water from one chamber into the other is an *involuntary* act. The volume of the fluid and the rate of its motion are definite, and proportional to the organic wants of the animal. The movement by which water is drawn from without into the extra-branchial reservoir is *voluntary* †, and dependent in frequency of recurrence upon the quantity of food which it may bear in suspension, and upon the degree of its purity. The body of water which at any given moment the extra-branchial cavity may contain, is *sieved* by the cilia, which are distributed over the *external* surfaces of the branchiæ. These cilia, as will be subsequently explained, raise a broad current (see arrows on the branchiæ in figs. 6, 8, & 9), very visible to the naked eye, which always and systematically sets in the direction of the free or unattached borders of the branchial lamellæ. These currents *begin* at the attached or proximal edges of all the lamellæ.

They observe the same directions on the under as on the upper surface of each lamella (see arrows on the branchiæ in fig. 7^2). They are true food-searching currents. The pellets formed by their agency, having attained the free margin,

* In correcting what earnest and faithful observation and research have convinced me to be "errors," I deal in no flattery or hypocritical circumlocution. I do not honour great men the less because a repetition of their procedures has assured me that in some special particulars they may have approved themselves false. It is because *their* genius has first indicated a main highway through a tangled wilderness, that faithful observers amongst their successors are enabled to mark the points whereat the sin of minor deviations from the straight course may have been committed. It is in this spirit that I have ventured to criticise the acute labours of Mr. Hancock and Mr. Clark. It is in this spirit, I trust, that my criticism will be received. The brief limits of these papers, in which *results* rather than processes are embodied, preclude all reference to details, dissections, experiments, observations on the living animals, injections, &c. Once for all, I affirm, that no assertion has been rashly projected in these papers which has not been conscientiously submitted to the test of *fact*, and weighed in the balance of practical trial.

† The influence of the cilia of the *branchial lamellæ* upon this ingressing current has never yet been clearly perceived. Such influence is undoubtedly exerted.

are carried in the direction of the mouth and tried and tasted by the *palpi* (fig. 6, *i*, *i*). Those which are acceptable are swallowed; those which are unpalatable are carried completely out of the cavity indifferently by any one of its openings, lest they should again pass over the branchiæ. So incomparably adjusted are the cilia which render the gills a wondrous spectacle of infinitesimal currents, so precise and fore-ordained are the directions in which they move, that the act which sieves the food from the water drives also that water from the recipient into the refuse chamber (fig. 6, *f*; Pl. II. fig. 12, *h*), *through the meshes* circumscribed by the branchial vessels. *This* stage of the respiratory process is strictly involuntary. It is governed by inviolable organic laws, not volitional caprice. It is to the mollusk what the insensible involuntary physical exos- and endosmose of gases in the ultimate air-cells of the lungs are to the mammal. It differs physically and physiologically from the act in which water is drawn into the cavity of the mantle, as strikingly as the thoracic movements of respiration in Man differ from the ultimate process. Thus, whatever may be the number, size, or prominence of the openings* of the mantle, the functions of the great ventral chamber remain unchanged. They are and must be in every instance, under all general mutations of character, those of a reservoir from which food is drawn to the mouth and the aërating element to the branchiæ.

The *second* great cavity (Pl. I. fig. 6, *f*; fig. 7, *c*. Pl. II. fig. 8, *d*; fig. 9, *e*; fig. 10, *c*, *c'*; fig. 12, *h*), lying to the left, dorsal, or "the hinge" side of the imaginary line formerly defined, remains now to be described. It is limited ventradly by the branchiæ, dorsadly by the hinge, and posteriorly by the ex-current siphon.

The anal chamber does not in all genera communicate openly and directly with the interlamellar passages. The former really arises in the latter, when only one of the proximal borders of the branchial lamellæ is attached to the side of the visceral mass; the grooves, running antero-posteriorly and parallel with the length of the gill, and situated between its proximal borders and

* I would beg here to refer the student to the interesting papers of Mr. Hancock, in the 'Annals and Magazine of Natural History' during the years 1852 and 1853, for an account of the collateral openings which in some genera occur in the mantle. In *Chamostrea albida*, in addition to the normal siphonal orifices and pedal and ventral gapes, he describes another of minute size, which is situated under the lower siphon. A similar aperture exists in other Lamellibranchiates. Mr. Hancock has observed it in *Lutraria*, *Cochlodesma*, *Panopæa* and *Myochama* and Prof. Owen in *Pholadomya*. It is clear from the explanation given in the text, that these secondary apertures are really secondary in meaning. They do not in the least affect the physiological character of the cavity.

the visceral mass, although open, form really the commencement of the anal chamber.

Mytilus and *Pecten* exemplify the type of this condition (Pl. I. fig. 7^2). The outer plate (c, c') of each lamella is free or unattached at its proximal margin. This latter is thick and strong. It is composed of the large afferent and efferent trunks. In *Mytilus* and *Pecten* it is not fringed by a slender membrane as in *Cardium* and *Pholas* (fig. 6, *e*, *f*) and *Mya*, &c. The gutter or channel (fig. 7^2, *f*, *f*) formed by the attached or *lower* lamella of the superior gill and the free or unattached or upper plate, opens consequently into the extra-branchial or pallial cavity in a direct manner. The water flowing along this groove (fig. 10, *c*) does not however return into this latter cavity, except under extraordinary circumstances. It is conducted in a rapid course, impelled by the branchial cilia, in the direction of the cloaca (fig. 10, *e*). The groove formed at the proximal margins of the inferior, or as it is falsely called, the supplemental gill (fig. 7^2, c'), opens in like manner into the pallial cavity, but on the under surface. It receives the expiratory currents of the lower gill, and conveys them in form of a strong single current towards the exhalent siphon. In *Cardium* (Pl. II. fig. 9), *Pholas* (fig. 7), *Mya*, *Solen*, *Cochlodesma*, and *Pholadomya*, the two plates of each branchial lamella on both sides are attached, the upper to the side of the body and foot, the lower to the mantle. The groove bounded by the plates of the branchial lamellæ is divided off, therefore, in these genera by a continuous membrane (fig. 9 *f*) from the pallial chamber. Mr. Hancock says, that in the siphonal families this membrane forms a complete partition between the pallial and anal cavities, since it extends continuously from the anterior to the posterior extremity of the upper plate. The author's observations have convinced him, that, while in *Cardium*, *Pholas*, *Solen*, and *Mya* this membrane stretches posteriorly over the cloaca in a hood- or tongue-like form, it leaves between its edge and the side of the foot a fissural opening through which the two cavities freely communicate. The difference, then, between the siphonal and non-siphonal families as respects the parts concerned in respiration, may be defined as consisting in *the degree* in which the intra-branchial grooves are anatomically isolated from the open space of the pallial cavity.

Such points are non-essential distinctions: while they denote the existence of trifling structural varieties, they involve no diversities in the methods of action. Whether partially open or completely closed, the grooves (fig. 6, *f*) running horizontally at the proximal borders of the gills and between their component plates, convey the exhalent current received from the gills in the direction of the cloaca. When there exist two separate branchial lamellæ on either side, there exist two grooves; when one, only one.

The *anal chamber*, then, should be defined as beginning in these intra-branchial grooves, but remotely or primarily in the *inter*-lamellar water-passages of Mr. Hancock. The mode in which this chamber communicates with the water-tubes between the branchial lamellæ is thus described by Mr. Hancock:—"... the anal chamber (in *Pholas crispata*) was laid open, and its ventral wall was seen to exhibit four longitudinal rows of large orifices. These four rows of orifices, already well known to anatomists, correspond to the attached margins of the four gill-plates, which hang from the roof or dorsal membrane of the branchial chamber; this membrane being the ventral wall of the anal chamber, the membrane, in fact, which divides the chambers. These orifices lead into wide tubes, which pass between the two laminæ forming each gill-plate. These inter-branchial tubes lie contiguous and parallel to each other, and extend the full width of the gill, being bifid within its free margin. Thus it is evident that the tubes within the gill-plates *communicate freely* with the *anal chamber* *." This description is exact, but it should be thus qualified: In those siphonal families in which the gills are united posteriorly (this is the case in *Unio*, *Anodonta*, *Mactra*, *Cardium*, *Isocardia*, *Lutraria*) and prolonged into the inhalent siphon, the anal chamber is considerably more capacious than in those in which the branchial plates of opposite sides are distinct and ununited posteriorly (this condition is observed in *Pecten*, *Avicula*, *Arca*, *Pectunculus*, and *Pinna*), or in those in which the siphons are suppressed. In *all* cases, the anal chamber commences anteriorly (fig. 10, *c*) in grooves more or less extended, formed, as already defined, between the plates of the branchial lamellæ and the side of the visceral mass and foot.

These grooves terminate and pour their contents in a continuous stream into the anal chamber—a cloacal cavity common to the branchiæ and intestine. In all cases then the interlamellar water-passages open throughout the *anterior* half or third of the gills into the water-grooves at their bases, posteriorly *directly* into the cloaca or anal chamber. This definition, so positive, precludes all misconception. It leaves the cavities functionally distinct in all genera, though in some structurally continuous. It solves the problem of the Molluscan organism. The ingress and egress of the alimentary and respiratory elements are so ordered, that the œconomy of the conchiferous animal, hidden in a coat of mail, is rendered unequivocally clear to the understanding.

* Ann. & Mag. Nat. Hist., Nov. 1851.

All the *interlaminar* tubes, lately so fully described by Mr. Hancock, pour a *constant* current into this cavity, with which *all* the intra-branchial spaces openly communicate. Into this chamber, at different points in different genera, the intestine terminates (Pl. II. fig. 12, *b*). It receives the excrementitious products at once of the intestinal and branchial systems.

This simple definition was first established in all its details by the researches of Mr. Hancock. It is essentially founded upon the permeability of the branchial laminæ, first proved by Dr. Sharpey. The correctness of this description is denied in the most strenuous manner by Mr. Clark. It is impossible not to admire the ardent eloquence, and sagacious inventiveness of argument with which Mr. Clark defends his own views. The duty of the critic, however, is sacred. The solemn sentence of "error" must be pronounced alike over many of his "facts" and not a few of his "inferences."

Mr. Clark is indeed right in asserting, that frequently a *momentary in*-current occurs through the *ex*-current siphon. This accidental incident is utterly unimportant. The normal, systematic, and necessary direction of the current in this (the dorsal, upper, anal ex-current, ex-halent or *intra*-branchial) siphon is centrifugal. In all Acephalans, whether siphonal or non-siphonal, everything that passes through this siphon has an *outward* tendency. The centripetal movement is irregular and accidental. The stream bears far more strikingly a continuous character than that ingressing at the ventral or extra-branchial orifices. The uninterruptedness of this current was supposed by Mr. Hancock to be due to the action of *cilia* lining the interior of the siphon. The statement of this distinguished naturalist in this particular is indisputably erroneous. This siphon, like the in-current one, is *not* lined with vibratile epithelium. The stream by which it is traversed is not excited by any force within its own limits.

In denying the existence of cilia within this siphon, Mr. Clark is on the side of truth. But the current emanating from the excurrent-siphon is *continuous* in character. It always goes on except when the orifice is closed by voluntary muscular action.

The continuousness of this ex-current is due, not to cilia within the interior of the siphon, but to those at a distance, on the branchial bars. *All* the cilia distributed over the internal surfaces of the branchial laminæ (those facing the interlaminar tubes) excite currents tending in the direction of the dorsal or intra-branchial cavity and that of the ex-current siphon. The *proofs* of this interesting fact will be afterwards given *.

* See a subsequent paper "On the Minute Structure of the Branchiæ."

The character of this exhalent current is not the same in all genera. In *Cardium* it is much more regular than in *Pholas*, &c. It occurs quite as distinctly in the Asiphonophora as in the Siphonal classes. It is with this current that the rejectamenta escape.

The *evidence* upon which the doctrine of the independence of this cavity from the ventral is maintained, will be adduced when speaking of the *minute* structure of the branchiæ.

If the view supported by Mr. Hancock be true, that the dorsal or intra-branchial cavity is separated from the ventral or extra-branchial by a partitional membrane which is permeable nowhere but at the branchial stigmata, it follows that everything which passes from one chamber into the other, either in a progressive or regressive direction, must percolate through these minute foramina. The author's dissections, however, render it probable that a *fissural* opening (fig. 6, *e*) at either base of the foot exists in some of the siphonal genera, if not in others. It is seated at the base of the branchial lamellæ and the junction of the vertical partition of the mantle with each superior gill, and opens directly from the *intra-* into the *extra*-branchial chambers. The office of this fissure is that of a safety-valve.

When the outlet of the ex-current siphon is closed by sphincteric contraction, the intra-branchial cavity being rapidly more and more filled in virtue of the *continuousness* of the branchial ciliary action, the surplus fluid escapes through the lateral fissures back again into the ventral or extra-branchial chamber, again to pass through the branchial foramina, propelled by cilia. It is by thus repeatedly filtering the same water through the branchiæ that those bivalves, such as the Mussels, sustain life, though abstracted for a considerable time from their native element. The fissure in question is detectable only from the inside of either chamber, not from the outside view of the whole mantle, even after the separation of the animal by spirits of wine from its shell. If the exit of the water from this intra-branchial enclosure be due to the force exerted by the lamellar cilia, it follows that the egressing current should be equally as vigorous and marked in the non-siphonal as in the siphonal genera. The presence of the ex-current siphon does not affect the real branchial action of respiration. As a tubular extension of the cavity, it enables the contents of the latter to be delivered at a greater distance away from the body. This is its real office. Thus the sphere in which the animal lives is maintained in purity. The *in-current* which occasionally occurs through this dorsal or intra-branchial siphon should be regarded really as a momentary accident, as an irregular reversal of a normal current. Water thus drawn into the cavity of the ex-current siphon can

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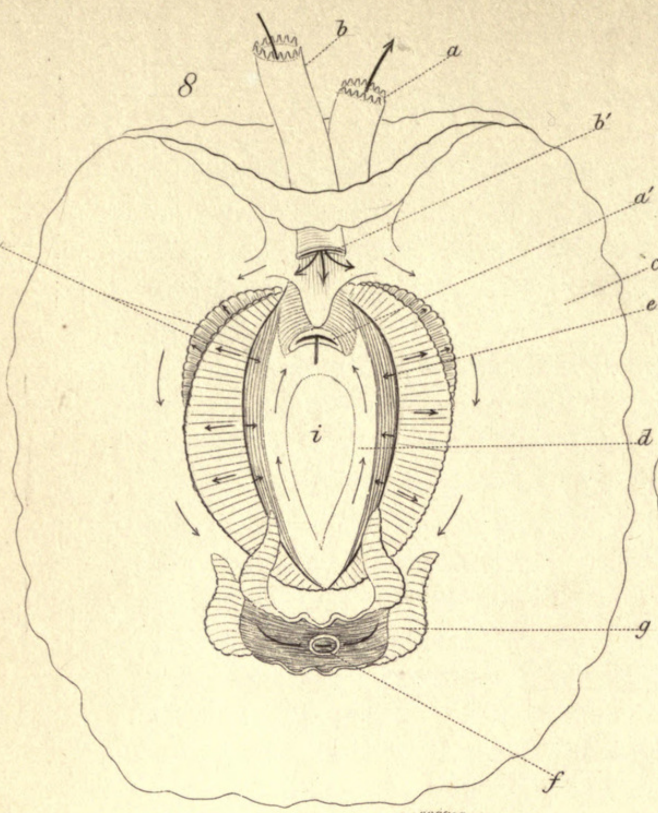
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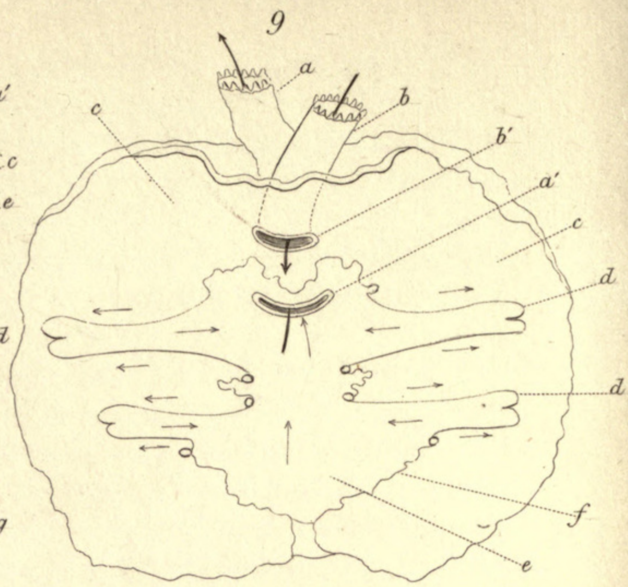
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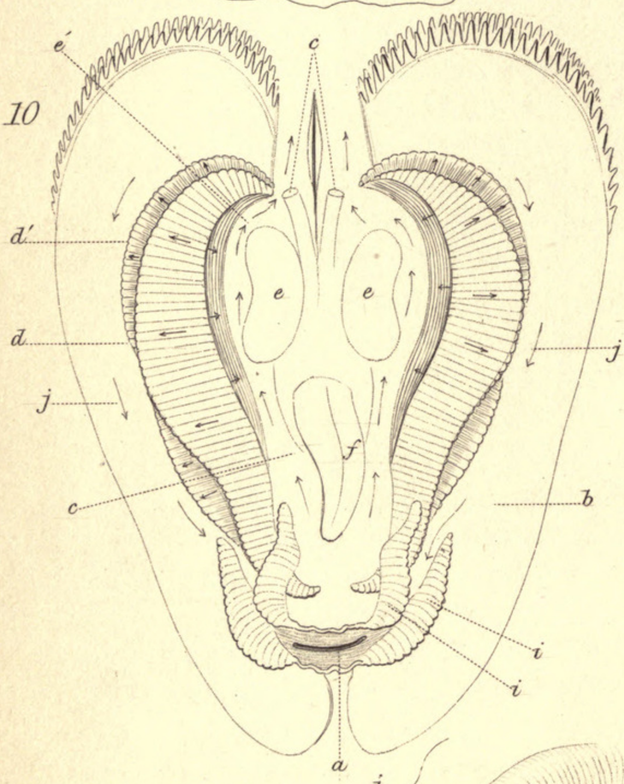
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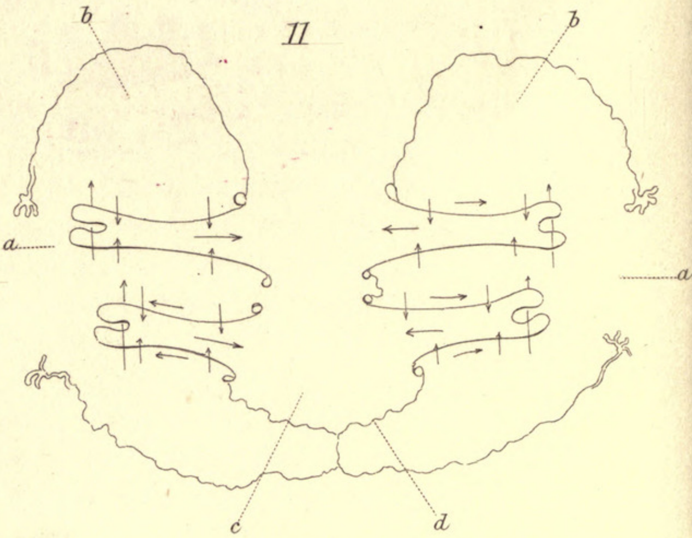
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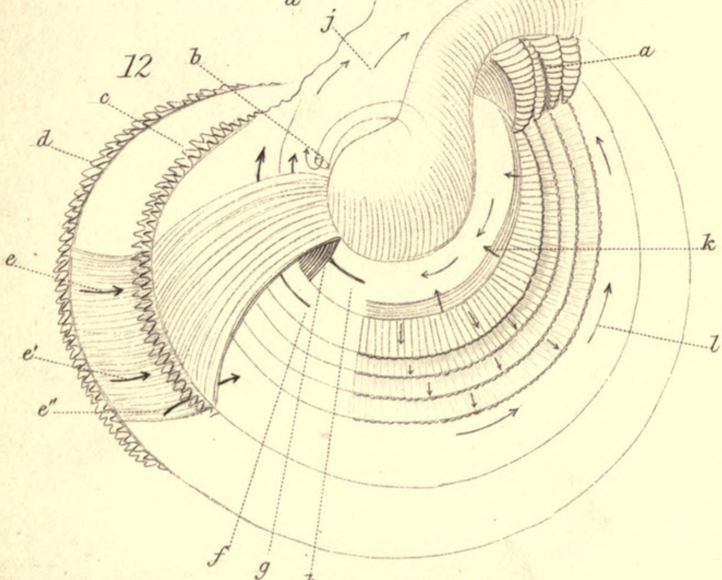
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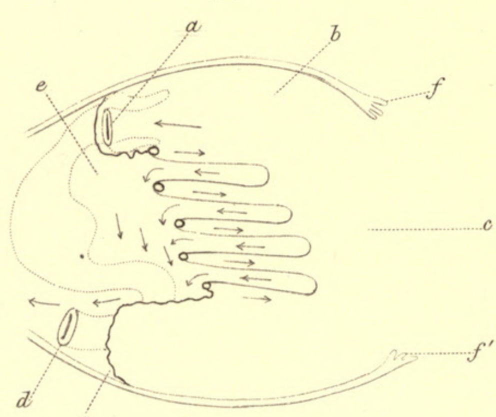
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