

**The structure, functions, and diseases of the lungs / by Thomas Williams.  
Part I., Water and air-lungs of invertebrate animals, and aquatic  
respiration.**

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THE

STRUCTURE, FUNCTIONS,

AND

DISEASES OF THE LUNGS,

BY

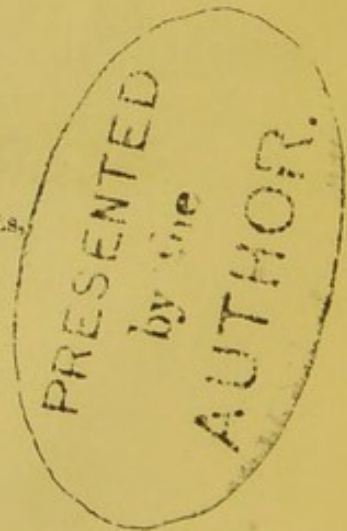
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AUTHOR OF THE COLLEGIAL TRIENNIAL PRIZE ESSAY ON THE "STRUCTURE AND  
FUNCTIONS OF THE LUNGS"; AND OF THE ARTICLE  
ON THE 'ORGANS OF RESPIRATION,' IN THE ENCYCLOPÆDIA OF ANATOMY AND  
PHYSIOLOGY, &c., &c.

PART I.

WATER AND AIR-LUNGS OF INVERTEBRATE ANIMALS,  
AND  
AQUATIC RESPIRATION.



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1857.



STRUCTURE FUNCTION

AND

THE

DISEASE OF THE LUNGS

BY

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WITH

ILLUSTRATIONS

LONDON

JOHN W. H. WATSON, M.D., F.R.C.P.

TO THE PRESIDENT

AND

COUNCIL

OF

THE ROYAL COLLEGE OF SURGEONS OF ENGLAND,

THIS WORK

(TO THE ORIGINAL OF WHICH, IN THE YEAR 1842-3,

THE TRIENNIAL COLLEGIAL PRIZE

OF FIFTY GUINEAS WAS AWARDED BY THE COLLEGE.)

IS RESPECTFULLY DEDICATED

BY THE AUTHOR.

NEARLY READY.

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PART II.—WATER AND AIR-LUNGS IN VERTEBRATE ANIMALS AND MAN.

---

PART III.—DISEASES OF THE HUMAN LUNGS (*preparing*).

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Each Part will form an independent Treatise.



ON THE  
MECHANISM OF AQUATIC RESPIRATION  
AND  
ON THE STRUCTURE OF THE ORGANS OF BREATHING  
IN  
INVERTEBRATE ANIMALS.

---

THE mechanism of breathing in the countless hosts of invertebrate animals which people the ocean, offers a problem which has never yet been satisfactorily solved. The mode in which life is sustained in those degraded forms, in which "a circulation of blood" is not to be discovered, has long stimulated the curious wonder of the naturalist. Fishes and Cetacea excepted, the invertebrate animals constitute the entire population of the ocean. Insects excepted, all invertebrate animals are aquatic. Hence the wide range of interest which belongs to this subject. How animals breathe is not second in importance to the question how they live. Every observer studies the latter, few the former. There are "habits" associated with the manner in which the function of breathing is performed which are well-fitted to win admiration. Wanting the knowledge of this process, not the smaller half of the history of an animal remains to be acquired.

It is the aim of this memoir to demonstrate first the anatomical conditions under which the office of respiration is performed in the invertebrate animals, and then to study the process itself. The anatomical conditions will prove as various as the classes of which this subkingdom is composed. Two primary divisions of this subject demand at once to be recognised;—1st, that comprising those organs which adapt the animal for atmospheric breathing; 2nd, that qualifying it to respire in water. The latter, embracing varieties more striking and numerous than the former division, should again be resolved into two denominations, of which one would comprehend the mechanism of those organs by which the *chylaqueous fluid* is sub-



mitted to the agency of the aërating element, and the other, that of those fitted to expose the true blood\*.

All vertebrated animals, fishes excepted, breathe on the atmospheric plan. All invertebrate animals, insects excepted, respire on the aquatic model. The organs used in the first method are more complex than those comprised in the second; while the chylaqueous fluid is subjected to respiration, through the *least* complexly arranged mechanisms. The simpler the fluid to be aërated, the less involved is the disposition of the solid parts through which the exposure is effected. Elaborately vitalized blood is circulated through respiratory organs of inconceivable complexity and subdivision. The study of the mechanical conditions of respiration should regard the *fluids* as well as the *solids* of the structures dedicated to this function. The floating cells of the fluids are concerned in, though not essential to the respiratory process. The *true capillary segments* of the lungs of *all* vertebrated animals, those of reptiles *not* excepted, are destitute of vibratile cilia. The branchiæ of fishes, without a single known exception, are clad only by a *non-vibratile* epithelium. The general proposition, that ciliary epithelium constitutes no part of the *active portions* of the breathing organs of vertebrated animals, rests therefore upon the stable basis of actual demonstration. This negative must be changed into an affirmative statement, with reference to the *air-passages*, which in the pulmonary vertebrated series are profusely and universally ciliated. The presence of cilia on the branchial structures of invertebrated animals is a common, but not a constant fact; the rule without intelligible reason is suspended in numerous instances. The operation of cilia is therefore *not* indispensable to the respiratory process, even in the invertebrate animal—not an *essential* constituent even of the aquatic model. The blood of all vertebrated animals is richly charged with corpuscular elements. It is invariably coloured red. In the invertebrated subkingdom not one example is known of a corpusculated *red-blood*. The blood of every known mollusc bears floating solid elements. In every articulated animal the true-blood abounds in organized corpuscles. In every annelid, without a single known exception, the blood-proper is perfectly destitute of morphotic elements; it contains no trace of visible cells. The perfect fluidity of the true-blood of all Entozoa can also now be affirmed. Every Echinoderm is endowed with an imperfect blood-system, the blood-proper bearing cells in suspension. The chylaqueous fluid of every animal in which it exists, is charged more or less abundantly with organized

\* The author would here beg to refer the reader, for a full statement of the grounds of this latter subdivision, to his paper on the Blood-proper and Chylaqueous Fluid, &c., in the Phil. Trans., Nov. 1852.



corpuscles. The generalization is thus incontrovertibly established, that there exists no single instance of a real animal, of which one or other of the circulating nutritive fluids of the organism, is not replete with morpious particles. What office, if any, these floating solids exercise in the *mechanism* of the respiratory act, it is the province of the physiologist to determine; their microscopic characters it is the duty of the anatomist to describe.

*Porifera*.—In the Spongiadæ, the fluids to be aërated are contained *in* and *between* the component cells of the gelatinous cortex. Each separate cell, like that of *Amæba*, is an independent organism. The included fluid, moved by the slow contraction of the cell-membrane, is a granulated, nutritive compound. That diffused between the cells, in composition, is less removed from the standard of sea-water. The latter replenishes the former. The inorganic fluid, entering from without into the interior of the living-cell-tissue, carries with it in solution a large amount of atmospheric air. In these lowly organisms, this dissolved air probably suffices to *oxygenize* their simple fluids. As the contained fluids are rapidly renewed, the nutritive and the respiratory process come to be performed by one and the same act. This is the history of the breathing function in the *Rhizopoda* and in *Actinophrys Sol*, recently described by Kölliker\*. The superficies of the whole gelatinous cortex of the sponge is overspread by a film of ciliated epithelium. It has now been proved by Dr. Dobie† and Mr. Bowerbank, that the “currents” of the sponge are due to the agency of these motive organules. These currents are simultaneously nutritive and respiratory.

*Polypifera*.—Three varieties of plan, in the mechanical conditions of respiration, prevail among Zoophytes: the *Hydraform* (Pl. XII. fig. 2), the *Actiniform* (fig. 3), and the *Asteroid polypes* (fig. 1) exemplify three minor forms of one type of structure. In the first the space between the stomach and the outer limit of the body (fig. 2, *a*) is subdivided by the intersection of delicate tissue into areolæ, in which the fluid to be aërated is contained ‡.

\* See Quarterly Journal of Microscopic Science, Oct. 1852.

† See Annals of Anatomy and Physiology, No. 2, May 1852.

‡ The author has stated in the text the impression which he has derived from numerous observations on the common hydra of our pools, that the tentacles open into the *perigastric* areolæ, as shown at (*a*) fig. 2, and not into the stomach, and that they are *tubular*, not solid threads, as shown at (*b*) fig. 1. If, as recently stated by Prof. Allman (Proceedings of the Royal Society, May 31st, 1853), they open directly into the stomach, the tentacles can only be injected by the contents of the latter, and their function would partake of a digestive as well as a respiratory character; and further, the digestive system of the hydra would conform with the medusan type which



The fluid penetrates along an axial channel to the furthest ends of the tentacles: they are *not* perforated at their distal extremities. In *Hydra viridis* and *H. fusca*, by means of the rolling granules, the fluid may be readily detected by the eye. It cannot be renewed *directly* from without. It is replenished *through* the walls of the stomach (*b*). The respiratory is here a function distinct and separate from the digestive. A living corpusculated fluid is submitted to the influence of the surrounding medium, by aid of the tentacles. These appendages in the hydraform zoophytes are furnished neither within nor without with motive cilia. They maintain the flux and reflux motion of the embraced fluid, in virtue of the contractile endowments of their parietes. In the *second* variety, illustrated by the sea-anemone (fig. 3, *b*), the open interval between the stomach and the integuments, though partitioned by dissepiments, is very capacious. The hollow axes (*c*) of the tentacles are continuations, in all species, of the perigastric space. They are filled with the same fluid as the latter. In some species of *Actiniæ*, the tentacles are perforated at the extreme ends: *Anthea Cereus* is an example. In the greater number they are cæcal. The *interior* of the tentacles, in common with the perigastric chambers, in *all* species are richly ciliated (*d*). The exterior of these appendages in many instances is covered only by an ordinary non-vibratile epidermis. The chylaqueous fluid\* is an inferiorly vitalized

is marked by the direct extension of canals from the stomach, and by the absence of a splanchnic cavity, the stomach being merely an excavation in the solid parenchyma of the body. The observations of Prof. Allman were instituted on *Cordylophora*, a genus of *Tubulariadae*. According to my researches very lately made on *Tubularia indivisa* and *Alcyonium*, the tentacles are tubular and open into the perigastric chambers, which they equal in number. From its interest, this question cannot remain long unanswered. If in the hydraform and tubularian zoophytes the tentacles are prolongations of the stomach, properly so called, zoophytes, as a class, might be ranged under two leading divisions; that 1st in which the tentacles are *gastric*, and 2nd that in which they are *perigastric* prolongations. The *fluids* would admit of a similar division.

\* Under this term (see Phil. Trans. 1852), the author has ventured to distinguish the fluid which occupies the gastric and perigastric cavities of *all* animals below the Annelida. He has elsewhere endeavoured to prove the proposition, that in all animals *below* the Echinoderms, it constitutes the *exclusive* nutritive fluid of the organism; that in those families, as in Zoophytes and inferior Echinoderms, in which it is readily ejected from the body and as readily replaced, it is very little removed in composition from salt water, and corpusculated only in a slight degree. It is simply albuminized sea water. But it has already undergone such preparation as fits it to enter the "protean" cells of the solids. Here, as illustrated in the examples of the *Amæba* and Sponge, it assumes a more highly vitalized and corpusculated character. It may be said that in the cells it is true blood, in the visceral cavity chylaqueous fluid. The difficult problem of respiration in the lowest forms of animal life can be solved *only* by determining



albuminous compound. It possesses higher organic properties in those orders in which the tentacles are closed, than in those in which they are open. In the former it sojourns longer in the visceral cavity under the influence of the Zoochemical forces. It is in the interior of the cells of the solid structures that the chylaqueous fluid acquires its final properties. It suffers here a second and higher nutritive and respiratory change, or derives from the chylaqueous mass, still in the visceral cavity, a further supply of oxygen. The chylaqueous fluid is aërated in two modes; 1st, every portion of the element from without, which is admitted into the splanchnic cavity, brings with it a fresh supply of highly oxygenized air; and 2nd, it exchanges its carbonic acid for the oxygen of the surrounding element, in accordance with the principles of ordinary aquatic breathing. It is therefore a reservoir of richly oxygenated fluid, fitted well to impart a renewed proportion of oxygen to the more highly vitalized contents of the cells. It is evident that it is only by a clear statement of these *apparently* irrelevant particulars, that the anatomist can arm the physiologist with an adequate conception of the *physical conditions*, under which the respiratory function occurs in these degraded organisms. In all actiniform polypes, the bottom of the stomach communicates, by means of a sphincteric aperture, with the perigastric chambers. It is by this route that the large mass of the

the real stages through which the fluids pass in the processes of animalization. If the great mass of the chylaqueous fluid contained in the polypedal and visceral chambers consist of pure, unvitalized, unalbuminized sea water, *then* the tentacles can subserve no respiratory purpose; since between two fluids (that within, and the element without the tentacles), of identical composition and specific gravity, there can occur no interchange of gases. But if, on the contrary, to this great reservoir of fluid be assigned the value of a chylaqueous compound, though it may have undergone only the first and lowest grade of assimilation, *then* the entire mechanism of respiration and nutrition becomes intelligible. This argument enforces the physiological principle, which, in order to demonstrate the true seat of the aërating process, demands that the real constitution of the fluids be *first* discovered. In studying the nutritive and respiratory actions in *all* invertebrate animals, one fact of singular interest should be remembered, the truth of which the author has established by numerous observations. The *cells* of the solid tissues are *contractile*; they *contract* and *dilate*: in the Cephalopods, the pigmented cells of the integumentary structures exhibit this property with remarkable distinctness. The pigment is deposited in the substance of the cell-wall. When the cell *contracts* the coloured point disappears, when it expands it assumes a conspicuous area. This is the simple explanation of the singular power, with which the Cephalopods are gifted, of *changing their colour*. It applies also to the chameleon. But in invertebrate animals it is not confined to the pigmented cells. It is exhibited by the non-pigmented cells of nearly all the structures of the body. The author has ventured in this place to bring it under the attention of the physiologist, because it is unquestionably a property of great importance in the circulation and aëration of the fluids.



contents of these latter cavities are derived from without. The contained fluid receives the first impress of the vital chemistry, in its passage over the gastric surfaces. It is then prepared to undergo the respiratory changes in the visceral cavities. The preceding observations apply to the *third* (fig. 1) variety of plan (exemplified in the *Asteroid* families), on which in zoophytes the fluids are elaborated. There is little difference of structure between the asteroid and helianthoid polypes. In the former the stomach is prolonged into the axis of the polypidom (*c*). The perigastric chambers (*d*) also communicate, but in a less direct manner than the stomach, with the channel of the stem. In these families, the tentacles, which are evidently the continuations of the perigastric chambers (fig. 1, *a*), are said to be perforate at their distal extremities: this point requires to be confirmed. The fluid filling the axial channel of the stem enters at the mouth of each polype, and descends through the orifice situated at the base of the stomach (fig. 1, *c*) into the polypidom. In this situation, in a great variety of species, the motion of the corpuscles contained in the fluid may be readily observed. They present all the characters of being driven by *cilia*. The presence of cilia is however controverted by some observers. From the polypidom the fluid passes upwards into the perigastric chambers, and thence into the tentacles in which it undergoes aëration. It is curious that the *corpuscles* of the fluid of the stem do *not* pass upwards into the tentacles. They are filtered back by the cribriform partition, which divides the chambers around the stomach from the axis of the polypidom. *New* observations are required on the whole family of the asteroid polypes, having special reference, 1st, to the arrangement and existence of cilia, and 2nd, to the distribution of the fluids.

The fluid by which the whole extent of the stem and visceral chambers of each individual polype are distended, constitutes one system. So rapidly is this fluid endowed with a low order of vital properties, enabling it to fulfil its functions as an element of nutrition, that it may be rejected *en masse*, to be replaced with a fresh volume of *inorganic* water. Such is the converting power of the vital chemistry in these simple organisms. This fact distinguishes the polype families from all other invertebrate animals. The true character of the breathing function must have remained beyond the reach of the physiologist, without the knowledge of these points. They prove that the *lower* the vital endowments of the fluids, the simpler the mechanical arrangements required to effect their aëration. In zoophytes the nutritive fluid is not exclusively vitalized through the agency of floating cells, it is vivified in part, catalytically by *contact* with the surfaces of the living solids. The morphotic elements, therefore,



which exist in the fluids of this group, are scanty in number, subordinate in function, and indeterminately organized. To detect the globules in the fluid of the polypary is easy. It is more difficult to trace its progress upwards into the space which surrounds the stomach, and thence into the tentacles. If, as lately stated by Prof. Allman\*, the axes of the tentacles in the tubularian polypes open directly *into the stomach*, and *not* into the space to the outside of this organ, these appendages cannot be intended to expose the chylaqueous fluid to the aërating medium. Arising out of the roof of the stomach, as already stated, at the side of the oral orifice, they can be injected only with the contents of the stomach, and that periodically by muscular force. Such a mechanism, for organs which are indubitably respiratory, is in the highest degree improbable. The tentacles of the distended polype are filled undoubtedly by a *fluid*. In *this* fluid no corpuscles have yet been detected. Those observed so readily in the stem cannot be traced upwards beyond the base of the stomach: Prof. Allman denies even in the latter situation the existence of cilia. The globules move, according to this observer, as "the effect of the active processes, going on in the secreting cells of the endoderm, —processes which can scarcely be imagined to take place without causing *local* alterations in the chemical constitution of the surrounding fluid and consequent disturbance of its stability." However these questions may eventually be determined, it is certain that there exists in all zoophytes but *one fluid system*.

This fluid is compounded of the surrounding medium, whether it be sea water or fresh, and the organic products of digestion. By this quasi-inorganic fluid the nutritive functions of the organism are performed. In the tentacles it undergoes aëration; in the actiniform orders it may be collected in large quantities: it contains corpuscles characteristic of species†. It affords distinct evidence of the presence of albumen; it is destitute of fibrine; it is the lowest example under which a living nutritive fluid occurs in the animal kingdom, and yet *the cells of the solids* of zoophytes are eminently irritable and contractile. An inverse proportion obtains generally in this respect in invertebrate animals. The simpler the fluids, the more irritable and contractile the solids, the cells of the latter being larger than the corresponding parts of vertebrated animals.

*Bryozoa* (fig. 4).—The marine and freshwater polyzoa are molluscan in the character of their alimentary system, zoophytic in that of the fluids. Their position in the scale must be allotted

\* Proceedings of the Royal Society, May 31, 1853.

† See the author's papers on the Blood, which are now in course of publication in the British and Foreign Med. Ch. Rev.



according to the relative importance of these two systems : judged by the fluids, they claim to rank at the summit of the zoophytic series ; by the alimentary organs, they would constitute the first link in the molluscan chain. The real signification of the fluids in the Polyzoa has never been understood. A perigastric cavity (*a, b*) is clearly described ; the *fluid* within this cavity and its floating corpuscles have been repeatedly observed, but the physiological value of these parts has never been explained\*. In these animals there exists neither a heart nor a blood-proper system. The fluids constitute an unmixed example of the chylaqueous system. They oscillate under muscular agency in the great visceral cavity (*a, b*) ; under the same force the fluid penetrates the tentacles which it traverses by a flux and reflux motion. These organs are plain, tubular appendages ; they are continuations of the visceral cavity ; —characters which are emphatically zoophytic. The tentacles of the Polyzoa differ from those of asteroid polypes in the presence of vibratile cilia. They are limited to the external surface, and arranged in a single row on either side : the interior of these branchial tubuli is not ciliated. Thus then is defined the whole apparatus of the chylaqueous system in this family. Henceforth the Polyzoa cannot be severed from the zoophytes.

*Acalephæ* (figs. 5, 6, 7).—The apparatus for breathing is, in

\* In justification of the statements made in the text, the author would refer to the admirable report, on the Polyzoa, by Prof. Allman, in the Trans. of the Brit. Assoc., 1850, in which the following statements occur. "The perigastric space and interior of the tentacula and locophore all freely communicate with one another, and are filled with a clear fluid, in which float numerous irregular particles of very irregular form and size.....That the fluid thus contained in the perigastric space, and thence admitted into the tentacles, consists really of water which had obtained entrance from without, there can, I think, be little doubt ; and yet I have in vain sought for any opening through which the external fluid can obtain admittance into the interior.....The fluid which circulates in the perigastric space is not perfectly homogeneous, and numerous corpuscles of various and irregular shape may be observed to float through it and be carried about by its current. Some of these corpuscles are perhaps spermatozoa ; others are of no definite shape, and look like minute portions of the tissues separated by laceration. May they not be some of the products of digestion, which have transuded through the walls of the alimentary canal, being thus conveyed into the *only* representative of a true circulation, with which these animals present us?" From the preceding passages it is undeniable that this excellent naturalist has not clearly seized the significance of that which he has described so graphically. He admits that the fluid of the perigastric cavity is the *only* fluid system discoverable in the organism of the polyzoon. He disputes the organic character of the fluid, while he *hints* at its nutritive properties. It is in truth a true and perfect *chylaqueous system*, and as adequate as blood-proper to the wants of the living organism. In the Polyzoa, there is discoverable no trace of a blood-proper system. They therefore *fail* in one of the most essential characters of the molluscan organism—the existence of a heart and an associated circulatory system.



this class, of simple construction : it consists of a system of cæcal canals in direct connection with the stomach. Four types occur—the Pulmograde, the Ciliograde, the Cirrhigraide, and the Phyllosograde. In the first examples (*Aurelia*, *Pelagia*, *Chrysaora*, *Rhizostoma*, *Cassiopea* and *Cyanæa*), the stomach is a central lobulated chamber, furnished with one external orifice, the mouth, and opening laterally into canals which reticulate at the margin of the disc : they end cæcally. In *Cyanæa aurita*, they are prolonged into the fringed appendages which depend from the circumference of the disc. The system of the gastro-vascular canals (fig. 5, *c, d* ; fig. 6, *c, d* ; fig. 7, *c, d*) in the *Discophoræ*, forming a horizontal plane, rest in immediate contact with the inferior surface of the disc—that is, the whole substance of the disc intervenes between them and the upper surface : the under surface of the disc externally, in every species, is ciliated ; the superior is not so. The stomach and the canals (*c, d*) to their remotest terminations are ciliated internally. This fact distinguishes these canals fundamentally from blood vessels ; they are filled with a fluid which is imperfectly vitalized, a chylaqueous compound ; it is replete with floating organized corpuscles. The flux and reflux motions of this fluid are excited, partly by cilia, and partly by the rhythmic contractions of the disc. Respiration is accomplished in two modes ; partly by the interchange of gases on the under surface between the contents of the canals and the surrounding element, and partly by the air suspended in the external fluid, which is admitted through the mouth and stomach into the gastro-vascular channels directly from without.

The basis and bulk of this fluid is composed of salt water, but qualified by the impresses of the zoochemical influence to sustain the life of albumen, fibrine, and to evolve definitively organized floating corpuscles. The refuse portions of this fluid are rejected *per os* ; there is no anal outlet. The cells of the solid structures of the Acaleph are filled with a semifluid hyaline jelly ; it is the chylaqueous fluid in its highest grade of organization. In the Medusa, it is to the chylaqueous fluid, what the contents of the “protean” cells of the gelatinous cortex are to the currents of the circumambient element, traversing the passages in the sponge : thus, in brief, is conveyed a description of the machinery of the respiratory process in the Acaleph ; from it the nutritive processes cannot be distinguished. The Ciliograde family departs from the type of the former in one particular ; there exists here a second orifice to the digestive system (fig. 7, *b*). The fact alters not the principle of the mechanism, according to which the fluids are aërated. The gastro-vascular canals arise from the fundus of the stomach, attain the surface, and pass in meridional series



(fig. 7, *c, d*) from one pole of the body to the opposite, lying immediately underneath the external epidermis. Their courses are followed externally by rows of motive cilia, or vibratory fringes: all the canals peripherally terminate cæcally; they are furnished on *their internal* surfaces with cilia. The genera *Cydroppe*, *Cestrum* and *Callianira* are illustrative.

In the *Cirrhigrade Acalephs*, the second orifice of the alimentary apparatus disappears. The canals, filled with the chylaqueous fluid, radiate, while they multiply in the direction of the circumference of the disc. Like those of the preceding families, they are ciliated internally, while they are distributed in close proximity to the under surface of the dome.

The organization of the *Physograde Medusæ* is little understood\*.

It cannot be doubted, that in the *fluids* of the Acalephs, floating corpuscles, from their multitude and their determinate structure, exercise an important part. They animalize the fluid; they endow it with life. Directly or indirectly they develop the proximate principles out of the inorganic elements. Both the corpuscles and the fluid contained in the gastro-vascular canals are nearly colourless. Here, as in many other instances amongst the invertebrate animals, the lesson is taught, that *colour* has little to do with the capability of vital fluids to absorb oxygen. In this class, it is beyond question, that sea water is admitted directly into those canals in which the chylaqueous fluid is contained. The former is so rapidly assimilated with the latter, that the nutritive and vital character of the compound fluid resulting from the admixture is readily maintained at the required standard.

It is important to remark, that in all Acalephs the gastro-vascular canals are distributed as closely as possible to some *external* surface; in *Rhizostoma* to the under surface of the dome, in *Beroë* in meridional lines over the globe, in other species along the margins, &c. Such disposition has reference to the respiratory process: vibratile cilia in general are developed on those portions of the external surface which coincide with the gastro-vascular canals.

*Echinodermata*.—In this class the same questions arise, as important preliminaries to the study of the respiratory process, with those as to the *meaning of the fluids*, which were discussed with reference to the inferior Radiata;—which of the *three* orders of fluids, present in the œconomy of nearly every Echinoderm, is made the *special* subject of this process? 1st, the cavity of the

\* See a paper in the Ann. des Sc. Nat. tom. xviii. "Sur la Structure des Physalies et des Siphonophores," by Leuckart.



body (figs. 8, 9, *d*; fig. 10, *n*) (*i. e.* the spacious interval which separates the digestive from the integumentary system) is filled in *all* species with a fluid which the author has called the *chylaqueous*: 2nd, the protrusile suctorial feet (Pl. XII. fig. 8, *g*; fig. 9, *f*) are occupied by another class of fluid; this system constitutes the water-vascular system of Tiedemann and Müller; 3rd, the blood-vascular system (fig. 10, *j*), of Tiedemann, Delle Chiaje, Valentin, Agassiz, Dr. Sharpey and Müller: these three systems are defined as severally distinct and independent, and their functions respectively are alleged to be distinct and independent. In what conceivable manner is the descriptive anatomist to depict the breathing systems of these animals, unless by that of first adjusting these long-controverted questions? The ultimate structure of those solid parts, on which the office of aërating the vital fluids is represented to devolve, must be first determined. This inquiry alone can prove to what extent, if at all, these parts are capable of answering the purpose which they are stated to fulfil. The chylaqueous system of fluids exists in *every* Echinoderm; the water-vascular system does *not* exist in every species. In the *Sipuncles* and the *Ophiuridæ*, it has no place. The blood-vascular system is very imperfectly known. Little has been done to demonstrate its presence in the asteroid Echinoderms, and still less in the Echinidæ. Its history has been most fully developed in the Holothuridan and Sipunculidan genera.

#### 1. *The Chylaqueous System of the Echinoderms.*

Is it capable of subserving a respiratory purpose? Is it constituted such that it is physiologically capable of executing this great function? And is it also *distributed* appropriately?

The mass of fluid occupying the visceral cavity, bounded on one side by the digestive system, on the other by the integuments, has been described, by the classical authorities upon this subject, as consisting purely of sea water, admitted *directly* from without through the skin, for the exclusive purpose of aërating the blood-proper, said to circulate in a *capillary* system of vessels wrought in the solid parietes circumscribing the cavity. This, in succinct expression, is the doctrine of the schools, as to the mechanism of respiration in this interesting class of animals. It supposes the existence of a profuse plexus of capillary vessels carrying true-blood, distributed over *all* the visceral and parietal surfaces limiting the chamber in question. It may be at once stated, that no approach to a demonstration of the presence of this system has ever been made by *any* modern or ancient anatomist. Is it logical to erect one hypothesis upon another? Let *facts* be first represented. In the Asteridæ, Echinidæ, Ophiuridæ and Ophio-



comidæ, the fluid contained in the peritoneal cavity has been described by every comparative anatomist as pure unmixed sea water. It cannot be denied that the cavity itself is the anatomical homologue of the real perigastric chamber of zoophytes and of the gastro-vascular canals of Medusæ. It is therefore the anatomical *locale*, in which the chylaqueous fluid *should* accumulate; but under what character does it occur in the higher vermiform Echinoderms? In the Holothuridan and Sipunculidan genera (fig. 10, *n*), it presents itself as a chamber filled with a chylaqueous compound, under the unquestionable form of a thickly corpusculated milky fluid, organized in a high degree, and oscillating as a living nutritive fluid: it is by tracking the characters of this fluid from above downwards, that its real signification in the inferior Echinoderms, in which it offers the *apparent* properties of simple sea water, can be unerringly ascertained. The floating corpuscles of the chylaqueous fluid of the Sipuncles (fig. 10, *h*) present the features of *constancy* in structure and proportion; they are always the same in the same species. The cephalic appendages in this genus, as well as the whole integumentary system of the body, are organized with express reference to the exposure of *this fluid*, and this fluid exclusively, to the agency of the external aërating element.

The skin is *fenestrated* (fig. 11, *d, d, d*), that is at regular intervals the muscular layer disappears, and an interval of elliptical figure, covered over only by a single layer of epidermis, results. In the *solid* structures of the integuments there is no trace whatever of a capillary vascular system to be detected. It is a simple membrano-muscular partition, intervening between the chylaqueous fluid within and the surrounding element without: it is *through* this veil that these two divided fluids interchange their dissolved gases. The tentacles present the same precise mechanism (Pl. XII. fig. 10, *a & C, & B*); they are merely hollow appendages, musculo-membranous, lined *within* and *without* by a ciliated epithelium. A *few* proper blood vessels reach their bases from the circular vessel; but *no* trace whatever of a vascular plexus, in the *structure* of these parts, can by any manœuvre be discovered. The inference is irresistible, that, like the skin of every part of the body, which *internally* is universally ciliated, the tentacles are designed almost exclusively as instruments for the oxygenation of the chylaqueous fluid (*not* the blood proper), which oscillates by a flux and reflux movement in their hollow interior. To the genus *Holothuria* these observations in every detail are strictly applicable. The tentacles, however, though hollow membranous appendages, are furnished, *in the substance of their parietes*, with a few more blood-vessels: the skin is fenestrated like that of the Sipuncles (fig. 11); the open cavity



of the body is occupied by a highly organized corpusculated fluid which the solid parts just described are expressly fitted to aërate. From its volume, its organic composition and its suspended cells, its importance in the organism cannot be disputed. It cannot acquire nutritive properties unless through the agency of oxygen. This element can be received through no other provisions than those exhibited by the skin and the tentacles: thus the *theory* of respiration, with respect to the chylaqueous fluid, in these superior Echinoderms is complete. Although attenuated at regular points, with a view to approximate as closely as possible the chylaqueous fluid to the external medium, no *open perforation anywhere* exists in the tentacular or integumentary processes. The surrounding fluid cannot therefore penetrate *directly* from without into the peritoneal cavity\*. It is introduced through the mouth and the digestive system.

In the *Ophiuridæ* and *Ophiocomidæ*, the visceral cavity is filled with a fluid, which, though not so highly organized as that of the preceding genera, is undoubtedly the same system: it is not so milky in appearance; it approaches more to that of pure salt-water. Its floating corpuscles are far less abundant, and more indefinitely formed; its oscillations are ceaseless under the movements of the arms and action of cilia. At the flexures of the articulated pieces of the arms, soft, membranous, hollow processes, opening into the peritoneal cavity, protrude.

They are designed to aërate the fluid contents of the visceral chamber: unlike the membranous integumentary projections of the *Asteridæ*, they are neither ciliated within nor without. They may be seen perfectly in the smaller species, as transparent objects. If any vestige of a blood-proper system of vessels occupied the substance of their parietes, it could not, thus examined, escape detection; none such exists. Wherefore then are these specific organs provided, if not to arterialize the great system of fluid which penetrates into their interior? The answer cannot be withheld; it is to aërate the chylaqueous fluid exclusively†. The chylaqueous system of the *Echinidæ* (fig. 9), comprehending a considerable mass of fluid filling the cavity of the spherical shell (*d*), has never yet been recognised by the anatomist as a vital organic system. The great authorities, Agassiz especially, formerly

\* The author would again refer the reader to his recent memoir in the *Phil. Trans.* (1852), for a full and complete statement of the anatomical and experimental evidence, by which are substantiated the general propositions enounced in the text.

† It will be afterwards shown, that comparative anatomy has done absolutely nothing towards the demonstration of the blood system of these Echinoderms. A circular vessel is stated by Müller only to surround the mouth.



quoted, state that sea water streams into the visceral cavity through perforations in the membranous processes (fig. 9, *f, f*) of the shell, especially in those under the name of *branchiæ*, which are distributed in groups around the circumference of the oral membranous disc. The latter are *not* connected with the suctorial or water-vascular system; they are distended by injections thrown into the open chamber of the shell.

They are protruded only by the force of the fluid driven into their interior. They collapse by contractility of their parietal structures. They are *not perforated* at their extremities (*b*). They *cannot* therefore serve as open passages for the direct admission of the external medium into the visceral cavity. They are unquestionably in part tactile appendages. In addition to the meridional rows of suctorial feet, the shell of *Echinus* is perforated by numerous hollow membranous processes (fig. 9, *f, f, f*), lined within and without by vibratile cilia, and *penetrated* exclusively by the fluid of the visceral cavity. Like the integumentary structures of the higher genera, they bear no evidence whatever of blood-vessels. These facts impel the physiologist to the adoption of one inference. They *can* only subserve a respiratory purpose on the supposition that the *subject* of that process is the chylaqueous fluid. *Then* the conclusion cannot be evaded, that, although in the *Echinidæ* the fluid contained in the visceral cavity may *look* like simple sea water, it must be something more; else *nothing* would be signified by the express provisions supplied, to subject it to the process of aëration. It is, in truth a dilute albuminous solution, charged with corpuscles indeterminately organized. It possesses a higher solvent power for oxygen than simple sea water. It is the reservoir out of which the elements of the true blood are drawn. Injection thrown into the hollow of the shell of *Echinus* distends beautifully, in relief, numerous membranous appendages belonging to the integumentary system. In *no instance whatever* can any *perforations* in the extremities of these processes be detected. There is therefore no direct evidence for the opinion commonly entertained by the best observers of the Echinoderms, which affirms that the external water enters immediately through openings in the *integuments* into the peritoneal cavity\*.

\* On the subject discussed in the text, Müller, in his recent elaborate essays on the Echinoderms, published in his 'Archiv,' offers the following remark, which I produce in the original:—"Die baumförmigen Kiemen der Seeigel, die äusseren Kiemen Valentin's sollen an den Enden ihrer Aeste nach Tiedemann offen sein, auch das Wasser in das Innere des Seeigels aufnehmen. Diese Ansicht gründet sich auf Injection mit Quecksilber unter gleichzeitiger Anwendung von gelindem Druck. Valentin fand diese Organe dagegen an den peripherischen Enden geschlossen, so dass sie also hohle Verlängerungen der Leibeshöhle nach aussen darstellen, und die



The preceding questions admit of more easy and satisfactory solution in the Asteridæ than in the classes of Echinoderms already reviewed. *Asterias rubens* is a large animal; the fluid by which the visceral cavity (fig. 8, *h*) is filled is considerable in volume. The whole integumentary structures are more readily subjected to demonstration. Everything is favourable to a final conclusion of the controversy which has long divided anatomists as to the real signification of the fluid contained in the visceral cavity: it can be placed, in several modes, beyond doubt, that *no open perforations exist in any part of the integumentary parietes of Asterias*. The membranous processes (fig. 8, *f, f'*) *openly* communicating with the visceral cavity are so remarkably elastic and protrusile, that, by means of coloured size forced carefully into the cavity, they distended to a great distance above the plane of the external surface. They are *cæcal* at their distal extremities.

This injection escapes externally only by rupture: this simple expedient proves the *cæcal* character of these parts; they are *not* consequently designed to admit sea water into the interior of the body. It is perfectly easy to repeat and confirm the first observation of Dr. Sharpey, that the corpuscles of the visceral fluid advance to the distal end of these processes, and then return under the impulse of ciliary agency\*. Although an injection so thick as size will not escape through these membranous processes, a thinner fluid, such as coloured water, will slowly ooze through; it is not therefore improbable that an interchange of the fluids, which their attenuated parietes only divide, may *to some extent* occur through endosmose. This fact, however, cannot shake the stability of the conclusion, that anatomy does not furnish *any* grounds for the belief that the fluid contained in the peritoneal cavity is derived directly from *without*. The microscope renders it certain that the hollow membranous processes,

Athemfunction auf ihrer äussern Oberfläche stattfindet. Auch ich habe bei wiederholter mikroskopischer Untersuchung dieser Theile von lebenden Seeigeln *keine* Oeffnungen an den abgerundeten Enden wahrgenommen." Müller, however, does not explain in what manner the "Athemfunction" of these appendages, which he argues to be *cæcal*, is possible. His conclusions as to the *imperforate* character of these parts I have repeatedly confirmed by variously devised methods of examination.

\* Müller confirms the conclusions stated in the text—"Die respiratorischen Röhren auf dem Rücken der Asterien, welche mit der Bauchhöhle communiciren sollen zufolge der Injection von Tiedemann am Ende offen sein, und zum Wechsel des Wassers des Leibeshöhle dienen. Nach Ehrenberg dagegen sind die Röhren am Ende geschlossen, er sowohl als Sharpey sahen die Strömungen im Innern am Ende umkehren. An jungen lebenden Exemplaren des *Asteracanthion violaceus* sah ich dasselbe, und es gelang mir nicht eine Oeffnung wahrzunehmen."—Anatomische Studien über die Echinodermen. Müller's Archiv, 1850.



filled by the fluid of the visceral cavity in *Asterias*, bear in the solid substance of their parietes no trace of true blood-vessels; they are lined within and without by vibratile epithelium, and composed only of interlacing elastic fibres. What conceivable office can such organs execute, if not that of exposing the chylaqueous fluid to the renovating influence of the surrounding medium? In *Asterias* this fluid approaches "simple sea water" closely in physical properties. It is, however, in reality a dilute albuminous, opalescent solution. It is charged scantily with imperfectly formed corpuscles always the same in the same species.

In other species of Asteridæ the membranous appendages of the skin present other varieties in size and figure, none in character and structure.

In *Uraster papposa* the membranous intervals in the calcareous trellis are large and favourable for examination. They may be readily seen with the naked eye in the living animal to be capable of being bulged out under the pressure of the fluid in the visceral chamber.

The Cribellidæ present another modification of the soft part of the integument. The skin is smoother, the membranous intervals are smaller, and the membranes are less capable of protrusion outwards. In every other respect they are identical with the corresponding parts of the preceding genera. The proposition may now then be finally affirmed, that in the Echinodermata the chylaqueous fluid (*i. e.* the contents of the visceral cavity) is *itself first* aërated, and that by means of a machinery of soft parts expressly arranged with a view to this end; and that then *it aërates the blood-proper*.

## 2. Water-vascular and Blood-vascular Systems of the Echinoderms.

To what extent, in what manner, if at all, do these two fluid-systems, or either of them, participate in the mechanism of the respiratory process? In solving the curious problem presented by the Echinodermal organism, the highest interest attaches to this question. Let it be first seen whether the statements of Tiedemann, Sharpey and Müller, that these systems are perfectly independent of each other and of the chylaqueous system already described, are really founded on trustworthy demonstration. No anatomist up to the present time has done more towards elucidating the anatomy of the true blood-system of the Echinoderms than that of proving the existence of certain central trunks *only*. This system has never been traced to its peripheric distribution in *any species* (the Holothuridan *perhaps* excepted) by any comparative anatomist. An induction is unsafe which is



grounded upon hypothesis. The theory of respiration can only be constructed out of the materials supplied by the patient labours of the anatomist. It does not appear that Dr. Sharpey ever could verify the description of Tiedemann with reference to the blood-system. The tenuity of their coats however, and pale colour of their contents, render it extremely difficult to trace completely the distribution of the vessels\*. Müller concurs in the description of Tiedemann, stating that in *Asterias* a circular trunk surrounds the mouth and gives off branches to each ray—adding the confession, that “*die Injection vom Blutgefäßring gelang nur bis zum Anfang dieser Gefäße.*” And this is all that the author of this memoir has ever been able to accomplish to prove the existence only of the central trunks. This is the sum of the existing knowledge with reference to the blood-proper system of the Asteridæ. Of that of the Echinidæ very little also is known. Müller describes a circular vessel embracing the œsophagus immediately underneath the lantern; from this a trunk proceeds coursing along the curves of the intestine, and ending in the *circulus analis*. This learned anatomist observes, “*Um eine klare Vorstellung vom Herzen zu bekommen, muss man es bei Cidaris untersuchen; es ist bei Cidaris ein weiter, ganz gerader Canal mit dicken weichen Wänden†.*” In *Cidaris* the heart is not a circular vessel, but a fusiform trunk lying parallel with the intestine. The circumference of the blood-system in the preceding genera has never yet been brought under demonstration. In science negative is inferior in value to positive proof; but at present it is only possible to declare that no care can succeed in discovering any evidence whatever of the presence of a blood-proper system in the solid structures of any part of the body of the Echinoderm. The parietes of the alimentary canal are *most certainly* not ramified by blood-vessels. The soft parts of the integumentary system are literally destitute of vascular tissue. The contents of the central trunks of the blood-system are identical in appearance with those of the visceral cavity, and with those of water-vascular or suctorial system; that is, when the morphous elements of these *three* fluids are placed in juxtaposition under the microscope, it is impossible to indicate between them any difference whatever in structure or shape. The fluids themselves are also identical in every physical appearance.

The *blood-vessels are internally and externally lined with cilia*, the water-vessels are so, and the visceral cavity is richly so. What can these extraordinary facts mean? Can they mean any thing, but that these three systems are reciprocally connected?

\* Art. Echinodermata, by Dr. Sharpey.

† *Op. cit.* p. 127.



A suspicion to this effect has been expressed by Milne-Edwards and M. Quatrefages; but the author claims the merit of having first produced demonstrative facts which impart to this suspicion a very probable character. The question admits of more confident answer in the higher genera. The blood-vessel of the *Sipuncle* may be readily exposed: it lies on the intestine in form a bright pink thread (fig. 10, *m, j*); it exists only on one side; it has no discoverable correlate on the opposed side of the cylinder; it is filled with pink fluid, the corpuscles of which are identical *unquestionably* with those floating on the fluid of the peritoneal cavity. The vessel may be readily isolated and placed detachedly under the eye of the microscope. The blood-corpuscles while in the vessel continue in ceaseless motion; this motion instantly ceases upon their escape from the vessel. Vibratile cilia may be actually *seen* on the internal lining membrane of the vessel: the motion is due to *their* vibration. Müller and Quatrefages and Dr. Peters incidentally refer to this phenomenon; by neither of these observers has it been referred to its true cause. In *no* other class of animals are the *internal* surfaces of true blood-vessels lined with cilia; it is because in the Echinoderms the blood-system is rudimentarily formed, that this aberrant phenomenon is intelligible. It is in the Echinoderms that the blood-proper system *first appears* in the zoological series. Nature's first effort is imperfect; the system is *not* independent of, closed off from, the other fluid systems of the organism; it derives its contents from those of the visceral cavity. The *water-vascular system* is exclusively locomotive and suctorial in function; it nowhere exhibits connexion with the branchial organs. Its fluid contents however indubitably communicate in some manner with those of the peritoneal cavity; the microscope *proves* them to be identical. In the Holothuridan genera these admit of more complete solution. In them the *three* systems exist under a pronounced form. The blood-system is more highly developed than in the inferior Echinoderms; it supplies branches to the tentacles, to the integuments, and forms a mesenteric plexus. The cavity of the body is notwithstanding filled by a highly corpusculated fluid, which penetrates into the hollow of the tentacles, and comes into near contact with the surrounding element through the *fenestræ* of the integument. In this genus then the *two* fluid systems are *separately* submitted to the process of aëration. The *parietes* of the tentacles bear a ramification of true blood-vessels. Their hollow axes are filled with chylaqueous fluid. But in the Holothuridæ a *fourth* system of fluids is superadded—that of the respiratory tree. The meaning of the respiratory tree is even now enigmatical; it consists of a cæcal, subdivided tube, filled with sea water, and communicating



openly with the cloaca. *It floats in the fluid of the visceral cavity.* Its parietes are *not* supplied by a plexiform vascular system. The plexus formed by the blood-vessels lies in the folds of the mesentery, and belongs to the intestine; it exhibits no connexion with the *respiratory tree*. What then can be the signification of this excentric and paradoxical organ? Every comparative physiologist from Tiedemann to Müller has recognised in it a true respiratory organ; but in what possible manner can it accomplish such a function? The sea water admitted into its interior cannot affect the true blood; its parietes are *not* supplied by blood-bearing plexuses. The latter are remotely situated. To what uses then is it dedicated? It is surrounded by, it floats in the mass of the chylaqueous fluid. From their relative positions, it is manifest that the fresh sea water admitted into the *respiratory tree either itself, or the air by which it is charged*, passes by endosmose through the partition of the parietes, and that the chylaqueous fluid in the closed visceral cavity, *either itself, or the effete gases by which it becomes impregnated*, passes out *into* the *respiratory tree* by exosmose. *This is the real function of the "respiratory tree of the Holothuria."* It is an excentric apparatus artfully provided, to renovate the composition and replenish the volume of the chylaqueous fluid. Thus is presented a summary statement of the *mechanism* of respiration in the Echinoderms.

*Rotifera.*—It is the undivided belief of all recent observers that a blood-proper system does not exist in the Rotifera. These animalcules are provided with a rudimentary water vascular system, which entitles them to rank near the Echinoderms. The cavity of the body is capacious; it is filled with a fluid which is sustained in motion by provisions expressly designed for this purpose. Vibratile 'tags,' accurately described by Ehrenberg and Dalmryple, aided by ordinary cilia on the external surface of the digestive canal, are well fitted for this office. The cavity external to the viscera is filled with a fluid, remarked by all observers, but specially described by none. Its nutritive character may be confidently inferred: 1st positively, from its anatomical locale; 2nd negatively, from the absence of every other fluid. 'Tags' and 'cilia' cannot aërate a vital fluid; they can only set it and maintain it in motion. Confusion has brooded over this simple point. Only the thin structure forming the exterior enclosure of the body intervenes between the fluid of the visceral cavity and the surrounding element. Thus is the former submitted to the influence of the aërating agent\*.

\* See the excellent Art. *Rotifera*, by Dr. Lankester, in Cyclop. Anat. and Phys. "Contributions to the Anatomy and Physiology of the *Rotifera*,"



*Entozoa*.—Mystery has long enshrouded the natural history of the Entozoon. Living in situations beyond the access of the atmosphere, and totally uncomprehended in the real character and distribution of its fluids, the mechanism of the respiratory process has proved only the arena for conjecture and speculation as erroneous as various and contradictory. M. E. Blanchard has long misled the helminthologists of Europe. In the Cestoid and Trematoid Entozoa he has pictorially represented a *blood-proper* system of extreme complexity and development. He has figured with elaborate minuteness that which has no existence in nature \*. He has confounded an apparatus of irregular, ramifying

by Mr. Huxley in *Micros. Journal. Annales des Sciences*, 1851, Art. *Lacinularia*, par M. Udeken. Leydig on *Lacinularia socialis*, in Siebold and Kölliker's *Zeitschrift*, Feb. 1852.

\* The author would desire to speak with respect of the researches of M. E. Blanchard on the Entozoa. His memoirs on this subject enrich the pages of the '*Annales des Sciences Naturelles*' for the years 1847, 1848 and 1849. His illustrative figures, which are copied into Crochard's edition of the '*Règne Animal*,' executed in the highest style of French art, are designed to display the true-blood system of the Cestoid and Trematoid worms. With reference to the latter order he remarks:—"Au moyen de mes injections, je me suis assuré qu'il existait chez ces animaux un appareil de vaisseaux à parois propres, se ramifiant dans toute l'étendue du corps. On ne distingue ici ni veines, ni artères proprement dites; les deux fonctions paraissent appartenir aux mêmes vaisseaux!"—Is it not extraordinary that such a distinguished physiologist as M. E. Blanchard should offer *such* a definition of any apparatus designed to circulate true *blood*? where in the animal kingdom could a parallel to such a system be indicated?—"Nous le voyons consister en un ou plusieurs vaisseaux principaux, offrant de nombreuses ramifications s'anastomosant sur une infinité de points; en sorte qu'il existe là un véritable réseau vasculaire." In principle how totally this definition differs from the former!

Bojanus and Nordmann have described almost in the same words the same system, indicating it as the apparatus for the circulation of the blood-proper. In relation to the Cestoid worms M. E. Blanchard observes: "Pendant longtemps, partageant l'erreur commune, je pensais qu'il n'existait point de système vasculaire proprement dit chez les Cestoïdes. Les canaux gastriques, communiquant de l'un à l'autre dans chaque Zoonite, étaient regardés très-généralement comme destinés à remplir les fonctions des deux appareils. Mais récemment, dans les *Tænia*s du chien et de la fouine, j'ai constaté, indépendamment de ces canaux gastriques ou intestinaux, l'existence d'un système vasculaire très-complexe, consistant en vaisseaux longitudinaux pourvus de ramifications et d'anastomoses nombreuses. Ainsi ces animaux remarquables, considérés par les zoologistes les plus éminents comme des Vers *parenchymateux* complètement dégradés, sont au contraire des êtres dont l'organisation est loin d'être très-simple." (*Annales des Sciences*, tome viii. 1847, p. 119.)

In the *Cestoid* worms M. Blanchard describes a perfect blood-vascular system, independently of that of the straight lateral canals which constitute the gastric apparatus. He describes an artery, a vein, and an intermediate order of straight parallel capillary vessels. In the *Trematoda*, in one place he states that the extreme vessels form a ramifying plexus; in another he remarks, "Il est à remarquer aussi que les vaisseaux de la



channels destined to contain a real chylaqueous fluid with a system of *true* blood-vessels. M. Blanchard's inferences are drawn from *injected* specimens. In such investigations the method of injection is liable to numerous fallacies; it imparts a uniform diameter to canals which are remarkable for variety of calibre. The real characters of such structures can only be determined by direct inspection of the living individual. Thus *only* can the fact be demonstrated, that the so-called *blood-vessels* of the parenchymatous worms *neither rhythmically contract nor pulsate*. Among blood-vessels such a circumstance would constitute an irreconcilable anomaly. The blood-vessels described by M. Blanchard, and in common with him by nearly all helminthologists, in the Cestoid and Trematoid Entozoa proceed from *one or more central spaces*. When these spaces are cylindrical in figure they assume the apparent characters of blood-trunks. They *really* represent the splanchnic or visceral *cavity*. Such is the form under which this cavity, so conspicuous in the Nematoid Entozoa, occurs in the Sterelmintha. The main central channels present a general coincidence of disposition with those of the alimentary system (Pl. XIII. figs. 3, 6, 8, 9). They do not present a uniform diameter according to the customary manner of a vascular trunk. They exhibit irregular outlines, now contracting into narrow necks, and now dilating into lacunæ. This is especially true of those of the Trematoid worms. In the Cestoid orders (fig. 6) the main trunks follow the margin of the "Zoonite," the lesser crossing in the parallel spaces between the transverse annuli into which the integuments are wrinkled. These secondary channels in *Tænia* are

partie antérieure (speaking of the vessels in *Amphistoma conicum* (Règne Animal, pl. 28)), et surtout ceux de la partie postérieure du corps, *se terminent sous la peau en de petites lacunes*, du reste très-nettement circonscrites." No instance is known in the whole animal kingdom of a *blood* system terminating in cæcal extremities. The apparatus which exhibits such characters cannot fall under the denomination of a blood-proper system. The method of investigation adopted by M. Blanchard has distorted the features of the object sought to be studied. Forcible *injections* into textures fragile and delicate will enable a preoccupied fancy to construct any results, to recognise grounds for *any* conclusion. The views stated in the text are founded upon examinations conducted with extreme care, and instituted on *living* specimens. To a great extent the author's researches have corroborated the *descriptive* anatomy of M. Blanchard: in many essential respects however they stand in direct opposition. If the system of vessels depicted in the figures of M. Blanchard were really a *true blood system*, the Cestoid and Trematoid Entozoa would be entitled to rank high in the zoological scale. They stand really below the Annelida. To this position they are assigned on the ground of the *general* affinities of their organization. The author is persuaded that the French helminthologist has mistaken a *modified* chylaqueous system for a blood-proper apparatus.



much more irregular in outline and distribution than the blood-vessels (*sic*) depicted in the drawings of M. Blanchard: they penetrate intimately the *substance* of the integuments. With reference to these channels, large and small, one important fact should be noted: *they are not gifted with separate membranous parietes*. This fact alone is enough to prove that they are *not* channels for the conveyance of true blood. Every true blood-vessel is endowed with a special power to circulate its fluid contents. Its parietes are *contractile*. The bore of the channel rhythmically increases and decreases. Such movements would be mechanically impossible if the parietes of such 'vessels' were adherent to the surrounding solid and fixed tissue. In a channel destined to convey chylaqueous fluid the latter case is the *rule*. They possess no inherent circulating power. *Their* contents are impelled to and fro under the conjoint force of ciliary and muscular action. Here then is a clearly defined distinction between a chylaqueous channel and a true blood-vessel. Let the wonderful vascular system, which M. Blanchard has delineated from artificial injections in the Cestoid and Trematoid worms, be tested by this anatomical principle. This excellent observer has omitted to investigate the histological characters of these parts. He has not in any case determined the relation between that system which he describes as the true blood system and the surrounding solid structures. In no instance has he reduced to demonstration the physical characters of the fluid by which his so-called blood-vessels are filled. The same criticism will apply with equal justice to the illustrations, by aid of which he defines the alimentary system of *Tenia* and *Bothriocephalus*. The *blood system* described by M. Blanchard in these worms *does not exist*. That which he so beautifully pictures as the *gastric* apparatus, consisting of straight capacious lateral canals, joined by cross conduits, constitutes really an order of passages tunnelled in the solid parenchyma of the body, answering in every sense to a normal chylaqueous system. The contained liquid is not blood, but chylaqueous fluid\*: it is a fluid which is devoid of every trace of morphotic elements. *Why* it is so will be immediately understood.

In the Trematoid worms the blood-vessels of M. Blanchard fall unquestionably under the denomination of a chylaqueous system. In *Distomum hepaticum* it is perfectly easy to reduce

\* The author is here desirous to explain that he does not deny altogether the existence of a blood-proper system in the Cestoid worms. His researches enable him only to affirm with confidence that *those channels which are described by M. Blanchard as constituting an independent system of blood-vessels do not exist*; that his alimentary is really a chylaqueous system, and that his ovary is truly a grand digestive organ.



to demonstration its entire characters. A large median, irregular channel commences in *smaller* passages near the posterior or generative sucker, and proceeds as far as the caudal end of the body of the worm, exhibiting a gradually diminishing diameter. Viewing the object transparently, it may be proved first that this channel is a hollow space by the rolling to and fro of a contained fluid; the movements of the fluid being rendered apparent to the eye by the presence of minute *accidental* molecules. In other respects, it is a perfectly homogeneous non-corpusculated fluid. By Bojanus, Mehlis, Nordmann, and other observers this channel is defined as terminating in an orifice posteriorly, and the channel itself, from the limpid character of its fluid contents, is described as the great duct of an excretory system. This is an error. This system in the Trematoid Entozoa has neither an inlet nor an outlet. It is a *closed* system, but not therefore a blood-system. In *Distomum* there is only *one* central space: it is not a blood-trunk; it represents unquestionably the *visceral cavity*. These worms are not literally therefore sterelminthous, solid, or parenchymatous worms (*Vers intestinaux parenchymateux*, Cuvier). The cavity is *distributed* in form of irregular, imparietal, reticulate passages. These passages can be traced with facility throughout the whole substance of the body. They ramify profusely underneath the skin and amid the digestive diverticula. They arise in the most unequal manner from every point of the circumference of the central trunk. They end peripherally in numerous instances in *cæcal* terminations, corresponding with the mode in which the blood-vessels (*sic*) of M. Blanchard terminate in *Holostomum alatum*, *Amphistoma conicum*, *Tristoma coccineum*; in others they form re-entering branches. The figure of M. Blanchard\* represents the secondary trunks in *Distomum* as proceeding from the primary with far too great regularity. To this trunk he seems to indicate a caudal orifice, and yet calls it a *blood-vessel*! It is susceptible of proof that this central channel in *Distomum* is *not contractile*. The adjacent trunks of the *digestive* system contract and dilate in regular periods. The walls of the central channel are perfectly stationary. Its interior is not lined with cilia. Its fluid contents do not move in one systematic orbit: they oscillate to and fro. Such characters can belong only to a chylaqueous system.

In *Holostomum alatum*, *Amphistoma conicum*, in *Tristomata*, in *Brachylemus variegatus*, sometimes found in the lung of the Frog and Toad, in *Monostoma verrucosum*, &c., the main primary

\* See plate 36,—Zoophytes: Crochard's French edition of the 'Règne Animal.'



channels of the fluid system coincide with those of the digestive. The latter are *embraced* by the former. This anatomical fact is significant of a physiological principle. It points to the manner in which the contents of the chylaqueous passages are derived by *exosmosis* from the chymous fluid contained in the digestive *cæca*. In those species of Trematoid worms in which the central conduits are *more* than one in number, it is important to observe that they are always joined together into *one* system by intervening passages. They do not convey opposite currents. In *both* the contained fluid flows and ebbs with great irregularity, in obedience to the contractions and expansions of the muscular integumentary envelope. In these essential particulars the standard definition of a true-blood system is violated. M. Blanchard defines thus the *Appareil vasculaire* of *Distomum hepaticum*:—"Cet appareil consiste en *un* vaisseau principal et médian." A *true* circulation requires *two* primary trunks, an artery and a vein. In another place this helminthologist observes generally with regard to the Trematoda—"Chez tous ces vers, le sang n'est certainement pas transporté, d'une manière régulière, d'arrière en avant par certains vaisseaux, et d'avant en arrière par d'autres, comme l'a pensé M. Nordmann. Dans les Trématodes en général, le fluide nourricier est transporté et ramené alternativement et plus ou moins irrégulièrement par les mêmes vaisseaux; *c'est un mouvement de va-et-vient plutôt qu'une véritable circulation.*" (Annales des Sciences Nat. tom. viii. 1847, p. 336.) Ample evidence is thus drawn from his own observations to convince the physiologist that the system of vessels described by M. Blanchard constitutes not a blood-proper but really a clearly defined chylaqueous system. The presence of this fluid implies the existence of a *visceral* cavity: it is its normal anatomical *locale*.

With reference to the blood-proper of the Cestoid and Trematoid Entozoa the author will at present only remark, that *if it exists at all*, it must be under conditions of rudimentary abeyance. The following general statements will then serve to convey the corollaries which his recent researches appear to warrant. In the Cestoid and Trematoid worms the whole substance of the body is pervaded by a highly albuminous but homogeneous non-corpusculated fluid, which is distributed extensively by means of imparietal and irregular conduits under the entire cutaneous surface of the body, *constituting the true apparatus of respiration*, and displaying alternate flux and reflux movements under external muscular agency, and embracing in every possible direction the diverticula of the digestive system, and *from which it extracts its reinforcements*.

It is adequate in every physiological sense to the ends of



a nutritive system. Abounding in albumen it is capable of ministering to the wants of the solids. Though destitute of morphotic elements, it yet conforms to all the essential characters of a chylaqueous system.

The *digestive* apparatus (Plate XIII. figs. 3, 6, 7, 8, 9) of the parenchymatous Entozoa is intimately concerned in the process of respiration. In the Cestoid and Trematoid orders it presents but one essential type. It has but one external orifice. A *stomach* properly so called does not exist. There is this remarkable and apparently anomalous fact to be stated with respect to the fluid with which the digestive cæca are filled:—it is charged *with definitely organized floating cells*, which exhibit *constant* differences in different species! These corpuscles are not formless molecules. They consist of a cell-wall and granular contents, and frequently a nucleus legible to the eye. They are flat, scaly particles, having a yellowish tinge. They are undoubtedly *not* fragments from the glandular parietes broken off by pressure. They oscillate with great regularity under the rythmic contractions and dilatations of the parietes of the cæca. It is contrary to no analogical argument to suppose that these floating cells are designed to raise the chyme in which they float to an organic standard above that of ordinary chyme. In the parenchymatous Entozoa they execute the required changes in the nutritive fluids, *while the latter are yet within the alimentary system*. Among the Annelida several exceptions occur in which the same peculiarity is illustrated. The Nemertine orders (Plate XIII. figs. 1, 2) will be afterwards shown to fall under this category. In *Aphrodita aculeata* (fig. 5, *d*) the digestive *diverticula* are filled with a corpusculated fluid, which is exposed by an express contrivance to the agency of the surrounding aërating medium. This is also the case in several species of freshwater planariform leeches (fig. 4). It prevails too in the true marine Planariæ (fig. 3). To the value which the author has endeavoured to assign to the fluid systems of the Cestoid and Trematoid Entozoa, no sound analogy is opposed. These worms are, on the ground of the interpretation of the fluids now first offered, naturally linked into a continuous zoological chain with the lowest parenchymatous Annelids. Notwithstanding the meritorious researches of M. Blanchard, the organization of the Cestoidea is even now a theme prolific of controversy. The large, branched, flocculent organ (fig. 6) forming the bulk of each segment in *Tænia* and *Bothriocephalus* is designated by all recent writers after M. Blanchard as the ovarian apparatus. It is really the alimentary organ. It opens externally by an orifice proper to each segment. This organ in each segment is therefore independent. It sucks nourishment



from without by its own separate mouth. It is a *Planaria in itself*.

What are ordinarily described as the straight canals along either edge of the body are *not gastric* but chylaqueous. They are a part of a system of open channels ramifying through the cells of the parenchyma in which the gastric cæca are lodged. The latter are almost surrounded externally by the fluid filling the former. This fluid, as formerly explained, although non-corpusculated, constitutes the real chylaqueous system of the Cestoid and Trematoid Entozoa. It is through its agency that the breathing function is chiefly accomplished.

In *Tænia* this fluid system is common to the whole body of the animal. The 'segments' therefore are separate units only as respects the alimentary and reproductive organs. The chylaqueous fluid attains its enclosing channels by exosmose from the alimentary organ, not directly *ab extra*. The *posture* of the animal in its native habitat favours this interpretation of its organism. The orifice of each segment is applied to the surface of the infested part. The necessity for the preceding explanation illustrates the intimacy with which the respiratory function is interwoven with all the other nutritive operations of the body. In the *Tæniæ* then the respiration is *cutaneous*, but *not* in the mode commonly supposed. The skin is *not* the scene of a rich plexus of true blood-vessels. It is permeated and pervaded everywhere by that fluid which embraces the alimentary organ, and which is distributed throughout the parenchyma of the body by means of the irregular canals already described. It reaches the surface sufficiently nearly to receive the influence of the surrounding medium.

It is impossible therefore that the blood-proper can in this worm be the immediate subject of the respiratory process. Its existence is insusceptible of demonstration. If present at all, it can only receive oxygen indirectly through the medium of the chylaqueous fluid. This explanation is simple. It is founded on fact, and supported by analogy. The organization of the Nemertine Annelida conforms in every essential particular to that of the Cestoid Entozoa\* (see figs. 1, 2).

\* From the following extracts it will be seen how *little confident*, nay how confused and obscure, the best and latest author appears to be with respect to the real significance of the most important element of structure in the *Cestoid Entozoa*:—"On a généralement regardé les canaux longitudinaux dont il sera question après cet appareil, comme digestifs. Quelques auteurs ont même été jusqu'à leur accorder une, deux ou quatre bouches, par exemple dans les *Ténias*: tout récemment on leur a attribué une *quasi-bouche*, parcequ'il fallait bien trouver un moyen de faire arriver les aliments dans ces canaux. *Je crois qu'aucune de ces opinions n'est fondée, que ces vers se nourrissent par toute la surface de la peau, et qu'il n'y a pas plus d'organe spécial ou d'appareil particulier pour la digestion que*



The latter are illustrated and explained by the former. The alimentary organ in the Nemertiniidæ\* is precisely conformable to that of *Tenia*. In the former the whole organ has but one external opening, which is situated, in form of mouth, at the anterior end of the body. In the latter each segment has its separate opening (fig. 6, *a*). In both the digestive diverticula are filled with a corpusculated fluid. In both the spongy tissue, in the midst of which the alimentary organ is lodged, is chambered into capacious areolæ in which the real chylaqueous fluid is observed irregularly to roll. In the Nemertiniidæ†, however, the entire external cutaneous surface is ciliated. In the Cestoid worms no

*pour la respiration.* Plusieurs anatomistes ont pensé, Rudolphi entre autres, que les segments qui se détachent peuvent se nourrir, pendant quelque temps, par l'ouverture qui s'est formée à la suite de la séparation; cela me paraît évidemment erroné. Quand ces segments se détachent, le corps s'est resserré de plus en plus au bout, et au moment de se séparer, il ne tient plus que par un mince pédicule!" From the above observations, it is undeniably evident that Van Beneden is perplexed with doubt as to what really *should* be regarded, and what should not, as the *digestive system* in the Cestoid worms. Without a *definitive* knowledge of this system, how is it possible to form a correct conception of the disposition and functions of the nutritive fluids? Nor are the ideas of Van Beneden with reference to the circulating system of these worms more clearly defined:—"M. E. Blanchard croit devoir admettre pour tous les animaux de ce groupe une circulation véritable ayant lieu par des troncs principaux et dans des tubes à parois propres. J'ai étudié, sous ce point de vue, les parties minces et transparentes chez des individus très-frais, et je suis persuadé que le mouvement circulatoire a lieu dans de grandes lacunes, qu'il n'existe pas de vaisseaux à parois propres, et que le liquide correspondant au sang ne peut suivre un cours déterminé; il y a plus, des brides s'étendant de l'une paroi à l'autre; elles maintiennent les organes en place, et c'est dans l'espace laissé par les brides que la circulation sanguine s'effectue. Voilà le résultat d'études faites sur des parties vivantes, minces, voisines de la périphérie du corps et sans avoir fait subir aucune préparation à l'animal." "*Je ne crois pas me tromper en disant que les Trématodes et les Cestoides n'ont ni appareil digestif, ni appareil circulatoire*"!!—a conclusion perfectly marvellous, for a comparative anatomist so circumspect and laborious as Van Beneden. The preceding quotations will be found at pages 35 and 36 of his work entitled "*Les Vers Cestoides ou Acotyles*," Bruxelles, 1850.

\* These Annelids are abundantly illustrated on our coasts by the genera *Borlasia*, *Polia*, and *Lineus*.

† The author is anxious here to bear witness to the excellence of the memoir by M. Quatrefages on the Nemertine Annelids (*Annales des Sciences Naturelles*, t. vi. 1846), with which he has only just become acquainted. While his essay is acknowledged as a master-piece of minute descriptive anatomy, the author is constrained to differ *toto cælo* from M. Quatrefages in the physiological interpretation of parts. In these worms the French naturalist indicates correctly the mechanism of the respiratory function:—"Si c'est la surface entière du corps qui joue le rôle d'organe respiratoire, il s'ensuit que la respiration doit s'exercer principalement et plus immédiatement sur le liquide qui remplit les grandes cavités que sur le sang lui-même, puisque celui-ci est renfermé dans des vaisseaux qui sont entourés par le liquide dont nous parlons."—*Op. cit.* p. 269.



vibratile cilia in *any situation* have been proved to exist. It is a remarkable fact, that in *all Entozoa* the ciliary variety of epithelium is entirely suppressed. The agency of these organules is not essential therefore to the process of cutaneous respiration.

The *Trematoid Entozoa* are allied to the Cestoid by the most intimate affinities of structure. In the former type as in the latter, there exists but one orifice to the alimentary system. The gastric diverticula, which in several species amount only to two in number, in all Trematoid orders terminate cæcally. These cæca are filled internally by a corpusculated, and surrounded externally by a non-corpusculated fluid. The oscillations of this latter fluid have been observed by Nordmann, Dugès, Rudolphi, Blanchard, and others. It constitutes the true chylaqueous system. *Such* a development of the blood-proper system in the Trematoid Entozoa is opposed unqualifiedly by the analogy of the whole Planarian family, after whose type the former are constructed. The parenchyma, which intervenes between the digestive system and the external surface in these worms, is loose and large-celled—readily traversed by fluid. This fluid reaches the cutaneous surface; it embraces and laves everywhere the digestive cæca. The Trematoid Entozoa then, like the Cestoid, respire cutaneously. Every spot of the surface is utilized. The chylaqueous fluid is present everywhere, and immediately underneath the cuticle. It moves to and fro in its vacuoles. It is the immediate recipient of the external oxygen. It imparts it secondarily to the true blood, if this exists. Future science may demonstrate that the properties of oxygen are intensified (*ozonized?*) by passage through, or absorption by, a living fluid. Deep meaning may yet radiate from material collocations, over which now chaos broods.

It is a remarkable fact, that the body of every Entozoon, whether imbedded in the parenchyma of solid organs or lodged in the cavitory viscera, is *immersed in a reservoir of fluid*. The *Tæniæ* and *Bothriocephali* are applied *closely to the walls* of the intestine (the orifice of each segment being adherent to the infested surface and surrounded by a mucous capsule filled with fluid). This fact is easily verified in the instance of those species of Cestoid worms which inhabit the intestine of fishes, birds and reptiles\*.

The Fluke swims in a pool in the biliary ducts of the sheep. The Trichina in the substance of a muscle floats in a reservoir

\* *Bothridium Pythonis* inhabits the large intestine of the Cod.

*Acanthobothrium coronatum* is found in the intestine of the Ray-fish.

*Trienophorus nodulosus* lodges itself on the peritoneal surface of the liver of the Perch.

*Floriceps saccatus* in the intestine of many fishes, &c.



of fluid, and the *Filaria* in the cellular tissue is surrounded by a stratum of serous liquid. These enveloping fluids are effused by the living vessels of the part upon which the animal preys. These circumstances present a fact which demonstrates that the life of Entozoa is essentially aquatic. The fluid is no essential constituent of the organism of the parasite. It is extravasated by reason of the irritation excited by the presence, the worm on a living surface, or in the midst of a living organ. It is however a fundamental condition of existence. *It is the medium of respiration to the Entozoon.* How could this vital process occur if the animal were surrounded by a *solid* substance? The fluid contained in these cysts must be *frequently renewed*, because the blood-corpuscles revealed in it by the microscope are always fresh in appearance, plump and perfect in outline. This fact also proves that it is derived directly from the blood of the infested animal; it is therefore charged with oxygen in the same proportion as the latter. Thus is explained an important *external* condition of respiration in the Entozoa.

The *Nematoid Entozoa* (figs. 10, 11 & 12) are distinguished from the parenchymatous orders in one essential respect. In the Nematodea the viscera float more or less freely in a spacious cavity filled with fluid. They agree in organic type with the cylindriform Annelids. From the latter, however, they differ in one extraordinary particular. The Nemertinidæ, Planariæ and Clepsinidæ excepted, in all Annelids the chylaqueous fluid is corpusculated, and the blood-proper is entirely destitute of all morpous particles. In the Nematoid Entozoa *these conditions are reversed.*

In the Cestoid and Trematoid genera the fluid contained in the digestive *diverticula*, through its floating cells, enacts that office, which, in the example of the Nematoid worms, is transferred to the blood-proper, and in that of the Annelids in general to the chylaqueous fluid. This circumstance, however, does not imply that in the Nematodea the blood-proper system is preponderantly developed. It consists only of two principal longitudinal trunks, adherent at the ventral and dorsal median lines to the internal surface of the integumentary cylinder. Cloquet has described the blood-system in several species. Ecker\* has also defined a blood-system in a species of *Filaria*. The blood-vessels of the Nematoid worms exhibit a distinct red colour. It is not yet certain that the contained *blood* partakes of the same colour†. Rudolphi has characterized these and all Entozoa as white-blooded worms. The primary trunks are connected together by

\* Müller's Archiv, Ueber ein Gefässsystem in eingepuppten Filarien, S. 506. t. 15. figs. 3, 4, 1845.

† For a further statement of the author's researches on this subject, see his papers in the 'British and For. Med. Chirur. Rev.'



means of transverse secondary branches: these latter can only be discovered in the substance of the integuments, not on or in the parietes of the viscera. The blood-proper of the Nematoid worms is indeed a very subordinate constituent of the organism, quite insufficient to supply the solids with the materials of increase, and not less unequal to the function of breathing. A few blood-vessels distributed scantily over the cutaneous surface would present too limited a surface of contact with the surrounding element to receive a proportion of oxygen adequate to supply the wants of an organism so large as that of *Strongylus Gigas*. By inference it becomes obvious that some other fluid element of nutrition in these genera is required to minister to the exigences of the solid parts. It is accordingly found that in the Nematoid orders the chylaqueous fluid is relatively abundant in quantity: this fluid is contained, as in the cylindriciform Annelids, in the peri-intestinal or visceral cavity (figs. 10, c; 11, d; 12, c). In the round worms this cavity occurs under two distinct anatomical conditions. In one case, illustrated in the example of *Ascaris Lumbricoides* (fig. 11), the intestine is tied by frequent transverse bridles to the integumentary cylinder: these bridles intersect the cavity, and limit the motion of the contained fluid. They stretch outwards through the whole thickness of the integument under the character of transverse muscular fasciculi. They are accompanied by open passages by which the chylaqueous fluid reaches the cutaneous surface for the purposes of aëration. The longitudinal muscular bands, with their embracing spaces, establish between the transverse, free communications. It is thus clear, that although the integuments in certain species of Nematoid worms are remarkably dense and resisting, they are permeated by chylaqueous fluid to an extent enough to subserve the purposes of breathing. The intimate connexion which in some Nematoid worms subsists between the intestine and integument, limits the movements of the intestine. It is to this anatomical circumstance that the motionless state of the chylaqueous fluid in these worms is to be ascribed. In consequence of the absence from this fluid of all visible globules, to detect its existence is not easy to the uninitiated observer.

It is upon the freedom with which the intestinal cylinder moves within the concentric integumentary, in many species of Annelida, that the rapid and unobstructed oscillations of the interposed chylaqueous fluid depend. Why should the same fluid, occupying the same locality, be required to move so little in the Entozoa? The answer probably is, that in the two indicated instances the fluid differs materially in chemical composition. The second type (fig. 10) of Nematoid Entozoa is exemplified



best in the case of the large *Strongylus*, constantly to be found in the small intestine of the sheep. Here the intestine, a straight tube, is considerably smaller in diameter than the space included by the integuments, while it is tied at few points to the latter. The visceral chamber is therefore unusually capacious in dimensions, and the enclosed fluid is considerable in bulk. It is a fact of unusual interest, that the chylaqueous fluid, whether stationary or moveable in its containing chamber, of all Nematoid Entozoa, is perfectly homogeneous and destitute of every trace of visible element. In these worms the digestive system does not lodge a corpusculated liquid, of which the suspended cells supersede the necessity for the agency of similar cells in the extra-intestinal chylaqueous fluid. It must therefore be inferred, that the true blood of these worms is the seat of the floating cell agency. If it should be hereafter proved by exact observations, that neither the true blood, nor the chylaqueous fluid, nor the intra-intestinal chyme is charged with floating cells, these animals will constitute an exception unique in the animal kingdom, in which an animal organism is sustained without a single corpusculated nutritive fluid.

The principle is at present inadmissible in science, which supposes that the intervention of cells in the nutritive fluids is neither indispensable to the process of solid nutrition nor to that of respiration.

It is a fact of surpassing physiological interest that the chylaqueous fluid in the *Strongylus* of the sheep, which can be collected by spoonfuls, is nothing but a thick solution of albumen. After even prolonged standing, it does not throw down the slightest vestige of fibrine-clot. If "the blood" of the infested animal permeated through the integuments of the parasite, and thus reached the visceral chamber of the latter, it appears probable that both the fibrine and the red corpuscles of the former would be capable of detection in the chylaqueous fluid of the latter. This, however, is not the case. The cyst in which *Trichina spiralis* is lodged in the substance of the muscle is filled with a fluid in which both the fibrine and the red corpuscles of the infested animal can be readily shown to exist. The inference is obvious. The chylaqueous fluid of the worm is not derived directly from without by filtration through the partition of the cutaneous structures.

In the order of Nematoid worms, typified by the *Strongylus* of the sheep, the integuments are very thin; the spaces between the circular muscular fasciculi being covered by little more than the epidermis—conditions well-fitted to favour the interchange of gases between the chylaqueous fluid within and the aërating medium without. No indications of vibratile epi-



thelium in any structure in any species of Nematoid worms can be discovered on the general cutaneous surface, dedicated though it be unquestionably to the office of respiration: they exist in no instance. *Why* do they *not* exist? The organic law presiding over the development of these motive organules is still beyond the ken of science.

Henceforth it will not satisfy the physiologist to affirm, in the vagueness of a general phrase, that "the respiration is cutaneous." He must know, with exact definition, by which order of fluids that function is enacted, and whether the living fluid, immediately influenced by the external element, be charged or not with morphous particles. Superstition for ages has wrapped these uninviting beings in unresolvable mist. The assertion has now been abundantly supported, that the process of respiration in *all* Entozoa is conducted on the aquatic model—that the chylaqueous fluid, though non-corpusculated, is by far the most voluminous and important fluid element in the organism, and that which directly performs the function of breathing. The true blood when it exists is only *secondarily* aerated. The 'value' of the respiratory function is directly proportional to the organic complexity of the fluids. The figure expressive of its amount progresses upwards with the zoological standard of the organism. This principle explains the faculty conferred upon the Entozoon, by a Nature exhaustless in expedients, illimitable in resources, by which it is enabled to extract oxygen enough for *its* wants from the least oxygenated of the animal fluids—venous blood—and securely to breathe amid the pestilential atmosphere of the colonic intestine.

These parasites are capable of sustaining life in any and every recess of the animal body. This fact proves inferentially what the physiologist cannot reduce to positive demonstration, that every part, every fluid, whether in or out of the vessels, is pervaded by the electric presence of oxygen. It proves that the respiratory process is really an inseparable attendant on, and an integral and essential part of, the nutritive actions of the body—that it is ubiquitous, not partial—that it vivifies every constituent atom, fluid, and solid of the entire organism\*.

\* In order to facilitate the repetition of the observations upon which the general conclusions stated in the text are founded, the author appends here a short list giving the name and place of abode of the most familiar Nematoid Entozoa:—

Name.	Habitat.
<i>Ascaris megalocephala</i> (Cloquet) ...	Intestines of the Horse.
— <i>lumbricoides</i> .....	Small intestines—Man.
— <i>Salaris</i> (Blanchard) .....	In intestines of several fishes.



*Annelida*.—In the *Annelida* the function of respiration is discharged under two remarkably distinct conditions. Under the first, the chylaqueous fluid *alone* is subjected to this process; under the second, the blood-proper exclusively fulfils the office. The mechanical organs subservient to this function under the former, are constructed on a plan diametrically different from that of those provided under the latter circumstances. In the *Annelid* the true-blood and chylaqueous fluid, though coexistent in the same organism, constitute two perfectly distinct and independent fluid systems. There is between them no *direct* communication of any sort; they are *physically* very dissimilar fluids. An order of branchial processes, intermediate between the two preceding, must also be recognised, in which in equal or unequal proportions the chylaqueous fluid and the blood-proper, either in the same or in distinct appendages, participate in the process of respiration. The branchial appendages affect four different situations on the body: 1. on the head; 2. along the back; 3. along the sides, and 4. at the tail. The first rank under the *Cephalobranchiata*, the two succeeding under the *Dorsibranchiata*, the fourth are represented by the *Clymenidæ*. The *Abranchiate Annelida* resolve themselves also into two distinct divisions; those, first, which breathe through the agency of the chylaqueous fluid, and those, secondly, which expose the true blood. Both these groups would be comprehended under the *Cryptobranchiata* of Dumeril.

To these extremes, too, an intermediate order occurs; it em-

Name.	Habitat.
<i>Filaria equina</i> (Rudolphi) .....	Folds of the peritoneum of the Horse.
— <i>attenuata</i> (Blanchard) .....	Air-cells of carnivorous birds.
<i>Spiroptera sanguinolenta</i> (Rudolphi) .....	Stomach of Dog and Wolf.
<i>Spirura Talpæ</i> (Blanchard) .....	Stomach and intestines of the Mole.
— <i>Megastoma</i> (Rudolphi) .....	Stomach of Horse.
<i>Oxyuris vermicularis</i> (Dujardin) ...	Rectum—Man.
<i>Sclerostoma Equinum</i> (Rudolphi) ...	Cæcum of Horse.
<i>Cucullanus Percæ</i> (Müller) .....	Pyloric appendages of common Perch.
<i>Angiostoma entomelas</i> (Dujardin) ...	Lungs of Reptiles.
<i>Cyathostoma lari</i> (Blanchard) .....	Orbital cavity of Sea-Gull.
<i>Strongylus Gigas</i> (Rud. & Müller)...	Kidneys of Horse, Dog, and Man.
<i>Trichostrongylus axei</i> (Rudolphi) .	Trachea of Fox.
<i>Trichocephalus hominis</i> (Rudolphi)...	Cæcum of Man.

The order *Nematoidea*, *Cœlmintha* (Owen), includes the principal internal parasites of the human subject, viz. *Trichina spiralis*, *Filaria medinensis* (Guinea worm), *Filaria oculi*, *Spiroptera hominis*, *Filaria bronchialis*, *Trichocephalus dispar*, *Strongylus Gigas*, *Ascaris lumbricoides*, and *Ascaris vermicularis*. The Entozoa found in the blood have been recently described under the class-name of *Hæmatozoa*. Several species of *Filaria*, *Monostomata*, *Distomata*, and Infusoria, have been discovered in the blood of frogs, dogs, fishes, and mollusca (Micr. Journal, Oct. 1st, 1853).



braces the *Nemertinidæ*, the *Liniadæ* and the *Gordiusidæ*, the cutaneous external surface of which is wonderfully and richly ciliated. In these unfamiliar genera the chylaqueous fluid and the true blood share, in unequal measure, however, the office of appropriating oxygen. Thus in succinct language has been defined "the heads" under which, in this interesting class, the mechanical conditions of respiration must be studied by the anatomist. The breathing is accomplished in every species, the *earth-worm* not excepted, in strict conformity with the *aquatic* principle. No known Annelid respire on the atmospheric model. In every Annelid the blood, though variable in colour, is *non-corpusculated*. The converse is true of the chylaqueous fluid. No instance is known in which it does not abound in regularly and determinately organized floating cells. The physiologist recognises in these facts the presence of experimental conditions of the highest interest. When the branchial organs carry blood, perfectly devoid of morphous elements of any description whatever, yet fulfilling the purposes of breathing, the floating cells of the fluids are shown to be *not necessary* to the interchange of the gaseous elements concerned in this vital process. On the basis of these unequivocal and visible facts, it is not rash to erect the rule that the floating corpuscles of the organic fluids enact *no share whatever* in the *first* stage of the respiratory process,—that is, in that which comprehends the mere ingress of oxygen and the egress of carbonic acid; *their* office, however it may be hereafter defined, has reference to the subsequent assimilation of the oxygen with the proximate principles of the blood. Through the instrumentality of the corpuscles this quickening element is probably coerced into chemical union with the integral constituents of those principles from which a new compound eventuates.

No class of invertebrate animals unmasks so completely to the eye of the scientific observer of nature the physical machinery through which the function of breathing is fulfilled as that of the Annelida. Gifted with brightly coloured blood, every ramuscle of the blood system can be tracked to its finest extremes. Nature is more comprehensible in her humblest efforts than in her master-pieces. Her plans are susceptible of readier recognition. The intentions of the faultless Artificer are less equivocally apparent. Subtlety gives place to simplicity, obscurity to light.

The Annelids are emphatically inhabitants of the sea-shore. They are seldom afloat. Always accessible in their littoral haunts, they invite the zootomist to demonstrate in *their* organization those abstruse theorems of vital dynamics which in other beings transcend the genius of science.



The *branchial* appendages in the genus *Serpula* are grouped in erectile tufts around the head. Projecting in a comb-like form from the cephalic extremity, and tinted variously and beautifully in different species, they are admirably adapted for the exposure of the blood to the agency of the surrounding water. Each process is supported by a camerated frame or basis, large and distinct at the thick edge of the comb, from which, on one side only, projects a double row of secondary processes. This supporting framework is composed of an extremely flexible and delicate cartilage, the chambers of which are filled with a limpid fluid which is in communication with that of the peritoneal cavity; an afferent and efferent vessel, carrying red blood, disposed in parallelism, accompany this axial framework. In the secondary processes corresponding to the teeth of the comb, the two vessels affect the inferior margin, to which the vibratile cilia are limited. These cilia are large and vigorous in action. Those of all the gills conspiring, generate a current in the surrounding water which bears in the direction of the mouth. The cilia answer therefore a double purpose: they ceaselessly renew the aërating element in contact with the branchiæ and convey food in the direction of the mouth. It is difficult to avoid contrasting the importance of *such* results with the incomplex simplicity of *such* means. Tubicolous and sedentary in their habits, the branchial appendages in the *Serpulæ* subserve thus at once the two highest functions of the organism. In this genus, *Serpula*, it is the blood-proper exclusively that is subjected to the respiratory process.

The branchiæ in the allied genus *Sabella* conform in ultimate structure with those of the *Serpulans*; they present, however, a somewhat modified disposition around the head.

In *S. unispira* they exhibit an elegant spiral arrangement around a tapering vertical central pillar. When fully expanded, no object in nature is more beautiful: the elementary parts are comb-like; the straight processes, describing a graceful corkscrew curve around the axial stem, are multiplied by a double row of lesser filiform appendages; these latter are richly ciliated on the under surface. They carry each an afferent and efferent vessel: on the margin of extension they are strengthened by a delicate axial scaffolding of flexible cartilage. They are capable of being folded up in a small compass and withdrawn into the tube: they are extraordinarily irritable and contractile. The feet in this genus bear no branchiæ. In *Sabella à sang vert* the branchiæ rise above the head in gorgeously coloured and circularly arranged plumes: they coincide with those of the former in minute structure.

*Sabella vesiculosa* exhibits a slight variation of plan as compared with those of the former, in the character of the branchial



processes. They are supported upon a pedunculated base: this latter is painted with spots of the gayest colours. In *Sabella à sang vert* the blood displays a deep grass-green colour; in the other species it is red. How incomprehensible such capricious freaks of nature!

The genera *Sabella* and *Serpula*, then, may be thus characterized as respects the organs and the manner of breathing. In all species the branchiæ affect a cephalic situation; the blood-proper, and not the chylaqueous fluid, is aërated; in all, the pedal appendages consist only of setæ; in all, the inferior half of the alimentary canal is richly ciliated *internally*, a singular provision for propelling an incessant current of water from one end of the body to the other. Such a current must necessarily part at once with *its dissolved oxygen* and its suspended organic particles. The former acts upon the chylaqueous fluid contained in the *hollow* cylinder embracing the canal. This is artfully accomplished *internal* respiration!

The genus *Sabina* has been recently constituted by the author to receive several species of tubicolous Annelids which present an organization intermediate between that of *Sabella* and that of *Amphitrite*.

*Sabina Poppæa* expresses the generic type. The branchiæ consist of a group of short flexible processes pluming the head; they support short rudimentary secondary processes, highly ciliated; each carries a looped blood-vessel. *These* appendages aërate only the true blood: others, of a quasi-tactile character, and of unusually large size, are provided, which assume an occipital situation; they amount to three in number on either side; they are *tubular, non-ciliated, fleshy* appendages; they are penetrated by a large current of corpusculated chylaqueous fluid; they are obviously designed to oxygenize this latter fluid; they are, at the same time, subservient to purposes of touch and defence.

In *Amphitrite vel Sabella alveolata* these semi-tactile filaments, similarly situated, are considerably greater in number. Unlike those of the former genus, they are ciliated; they are hollow tubular filaments; destined to aërate the chylaqueous fluid, they communicate openly with the visceral cavity. In *A. alveolata* the true-blood branchiæ are distributed over the dorsal aspect of the body; they constitute tapering, prominent, blood-red, highly ciliated appendages carrying in their interior axially a single longitudinal blood-vessel, which at the distal extremity returns upon itself. The chylaqueous fluid also penetrates in small quantities into the interior of these processes. By M. Quatrefages\* a complex *subdivision* of the blood-vessels in these processes is figured and described. An *appearance* leading to such

\* "Organisation des Hermelles," Ann. des Sciences, 3<sup>me</sup> série, 1848.



an error may be easily produced by pressure. A *spirally* arranged line of vibratile cilia, coiling from the base to the apex of each appendage, provides for the constant renewal of the aërating medium\*.

In *Amphitrite auricoma* the branchial combs are attached by a single root, expand and divide in a pectinated manner, each tooth carrying only a single longitudinal vessel. This species indicates a transition from the typical *Amphitrite* to the genus *Terebella* (fig. 1. Pl. XIV.). In all the species of the latter genus the branchial organs appear under the form of blood-red tufts (fig. 1, *a*), proceeding from three or more separate root-vessels on either side of the occiput. The vessels divide for the most part dichotomously, forming an arborescent bunch of *naked* florid branches: each ramusculæ is enclosed in a delicate cuticular envelope (fig. 3, *a*<sup>2</sup>) *perfectly destitute* of cilia, and conveys to its extreme end a single vessel looping upon itself (fig. 3, *m*). Although extremely transparent and attenuated, the epidermal coating must include contractile fibres, since each branch may be emptied, rendered bloodless and shrivelled, by the compression of the parietes. This provision for reinforcing the central circulating powers exists in various parts of the blood-system of the Annelida. It may be affirmed, generally, that in all true *Terebellæ* the branchiæ occur under the character of naked, unciliated blood-vessels restricted to the occipital rings of the body. In *T. nebulosa* (fig. 1, *A*) they constitute thick, florid, resplendent tufts; in *T. conchilegia* they are fewer in number and less prominent. In the smaller species† the cephalic tentacles (fig. 2) of the *Terebellæ* constitute, unquestionably, auxiliary organs of respiration; they are copiously penetrated by the chylaqueous fluid; they carry vibratile cilia on their inferior side (fig. 2, *g*); they are capable of injection by the chylaqueous fluid; they open directly into the peritoneal chamber; they are *tubular*, flattened filaments, furnished with strong muscular parietes; they are admirably fitted to aërate the chylaqueous fluid; they are incessant in their motions; touch is obviously one of their functions; they also act as prehensile organs, conveying food to the mouth; but they are also organs of locomotion; they are fixed suctorially on a surface in advance of the animal, and used as ropes for hauling forwards the body.

In *Terebella conchilegia*, tubicolous and sedentary in its habits, the cephalic tentacles are inferior to those of *T. nebulosa* in num-

\* For illustrations of many of the parts described in the text, the reader is referred to the Report of the Trans. of the Brit. Assoc. for 1851, on the British Annelida.

† Several undescribed *small* species will hereafter be figured and defined.



ber and size. They are differently configured; they approach the prismatic in outline; in transverse section they present a tri-radiate shape; in minute structure and mechanism of action, they differ slightly from those of the latter; they are not for locomotive purposes; hence their reduced size and diminished number.

It is not a little curious that in the *Terebellæ* these organs, which are homologous with true cirri, should be so richly provided with vibratile cilia, while the true-blood branchiæ are entirely destitute of these motive appendages. Nothing but a correct conception of the nature and capabilities of the chylaqueous fluid will enable the physiologist to unriddle this apparent paradox.

The *Dorsibranchiate* order comprehends a considerable proportion of the class Annelida. "Ils ont leur organes et surtout leur branchies distribués à-peu-près également le long de tout leur corps, ou au moins de sa partie moyenne," says Cuvier. *Arénicola* represents the central genus. In this worm respiration is performed by means of naked blood-vessels projecting at the root of the setiferous processes upwards and outwards one-fourth of an inch, in the adult worm, above the plane of the surface. They are limited in number and distribution to the fourteen or sixteen middle annuli of the body. They are commonly described as forming an arborescent tuft; the division of the vessels is, however, regulated by order and symmetry. When fully injected, the vessels of each branchia form a *single* plane, rising obliquely above and across the body, and immediately behind each brush of setæ. In the adult animal each gill is composed of from twelve to sixteen primary branches, proceeding from a single trunk which arises from the great dorsal vessel: the vessels in the branchial tuft describe zigzag outlines; the secondary branches project from the salient angle of each zigzag. This mode of division, occurring in one plane and in all the smaller branches, results in a plexus of vessels of extreme beauty of pattern,—a captivating example of symmetry amid irregularity, harmony amid lawless variety. Each branchial tuft and each individual vessel possess an independent power of contraction; in the contracted state the tuft almost entirely disappears, so completely effected is the emptying of the vessels. The contraction or *systole* in any given tuft occurs at frequent but irregular intervals; this movement does not take place simultaneously in *all* the branchiæ, but at different periods in different tufts. As there exist no heart-like dilatations in the afferent vessels of the branchiæ, the contractile power with which the exposed branches are endowed, becomes an important means of reinforcing the branchial circulation. The vessels appear quite naked, and if



examined in the living state, each ramusculæ seems to consist only of a single trunklet; if this were really the case, it would of course resolve itself into a tube ending in a *cul-de-sac*, and the blood movement would be a flux and reflux; but by injection it is easy to show that the finest division of the branchial arbuscle contains a *double* vessel, enveloped in a common muscular though extremely diaphanous sheath. That these vascular sheaths, which are only fine productions of the integuments, are furnished with voluntary muscular fibres, is proved by the rapid and simultaneous retraction of *all* the branchiæ into the interior of the body, which follows when the animal is touched. This sheathing of the blood-vessels with true muscular coats is a frequent character of the circulating system in the Annelida. In *Arenicola*, as in *all* Annelids in which the vessels are naked, the branchiæ are destitute of vibratile cilia.

To the frequenter of the sea-shore the preceding description of the mechanism of breathing in the familiar lug cannot prove unacceptable. Its fæcal coils are encountered at every step. The animal is ceaselessly occupied in swallowing and rejecting *wet* sand. A considerable amount of water and sand is incessantly traversing the body of the animal from one extreme to the other. The organic particles are appropriated during the digestive process; the water in part yields up its oxygen and in part replenishes the large volume of chylaqueous fluid with which the visceral cavity is distended,—another example of *internal* respiration.

Provided the branchiæ convey to the surrounding medium the blood-proper exclusively, and these organs occur in form of naked vessels projecting above the external surface, the description now given of the branchiæ of *Arenicola* will apply in every minute respect of structure to all other Annelida. It will prove exact in relation to the structure of the gills in the several species of the beautiful genus *Euphrosyne* of Savigny.

In *Euphrosyne laureata* they rise under the protection of the setæ as brightly florid brushes on the back. They are fixed by means of three or four primary trunks. Viewed by transmitted light and under a high power, each ramusculæ is seen to consist of a single leafed vessel embraced in a very attenuated musculo-membranous sheath. They are destitute of ciliary epithelium.

An Annelid of great beauty of figure is described by Milne-Edwards and Audouin under the name of *Hipponoë Gaudichaudii*, in which the branchial appendages assume the character of arbuscles of naked vessels garnishing most ornately the entire dorsum of the animal. *Pleione tetrahedra*, the typical species of the genus *Amphinome*, exhibits the breathing organs under the figure of scarlet bunches mounting round dorsally each annulus of the body, and guarded in front by a bundle of strong bristles.



The branchiæ in *Pleione Alcyonia* affect a ventral situation, and exhibit a much less ornamental character.

*Chloeia capillata* (Savigny) is an Annelid of matchless beauty. The whole line of the back on either side of the median line is decorated with arborescent vermilion tufts. Each tuft is supported by single contracted stems embracing two trunks. They are clothed with a slender musculo-cuticular unciliated membrane. In this rare worm the chylaqueous fluid is abundant, yet no *external* organs are furnished for subjecting it to the agency of the aërating element.

The genus *Eunice* (fig. 4) presents another and different type of branchial vessels. Arranged in a prominent row of bright vessels (*b, c, d, e, f*), standing erect as florid visible combs at the dorsal base of each foot in the body, the branchiæ impart to all the species of this genus a graceful and characteristic appearance. In every species the branchial vessels divide on a uniform plan peculiar to this genus. The primary trunk (*a*) rises vertically along the inner side of the branchia, and detaches from its outer side at regular intervals, straight vessels, which gradually decrease in size from below upwards; each branch forms a straight undividing vessel (fig. 5, *i, j*), curving gently upwards and towards the median line; these branches become in their number distinctive of species. In some of the smaller species inhabiting the British coasts, the branchiæ are composed only of a *single* vessel; this is the case also with the *young* of the larger species; in others they vary the single to the number of six or eight. In *Eunice gigantea*, according to the figures of Milne-Edwards, the vessels of each branchia amount to thirty-six in number. These vessels, although perfectly naked and unciliated, like those of *Arenicola*, are both less contractile and retractile; they extend in this genus from the head to the tail, and equal in number the annular segments of the body. In the dorsibranchiate genera, the branchial organs of which are now being described, the true blood circulating in its proper vessels is exclusively the seat and *subject* of oxygenation.

The fluid of the peritoneal cavity, abundant in quantity and highly organized though it be in the genera under review, does not, at least by means of any external organs, participate in this great function. Judged by such a test, the genera of this grand order of worms should be marshalled under two primary groups, of which one would comprehend those in which the function of breathing devolves *exclusively* on the true blood, while the other would be characterized by the fact, that the branchiæ are so organized as to permit separately or conjointly the exposure of the chylaqueous fluid. When the branchial apparatus is penetrated by two separate and distinct fluids, coordinate probably



in organic properties, the vascular system of the body will be found in general by so much the less developed by how much the chylaqueous fluid supplants the blood-proper in the branchiæ. The *structure* of the branchial organs becomes thus a significant test of the position of any given species in the Annelidan scale—those being entitled to the highest rank of which the respiratory organs are designed to aërate the true blood, those the lowest in which the chylaqueous fluid alone circulates in the branchiæ.

The subgenera *Lysidice*, *Aglaura* and *Ænone*, of the genus *Eunice*, are distinguished in the circumstances now defined from all the former genera of the dorsibranchiate order. Naked unciliated blood-vessels no longer in them form exclusively the branchial organs; loose and large-celled tissue is superadded to the proper blood-vessels, which are far less in relative size than those in the former variety of branchiæ; into the cells of this tissue the fluid of the visceral cavity insinuates itself, its course being marked by a slow flux and reflux motion. There exists, however, another point of structural difference between the branchial organs of this group and those of the former; this difference admits of the following general expression—that wherever the chylaqueous fluid is admitted into the interior of the branchial organs, the latter are invariably supplied more or less profusely with vibratile cilia.

In the genus *Lysidice* the branchia consists of a flat, lanceolate process, more or less developed, surrounded marginally by a blood-vessel, the mid-space between the lines of the advancing and returning vessels being composed of large-celled lacunose tissue, into which the chylaqueous fluid penetrates by an advancing and receding movement. The branchiæ in *L. Ninetta* are situated dorsally, and are supplied at their bases with single rows of vibratile cilia. Those of *Aglaura fulgida* are similarly constructed, although they differ slightly from those of the former genus in size and figure. In *Ænone maculata* they occur under a more developed form, constituting flattened pointed trowel-shaped processes, the plane of which is vertical with reference to that of the body. A blood-vessel, as in the former case, trends along the borders, immediately beneath the cuticle. The course of these vessels is followed by a row of large and prominent vibratile cilia\*.

In the branchial system of the genus *Nereis* (Cuvier), *Lycoris* (Savigny), the minute anatomist encounters a structure strikingly dissimilar from anything hitherto described in the Annelids. Whether round, or laminated, or foliaceous, the true branchiæ in this genus are always penetrated by the chylaqueous fluid, and

\* See plates in the author's Report on the British Annelida, Trans. of Brit. Assoc. for 1851.



the blood-vessels assume a peculiar disposition. When the branchial process is conical in shape, its base is embraced by a *reticulated* plexus of true blood-vessels, which are situated quite superficially and immediately beneath the epidermis. These vessels are most prominently developed on the dorsal-most process, which therefore may be called the branchial, but they extend more or less over all the cirri. A better characteristic of the branchiæ in the Nereids is that of being penetrated by the fluid of the visceral chamber. In those species in which the branchial process is conical, the interior of the base only is hollow and filled with chylaqueous fluid. Floating in this fluid may be readily seen, when viewed by transmitted light, coils of naked blood-vessels; in those instances in which the branchiæ are laminated or foliaceous, as in *Nereis renalis*, the blood-plexus on the external surface does not extend beyond the limits of the base of the process, the flat, leafy circumference being tunnelled by straight spacious canals which radiate with great regularity from the root to the expanded border of the fan. In these canals the corpuscles of the chylaqueous fluid may be observed rolling to and fro, advancing and receding in the same channel. These movements are regulated by those of the current in the chamber of the peritoneum. This type of structure prevails in *Nereis renalis*, *N. longissima*, and in a slightly modified form, in consequence of the less flattened shape of the branchiæ, in *N. viridis*. The round or conical variety of branchial process obtains in *N. margaritacea*, *N. Dumerillii*, *N. fucata*, *N. pelagica*, and *N. brevimanus*.

It is difficult to explain why the branchial organs of the Nereids should be entirely destitute of ciliary epithelium.

The laminated or foliaceous type attains the point of maximum development in the branchial appendages of the genus *Phyllodoce*. Anteriorly to the discovery of the vital and organic characters of the chylaqueous fluid, the real uses of the rich leafy expansions ornamenting the sides of these attractive Annelids could only have been rudely conjectured. They look more like oars than branchiæ, natatory more than respiratory organs. In the absence of correct ideas tending to a knowledge of the nature and capabilities of the fluid contents of the visceral chamber, the real meaning of the radiating channels by which the respiratory laminæ are perforated, and therefore of the mechanism of the function of which they are the scene, never could have been rightly apprehended. It was only by mistaking the chylaqueous fluid for the true blood that the branchial office of these appendages could have been predicated, and this very mistake has been committed by M. Quatrefages.

The branchiæ in *Phyllodoce viridis* are prominent dorso-lateral



appendages; in this worm the blood-system can be traced only to a few scanty vessels distributed over the roots of these processes: nor are the canals very spacious and distinct; they are more like lacunæ in a spongy tissue.

In *P. bilineata* and *P. lamelligera*, radiating passages, distinct from each other and communicating only indirectly through intermediate cells, are readily observed. They carry the visceral fluid, the corpuscles of the latter being seen flowing and ebbing in the same channel. Nothing can, however, more conclusively prove the true branchial character of these laminæ than the presence of cilia, the vibrations of which can be observed only at the edges of the respiratory laminæ: these cilia are most conspicuous in *P. lamelligera*. This is a striking point of distinction between the *Phyllodocidæ* and the Nereids, in which ciliary epithelium has no existence. The chylaqueous fluid then may be clearly affirmed as that agent in the œconomy of the *Phyllodocidæ* which is the immediate, the first, subject of the respiratory process, the true blood receiving its supply of oxygen from this fluid, afterwards to convey it to the solid structures of the body.

In the genus *Glycera* the blood-proper is entirely excluded from the organs of respiration: this office devolves exclusively on the chylaqueous fluid. The latter in this worm is crowdedly charged with red-corpuscles, a remarkable exception to the Annelidan rule. The gills consist of hollow, cylindrical appendages, emanating from the base of each dorsal foot at its superior aspect, filled in the interior with the chylaqueous fluid. It is peculiar to and distinctive of this genus that the interior of the branchiæ is lined with vibratory epithelium. Cilia are not detectible on the exterior of these processes, but they exist in the interior: under the action of these oarlets, the corpuscles of the chylaqueous fluid by which the gill-process is penetrated, move with great rapidity in a definite direction;—peripherally on one side and centrally along the other, each corpuscle whirling on its own axis as it proceeds. The advancing stream, however, is not divided from the returning. The channel is one, open channel. This is the law which is applied to the chylaqueous fluid: it knows no exception. Its channels are always single and cæcal: its movements a flux and reflux. Contrarily the orbit of the true blood is circle-like, its channels closed, its colour red, its composition non-morphotic.

In the *Syllidæ* (fig. 6) the branchial organs are penetrated only by the chylaqueous fluid. It can be detected only at the bases of the feet (*d*). To this part the vibratile cilia are restricted (*c*). The long filiform, and in some species moniliform or leafy appendages which are described commonly as the branchiæ in these worms, have no central hollow; they are filled with lacunose



tissue (*f*) through which the *fluid* parts of the contents of the visceral chamber slowly penetrate. But in the spacious chambers occupying the bases of the feet, the *corpuscles* may be detected in whirlpools. From this fact the inference may be drawn that the corpuscles are not essential to the *first* mechanical stage in the respiratory process—that of receiving oxygen directly from without. The characters of structure just described are very perfectly typified in *S. prolifera*, the moniliform variety is best seen in *S. armillaris* and *S. maculosa*. A similar conformation prevails in the genera *Ioida* and *Psamathe* of Dr. Johnston. In the Syllidan family, which excels all others in grace and beauty, the blood-proper system is almost undetectable, in consequence of the colourlessness of the contents. The blood does not participate in the function of breathing: it is an office performed exclusively by the chylaqueous fluid.

Amongst the family *Ariciadae* several other varieties in the configuration of the breathing organs occur. In the genera *Nerine* (fig. 8) and *Aricia* the branchial appendages affect a dorso-lateral situation: they are traversed in every species from base to apex by a single blood-vessel returning upon itself (*i*). This vessel is supported by a lobule of spongy tissue (*f*), into the cells of which the chylaqueous fluid insinuates itself. In every species of this family the branchiæ are supplied by vibratile cilia, exhibiting in each a distinct disposition. In ultimate structure, those of *Amphitrite alveolata* and *Leucodore ciliatus*, remote specifically from the Syllidans, display the same construction.

In the genus *Spio*, abundantly common on our shores, the respiratory organs occur under forms of the highest beauty. They constitute flat membranous penknife-shaped appendages curving gracefully over the back and crossing over the median line, alternating imbricatively with the corresponding processes of the other side. The plane of each process is vertical in relation to the long axis of the body (fig. 8). They are less flat and close in *N. vulgaris* than in *N. coniocephala*; they are largest in size towards the middle of the body, smallest anteriorly and posteriorly. The blood-vessels, the afferent and efferent, run close to and parallel with the inferior border of the process; the upper part of each is composed of a membranous lobular (*g, f*) addition to the inferior and vascular portion. Into the cells (*g*) of this lobule the chylaqueous fluid slowly finds its way, and participates obviously in the office of respiration. In *N. coniocephala* it is remarkable that the cilia should be limited in their distribution to the margin along which the true blood-vessel runs. This fact is manifest in *N. vulgaris* in consequence of the smallness of the membranous lobule. In *Aricia Cuvieri* the branchial appendages are more conical in figure, more vertical in position,



and developed only at the posterior four-fifths of the body: they are covered with large vibratile cilia. Like those of the former, they are supplied with flat lobules of spongy tissue. In all the members of the preceding family the real branchial organ consists of an evolved or exaggerated development of the superior element of the dorsal foot.

In the genus *Nephtys* (fig. 7, A) which comes now under review, it is the inferior element of the dorsal foot which becomes the subject of this evolution. It is a curved conical process (*a*), attached to the inferior aspect of the root of the upper foot. It is hollow and filled with the chylaqueous fluid, the corpuscles of which are readily observed on external examination (B, *a*). No cilia exist on the interior surface: they are abundant and vigorous on the exterior. A rich vermilion coil (*b, c*) filling the hollow of the process and *floating in the chylaqueous fluid* may be seen by transmitted light. This is a true blood-vessel: it is a single vessel. It is a law in many Annelids that the ultimate blood-vessels do not form plexuses: this proceeds from the extreme mobility of the body. The *quantity* of the blood-proper varies as the Annelidan organism varies at different seasons; it is greatest during the reproductive season, a season during which the chylaqueous fluid is most *reduced* in amount. The two fluids, though coordinate in physiological capacities, are governed by *inverse* laws.

In *Cirrhatus Lamarckii* and in the allied genus *Ophelia*, a linear series of yellowish blood-red threads, remarkably irritable and contractile, project to a considerable distance from either side of the body throughout its whole length: at the occiput they are grouped over the dorsum. They convey the blood-proper *exclusively* in a *single* vessel of considerable length.

The *Aphroditaceæ* constitute a group of Annelids to which the term dorsibranchiate by no means correctly applies; that is, in the majority of the species embraced in this order no branchial appendages exist either on the dorsum or sides. In all the *Aphroditaceæ* the blood is colourless. The blood-system is in abeyance, while that of the chylaqueous fluid is exaggerated. But it is exaggerated only in bulk; it is not raised in organic composition; its corpuscles are scanty, and its albumen small in relative amount. This unusual fact is explained by the presence of organized corpuscles in the dark chymous fluid which fills the gastric diverticula. The scales or elytra fulfil an important purpose: they rise and fall. In rising under muscular action, they create a vacuum in the space between them and the back, into which the water rushes; in falling or collapsing, the water escapes in a current posteriorly. *These currents of water operate immediately upon the fluid contained in the gastric pouches.* The



latter are arranged so as most advantageously to receive the influence of the external aërating element. But they float also in the chylaqueous fluid: this is also in part oxygenized. It is the agent by which this vivifying element is conveyed to the solids of the body; it shares directly in the function of respiration; it receives its organic principles from the contents of the gastric cæca.

It cannot have escaped observation, that there prevails a striking resemblance between the general anatomy of *Aphrodita aculeata* and that of the Asteridæ among the Echinoderms. In the latter, however, the chylaqueous fluid fulfils exclusively the office of breathing. It intervenes between the contents of the digestive cæca and the aërating element. The link of zoological continuity between the Echinoderms and the Annelids is not more clearly constituted by *Aphrodita aculeata*, than the Cestoid and Trematode Entozoa are joined to the Annelids by the transitional family of the Nemertinidæ. From the Entozoa the latter differ in the extraordinary feature of being embraced in ciliated epidermis. Every part of the external surface of the body in the Nemertinidæ is the scene of active ciliary vibration. No approach to the development of this epithelium occurs in *any* Entozoon. The five genera *Valencia*, *Borlasia*, *Nemertes*, *Polia cerebratulus* and *Oerstedia*, into which M. Quatrefages has distributed the Nemertine Annelids, are exemplified on our coasts.

From the Cestoid and Trematode Entozoa several of these Annelids are distinguished by the presence of *corpuscles* in the chylaqueous fluid. In others of them the fluid conforms in character to that already defined in these parenchymatous worms. To the latter the Nemertinidæ are united by another striking peculiarity, that the cæcal *diverticula* of the alimentary system are filled with a *corpusculated* fluid, which, from the methodized distribution of these parts throughout the body, participates unquestionably in the function of respiration. The Nemertinidæ, intimate though their alliance may be with the Cestoid and Trematode Entozoa in general plan of construction, are separated from the latter in one important particular:—in the Annelids the blood system is obviously present, the blood-proper being brightly red in colour; in the Entozoa the existence of this system must for the present be held as doubtful.

It remains to consider the mode in which the process of breathing is accomplished in the *Abranchiate* Annelids, *i. e.* the leech, the earth-worm, and the Nais.

In all systematic works these worms are summarily dismissed as “breathing by the surface.” In *Nais filiformis* (fig. 10) the blood-proper is only very scantily distributed over the cutaneous surface; it is impossible therefore that it can be the imme-



diate subject of the first act of aëration. The visceral chamber (*d*) in this little worm is filled with a corpusculated fluid: in this fluid coils of blood-vessels (*f, f*) are suspended. The blood-proper systematically, by expressly provided vessels, thus brought into intimate contact with the chylaqueous fluid, interchanges constituents with the latter: the former yields up to the latter its carbonic acid, and the latter to the former its oxygen. The chylaqueous fluid thus becomes to the blood-proper the aërating medium. Respiration thus explained is literally *internal*, but not the less real.

In the instance of the earth-worm the chylaqueous fluid is almost entirely suppressed, and the visceral cavity obliterated. This vulgar worm, however, does not breathe on the atmospheric, but on the aquatic principle. It dies rapidly in perfectly dry places. Its cutaneous surface is the scene of a dense plexus of blood-proper vessels. It is always enveloped in a stratum of viscid fluid, which is remarkable for the property of absorbing and *dissolving* atmospheric air. This air, brought thus into immediate and intimate contact with the surface of the body, operates directly upon the blood-proper circulating in the cutaneous plexus. In the Abranchiate Annelids as in many of the tubicolous Annelids, the alimentary canal is profusely supplied *always* with a vascular tissue which shares in the respiratory process: this process may be distinguished as the intestinal respiration.

In the genus *Clumene* (fig. 9) the branchial organs are situated at the tail (*c*). In ultimate structure they correspond in every particular with those of the Sipunculidæ—they are *hollow* membranous projections (*B*) penetrated by the chylaqueous fluid (*e*) in which a coiled blood-vessel (*d*) floats. They are destitute of cilia. They afford the only illustration in the class Annelida of branchial organs specialized around the *outlet* of the alimentary system.

It has now been shown that the branchial organs in the Annelida arrange themselves under two leading divisions, between which a clearly legible line of demarcation exists. Under the one, the blood-vessel-bearing branchiæ occur; under the other, those range which are organized for the exposure of the chylaqueous fluid. Vibratile cilia are never superadded when the blood-proper alone enters the gills; *generally*, when this and the chylaqueous fluid participate in the process; *always*, when the latter alone enacts this function. The mechanism of respiration in the Annelid demonstrates beyond doubt that the agency of floating corpuscles is not required for the *absorption* of the external oxygen. The blood-proper, though coloured, is non-morphotic in *every* species. It has been proved that the tentacles are not simply organs of touch: with a single instrument



nature accomplishes various ends. They are subsidiary organs of respiration. They are injected always with the chylaqueous fluid. It is certain therefore that in the œconomy of the Annelid the blood-proper and chylaqueous fluid are co-equal elements; they are convertible proximate principles; they exhibit equal physiological capacities; both are capable of discharging the function of respiration, and both are capable of supplying the solids of the body with the materials of increase.

*Articulata.*—The annulose are most naturally succeeded by the articulate classes. The word 'annulose' differs in signification not more from the word 'articulate,' than in structure the annulose differs from the articulate animal. In the former a mechanically perfect *joint* never occurs. An 'articulation,' complete in all its mechanical appliances, is not produced in the animal kingdom below the Myriapod. The feet and tentacles of the Annelid, the spines and hard appendages of the Echinoderm, the soft processes of the Medusan, and the feelers of the Zoophyte are equally remote in construction from the leg of the insect or the claw of the crab. A '*joint*' is the symbol of organic superiority: it is not an arbitrary symbol; it is a unit in an *assemblage* of signs which proclaim a new and higher combination in the arrangements which constitute 'life.' At this limit in the animal series, the fluids and the solids of the organism undergo a signal exaltation of standard. The system of the chylaqueous fluid exists no longer in the adult organism,—it is present only in the embryonic. It is supplanted by that of the blood-proper. This capital fact supplies the material wherewith the physiologist forges the golden key which is capable of unlocking treasures long hidden from the eye of science. Coincidentally with the *joint*, at the frontier of the articulate subkingdom, there occurs a heart to circulate the blood, fibrine, and with it an order of floating corpuscles more highly organized in the fluids; a wondrous development of the muscular apparatus, striæ in the muscle-cell, a rapid increase in the dimensions of the cephalic ganglia, and in those of the organs of the special senses. It is here, in the history of the reproductive system, that the diœcious character is first unquestionably assumed. These are note-worthy events in the ascensive march of organic architecture! *Why*, at this particular link in the chain, are these events declared? How are they to be explained? Is it *necessary* in the scheme of creation that the Annelid should chronologically antecede the Myriapod? Are the fluids of the Annelid *plus* fibrine suddenly invested with such new building capacity as to be enabled to construct a Myriapod? The æra will assuredly arrive when organic science will satisfactorily answer such transcendental questions; there repose, beneath the curtain of the theories of



spontaneous generation, specific transmutation, progressive development, &c., truths more recondite than any yet projected by the genius of the author of 'The Vestiges,' &c., or defended by the ingenuity of his countless reviewers.

The Myriapod is the lowest articulate animal, the Annelid the highest annulose: though constituting juxtaposed classes, they are yet divided by deep differential characters. The circulating system of the articulated animal is distinguished by one remarkable fact: only the *central* (dorsal) vessel enjoys the power of contracting and dilating; *every other* part of the circulatory apparatus is *passive*. The *supra-spinal vessel* in the Myriapod and the insect is *not pulsatile*; it is like the abdominal aorta in fishes. It is separated from the contractile centre by the intervention of narrow branches, the aortic arches, which embrace the œsophagus. The pulse-wave imparted to the fluid current by the ventricular action of the dorsal vessel is *broken* by these straitened tubes. The system of the branchial capillaries in the fish converts the saltatory manner in which the blood moves in the interval between them and the heart into a continuous non-pulsatile current. Thus the velocity of the current, and the force with which it travels, are reduced. A slackened course is impressed upon the blood-stream in every part of the body. From these anatomical facts will hereafter flow physiological consequences of great importance; they will unriddle the arcana of the *second* stage of respiration. The parietes of the peripheral channels, though undoubtedly constituting independent membranes, are adherent externally to the solid structures amid which they penetrate. In this particular they differ strikingly from the corresponding parts of the true-blood system of the Annelid. In the latter case, *every* vessel, the minutest and the largest, is detached from all other structures, appearing everywhere in form of independent systolising and diastolising tubes.

The *dorsal* vessel of the articulate animal is much more perfect, viewed as an hydraulic instrument of propulsion, than that of the Annelid. In a few species of Annelids, indeed, a cordiform development of this vessel occurs; it is, notwithstanding, little distinguished from the rest of the apparatus; centralization is not required. Every segment of the system, periphery and centre, is actively operative in circulating the contents. In the instance of the articulate animal the mechanical conditions are different: the dorsal vessel *alone* is the active instrument of circulation.

The circumferential segments of the system *cannot* contract upon the contained fluid; the central organ therefore in this class is invested with additional strength; it is adapted for more powerful work. In its peripheric parts the circulatory apparatus



of the articulate animal may be described as inferior to the analogous divisions of that of the Annelid. The conditions are reversed with reference to the centres. This character is not restricted to the air-breathing or tracheary Articulata; it prevails amongst the Crustacea. From Hunter to Newport this question has formed an arena of microscopic controversy:—are the vessels provided with separate and independent coats, or does the blood only traverse fortuitous channels in the “cellular membrane” of the solids? It is not devoid of interest, in the study of the *material conditions* of solid nutrition: it is not difficult of solution: it will be afterwards answered in detail. No channel through which *chylaqueous fluid* circulates is contractile. In no invertebrate animal, from the highest Annelid to the Zoophyte, does this anatomical character know an exception. It is *this* character which is extended to the anatomical disposition of the blood-tubes in the Articulata; it will be subsequently shown to belong equally to the circulatory system of the Mollusca. Although the fluids of the Articulate and Molluscan organisms represent true blood, the conduits through which it moves are not detached and independent structures. Although *more* complex and *more* raised in vital standard than the chylaqueous fluid of the Annelid and the Echinoderm, the blood of the Articulata and Mollusca is *less* complex and *less* raised in the scale of composition than that of vertebrated animals. It is thus easy to demonstrate that there obtains a direct and constant relation between the vital standard and chemical composition of the living fluids, and the anatomical characters of the tubular apparatus in which they perform their circulatory orbits. These facts have especial reference to the theory of respiration afterwards to be propounded.

The muscular system of the Articulata, as compared with that of the Annulose classes, manifests features of great superiority. The muscle-cell is more densely charged with fibrinous contents: the property of contractility is far higher in degree. The ceaseless activity of these animals flows from their remarkable muscularity. It is mechanically obvious that such a powerful muscular system as that of the Articulata presupposes an apparatus of fixed solids on which to act, and through which to produce mechanical results. Contemporaneously with this system accordingly appears the dermal skeleton of these classes. It is quite certain that such a highly developed state of the muscle-system as that which exists in the articulated animal *implies of necessity*\* the presence of a considerable proportion of fibrine in

\* See the author's papers “On the Blood,” now being published in the British and Foreign Medical and Chirurgical Review, for a full exposition of this subject.



the blood. The production of *fibrine* in the fluids supposes a high standard of respiration, and a correspondently developed nervous system.

Of these several events, which takes the *lead*? Is it possible that an increase in the complexity of solid systems, the integumentary, the nervous, and the muscular, can *go before* the increasing complexity which occurs at this stage in the zoological series in the composition of the fluids? The question involves the absurdity of conceiving an effect without a cause, a sequence without an antecedence. Nature makes first the mortar, *then* builds; the fluids are first prepared, *then* the superstructure of the solids is raised.

The function of respiration always, in every animal, is inseparable from the blood-making physiological actions. It is commonly supposed that it is with the system of *the fluids* that the office of breathing immediately connects itself. Extraordinary facts will be afterwards adduced which will render this supposition no longer exclusively tenable. The tubular apparatus of the fluids evolves itself at some point or other of its periphery, such that the amount of oxygen received shall be proportional, not to the abstract *bulk* of that fluid, but to its vital composition. A very small *vertebrated* animal weighing fivefold *less* than a given *invertebrated* animal, will consume in equal times fiftyfold more oxygen than the latter. 'Respiration,' therefore, is not an isolated physiological act, separable physically and dynamically from that complex assemblage of events which conspire in the maintenance of the living organism: it is an integer in the arithmetic sum of life. Its real value can only be determined by a study of it in its connections. Given the vital and chemical composition of the fluids, to estimate the proportion of oxygen demanded by any appointed organism? The problem is not empirical; it is scientific in the highest degree. It is an absolute rule in the physics of organization, that the structure and the function are directly proportional. An imperfect instrument can only produce imperfect results. The complex fluids and highly organized solids of the articulated animal render indispensable the provision of an *adequate* machinery for the inhalation of the vivifying principle. Thus then are traced irrefutably the physiological circumstances which *necessitate* at this limit in the scale a new order of respiratory organs. The object is inimitably accomplished; for the *first time* in the serial history of animal life, an *air-breathing* being is introduced on the stage. Nature surmounts all difficulties by adroitly resorting to an unexpected but matchless variation of her former plan; all at once, and without apparent reason, a new and extraordinary system of organs is contrived; an exquisite apparatus of *aëriferous vessels* is so skilfully blended with all the



other and normal constituents of the living body, that an *air-breathing* animal results without deformity of exterior contour: in a small space a large result is realized. An insect is a diminutive animal; its muscular and nervous systems are intensely active; its fluids are highly corpusculated and fibrinized; a considerable proportion of oxygen is absolutely essential. Could it by any other expedient have been adequately supplied? But the simple distribution of patulous tracheæ throughout all the structures of the body, by which air is rather brought to the blood than blood to the air, would most imperfectly accomplish the great function of breathing. It was not enough to provide an elastic inimitable spiral, by which the passive patency of each tube is maintained. Such property as that of physical elasticity in a structure so singularly beautiful answers *another* end; it recoils on the *contracting* of the tube. The *contracting* of the tracheæ is in the insect the act of *expiration*; by this act the diameter of the tubes of the universal tracheary system is diminished, and the air is driven out through the spiracular orifices: this act is *rythmically* followed by that of *inspiration*, in which the physical elasticity of the spiral, by rebound, restores the tube to its former diameter\*. No part of the circulating system but the dorsal vessel is capable of contracting and dilating. This fact explains an observation which the author has often made, that, considering the exalted muscular activity of the Articulata, of insects in particular, the *current of the blood in its channels moves at a disproportionately slow rate*. This diminished velocity is compensated, in the most perfect manner, by the rythmic contractility possessed by the parietes of the tracheæ. In virtue of this property the required *motion* is imparted to the *air* rather than to the *blood*. As well observed by M. E. Blanchard, the voluntary muscles of the body by their peculiar distribution *favour* the course taken by the blood, both in the arterial and

\* I have diligently sought for the announcement of this fact amongst the varied and excellent writings of Mr. Newport, M. E. Blanchard, and M. Léon Dufour. No allusion whatever is anywhere made to this property of *rythmic* contraction and dilatation, which I have proved, by *repeated* observations on larvæ and adult insects and Myriapods, the tracheæ to possess. The omission is the more surprising, since, *without* such a property, the tracheary system would be *mechanically imperfect* as an apparatus of respiration. As the *vessels* do not contract, there would be no provision for renewing the air in the extremes of the system. The working of the general muscles of the body external to the system would obviously prove a most imperfect substitute. What is denied indeed to the vessels is conferred on the tracheæ. I cannot *prove* that the parietes of the tracheæ are capable of *originating* this movement. I cannot demonstrate them to be muscular. It is possible that the opening and shutting of the air-tubes may only follow from those alternate acts of contraction and dilatation in the abdominal segments by which the dorsal and ventral arches of the abdomen are alternately elevated and depressed like the ribs of the vertebrated animal.



venous moiety of the system. No valves exist. The mechanism of nutrition and respiration in the tracheary Articulata would be most unsuccessfully studied without the guiding knowledge of these general facts.

The characters then which distinguish an annulose from an articulate animal are more deeply graven in the interior of the organism and in its physiological actions than on the visible and exterior forms by which they are respectively characterized. There is deep meaning in the freaks of nature.

In the water-breathing Articulata the system of air-tubes just described suddenly disappears. The large size of the crustacean renders practicable the introduction of complex *branchial* organs. They accomplish that office which in the myriapod and the insect devolved upon the aëriferous tracheæ. Nature has nowhere blended the two methods of respiration in the same class. There exists no adult *water-breathing* myriapod or insect. An *air-breathing* crustacean can nowhere be found. Her plans are consistent.

One more *general* fact of organization with respect to the Articulata remains to be stated. *Nowhere* from the myriapod to the crustacean is any trace whatever to be discovered of the existence of a *true ciliary epithelium*! Why should a structure so constant and profuse in all classes *below* the Articulata so suddenly and so completely disappear at the lower limit of this class? If in the epidermic system of the articulated animal there be something incompatible with the evolution of the ciliary variety of epithelium, why should it *not* occur on the mucous? In no single instance, in any species of myriapod, insect or crustacean, on the mucous tract of the alimentary canal, or anywhere else, has any indication whatever of the presence of vibratile epithelium been ever yet discovered. This extraordinary fact cannot be arbitrary and unmeaning. Cilia are here suppressed for some reason and from some cause—what can it be? The solution should be sought in the rapid and unwonted evolution of the *muscular* system which takes place at this point. In the organism of the articulated animal there does not exist *motive force* enough to sustain *two* motive systems at one and the same time: one is supplanted by the other. Ciliary is commuted into muscular motion. While studying the mechanism of respiration in the articulated animal, vibratile epithelium will therefore nowhere demand attention: its agency will be found to have been substituted by other instruments.

An exposition of the preceding general principles has seemed to the author indispensable to an intelligent study of the novel and extraordinary details, upon which it is proposed next to enter.



The orbit of the blood-proper in the Annelid is conducted in obedience to the simplest hydraulic principles. The Annelid is vermiform in figure. A dorsal vessel carries the blood from the tail to the head, a ventral in the reverse direction. The intermediate currents invariably, in every species, bear *from* the latter *into* the former vessel. This fact is perfectly patent to the eye of every observer. The blood enters *into* the dorsal vessel from the viscera, *from* the ventral trunk *into* the viscera. In simplicity of mechanical principles nothing can exceed such an arrangement. The annulose 'circulation' observes two leading directions, longitudinal and transverse. The dorsal trunk is propulsive, the ventral distributive, the œsophageal ring connective. Let the circulatory system of the *articulated* animal be studied with reference to this comparative standard.

*Myriapoda, Insecta, Arachnida.*

These three classes are distinguished by *one type* of organization. The blood-system, the nervous, and the respiratory are constructed upon one essential plan. A law, true of one, cannot therefore suffer aberration in the other. The unity of nature's constructive principles are observed with rigid inviolability. The lowest Myriapod is removed from the highest Annelid only by a short distance: the former in the adult state has no chylaqueous fluid, the latter no tracheal system. Is it mechanically reasonable that the introduction of 'tracheæ' into the organism should involve a radical change of plan in the orbital direction of the blood-current? It must be so, if Mr. Newport's exposition of this subject be founded in truth. In the Annelid the eye follows with clearness and certainty the currents in all the lateral vessels attached to the dorsal trunk moving *into* or *in the direction* of the latter. In what Mr. Newport has called the *systemic arteries* in Myriapods and Arachnids, the blood moves in a contrary direction, from the dorsal vessel towards the viscera. Those very vessels which in the Annelid can be proved indubitably, by the eye, to be *veins*, are suddenly in the very next class reversed into *arteries*! Which is the more probable,—that her observers have perpetrated a paradox, or that nature has reversed her course? The subject deserves a more accurate examination.

All English and continental anatomists have implicitly followed Mr. Newport; where he is in error they are wrong, where he is truthful they are right. It is *his* exposition of this subject therefore that must be measured by the standard of actual nature. Disciples will obey the master-teacher.

Mr. Newport's researches on the "Circulation of the Blood"



in the Myriapods, Insects, and Arachnids, constituted a remarkable æra in the anatomical history of the Invertebrate animals\*. His researches are masterpieces of minute and difficult anatomy; they deserve, as they have received, the admiration of all scientific men. The age of authority is gone by. Truth must now be revered at her native shrine, and Mr. Newport must submit to the criticism of his peers. Mr. Newport's anatomy is exact, but his reasoning is unintelligibly contradictory. His researches relate exclusively to the *central parts* of the circulating system of the tracheary Articulata; he has not attempted to investigate the peripheric. This is a natural division of this subject. Let these heads be discussed separately.

*Central Parts of the Circulatory System in the Myriapoda,  
Insecta, and Arachnida.*

The researches of Baker, Carus, Wagner †, Lyonet ‡, Cuvier §, Treviranus ||, Latreille ¶, Straus-Durkheim\*\*, Mr. Bowerbank ††, Tyrrel ‡‡, Müller §§, Hunter, Lord ||||, Newport ¶¶, in connexion with this subject, should be historically signalized; they deserve the reverence, but not the servile acceptance, of the scientific scholar; they involve a vast mass of laboriously acquired knowledge; they constitute the foundation whereon all future additions must rest.

The myriapodal 'circulation' exists in its least complex form in the *Iulidæ*. Of this family the *Spirostrepti* and *Spiroboli* represent the lowest genera. Mr. Newport has proved that the chambers of the heart *decrease* in number as the articulate scale is followed upwards from the lowest Myriapod to the highest Arachnid. This principle is *not* observed in the larva of all insects. In several aquatic species, the great venous abdominal currents may be followed most perfectly with the eye, and seen to enter the dorsal vessel *only* at its posterior extremity, where alone auricular orifices exist (Pl. IX. fig. 4, b). The dorsal vessel (a) of

\* On the nervous and circulatory systems, and on the existence of a complete circulation of blood in vessels, in Myriapoda and Macrourous Arachnida, Phil. Trans. 1843. Also Art. *Insecta*, Cyclop. Anat. and Phys.; and various papers in the 'Linnæan Transactions,' by George Newport, Esq.

† Isis, 1832.

‡ Traité Anatomique de la Chénille, &c., 1760.

§ Leçons d'Anat. Comp.

|| Die Arachniden, 1812; and also his Vermischte Schriften Anatomischen und Physiologischen Inhalts. Göttingen, 1816 (Die Spinne), p. 5.

¶ Cours d'Entomologie, &c., Paris, 1831.

\*\* Considérations générales sur l'Anat. Comp. des An. Art., 4to, Paris, 1828.

†† Entom. Mag. vol. i. April 1833.

‡‡ Proceedings of the Royal Society, 1835.

§§ Nova Acta Nat. xii. 2.

|||| Medical Gazette, 1838.

¶¶ *Op. cit.*



the larva of the Insect therefore bears a closer typical analogy to that of the Annelid than that which is presented by that of the lowest Myriapod. The dorsal vessel of certain transparent aquatic larvæ may be readily defined under the microscope; its pulsations and currents may be perfectly observed. The corpuscles floating in the blood mark with great clearness the direction of the current. It is certain that in some species the *systemic arteries* (fig. 1, *f*, & fig. 3, *n*, *n*.) (of Mr. Newport) do not exist. In those in which these vessels are detectable, the current which they convey tends *towards*, not *from*, the dorsal vessel. Repeated observations have convinced the author upon this point. They are venous, not arterial; they return the blood from the viscera into the dorsal vessel; these vessels are described everywhere, in all his writings, by Mr. Newport, as *visceral arteries*; his dissections have notwithstanding traced them into anastomosis with branches coming from the *supraspinal artery* (fig. 1, *c*, fig. 3, *c*, *e*, fig. 2, *b*). In *this* vessel the blood moves from the head in the direction of the tail; it follows therefore that the currents conveyed by the anastomosing branches must meet each other in the *same* vessel! action and reaction are equal and contrary! stagnation results! The *subspinal* venous trunk (fig. 3, *e*, *l*) discovered by Mr. Newport in Insects and Arachnids does not exist in the Myriapod. In the latter, therefore, the *primary* channels of the system of the blood do not exceed two in number, the dorsal and the ventral. This is the case in the Annelid; the ventral vessel of the Annelid *undulates* much *less* obviously than the dorsal. It receives *all* its blood from the dorsal by means of the œsophageal collar-branches: it distributes it chiefly to the integumentary structures. Trunks of secondary size proceed backwards, in some species from the heart, in others from the œsophageal vessels, expressly to supply the walls of the alimentary canal\*. Now the *veins* which return this blood from the glandular parietes of the intestinal canal in the Annelid enter into the dorsal vessel precisely in the same manner as the *systemic arteries* are described by Mr. Newport to *proceed from* this vessel in the Myriapod, Insect, and the Arachnid. In classes so contiguous, why should the functions of the same vessels be reversed? Mr. Newport's views are drawn from anatomical structures; he has never *seen* the blood moving in these so-called *systemic arteries*; he ignores the argument of analogy drawn from the *living* circulation of the Annelid; he does not perceive the *mechanical* difficulty with which the blood would enter these vessels from the segmental heart, on the supposition of their arterial character. They arise from the latter at its extreme *posterior*

\* See the Author's Report on the British Annelida in the Transactions of the British Association for 1851.



end (Pl. IX. fig. 3, *n, n*)—at that very point at which they should enter if they were veins.

A large wave of blood rushing forwards may be clearly seen in the dorsal vessel of larvæ (fig. 4, *b, a*): the chambered dorsal vessel contracts from behind forward; it observes the law of the Annelidan; the hindmost chamber contracts first, that next to it in advance next, and so on. The systolic movement does not occur throughout the whole length of the vessel at the same time, but in parts from behind forwards as the wave of blood travels. In two adjacent chambers the actions of systole and diastole are alternate.

There is in fact no functional difference whatever between the dorsal vessel of the Annelid and that of the articulated animal; they are distinguished only in structure. In the Myriapod, the tubular vessel of the Annelid is reinforced with propelling power at successive points—the chambered hearts. In the articulated animal this *extra* power in the central vessel is absolutely required. In the Annelid every vessel in the body is an elastic tube *tightly embracing* the fluid contents. The *channels* through which the blood moves in the Articulata do not closely grasp the contained fluid (fig. 2, *g*); they are indeed bounded by definitive membranes, but they are not elastic contractile structures fitted mechanically to favour the circulation of the fluids (Pl. X. fig. 10, *b, c*). This circumstance ought not to involve an alteration in the *type* of the circulation. But if the systemic arteries of Mr. Newport be really arteries, then the plan and principle of the circulatory systems of the Annelid and the Myriapod must be diametrically dissimilar. If they be arteries, the circuit of the fluids cannot be explained without involving physical contradictions. The author is however convinced that Mr. Newport has committed the mistake of imputing to vessels an arterial character, which observation and analogy prove to be venous.

The orbit of the blood-current in the Myriapod conforms in every particular with the Annelidan type. All vessels attached to the dorsal vessel *behind the œsophageal collar* (fig. 1, *b*) are *afferent* with respect to that trunk. All branches connected with the great ventral or supraspinal vessel posterior to the same limit are *efferent* with respect to this vessel. The currents in these latter branches are divisible into two orders—that first which supplies the viscera, that secondly which is distributed to the integuments: the current from the first, after having traversed the viscera *en route*, returns into the dorsal vessel under a *venous* character by means of the *systemic arteries* (sic) of Mr. Newport. That from the second is poured from various sources into the great splanchnic sinuses which enter the dorsal vessel at the auricular orifices.



In the *dorsal* vessel, from the extreme tail to the extreme head, the blood moves *forwards*, in the ventral backwards: in *all* branches whether integumentary or visceral, *from* the latter *into* the former. The dorsal vessel is afferent only with respect to those parts which are situated anteriorly to the œsophageal ring; the ventral is efferent only to the same parts—it is distributive to all others.

The preceding account of the course of the blood in the Myriapoda embraces conclusions suggested by careful study and numerous observations; it is recommended by its mechanical simplicity; it entangles the physiologist in no hydraulic contradictions.

That of the *Insect* (fig. 2) is regulated in exact conformity to the myriapodal type. The dorsal vessel (*a*) in the *Insect* exhibits signs of concentration; it is only the *abdominal* portion that is multiplied into chambers; through the thorax the vessel is continued in form of a simple tube. The auricular orifice of these chambers is furnished with a more perfect valvular apparatus. The same observations apply to the so-called *systemic arteries* of *Insects* as to those of *Myriapoda*. To the presence of these vessels in this class, however, no allusion is made by Mr. Newport\*. If they exist in the *Myriapod*, they must also exist in the adult *Insect*.

The *supra-spinal* trunk (fig. 2, *b*) in *Insects*, as in *Myriapods*, is the great centre of the ventral circulation. It receives all its blood from the dorsal vessel by means of the anterior branches into which the latter divides; it supplies chiefly the external structures and the nervous chords. Either from the descending aortic branches or from the anterior part of the supraspinal artery, there proceed backwards along the ventral aspect of the viscera, one or more secondary trunks which correspond with those which in the *Annelids* are exclusively distributed over the parietes of the alimentary canal; in these, the direction of the blood corresponds with that in the great ventral artery; like the latter, they are afferent and distributive. All the blood, thus, by means of these trunks, entering the viscera from below, reaches again the dorsal vessel, conducted by the so-called “systemic arteries.” In *Insects* the vessels connected with the abdominal circulation are more perfect, mechanically, as conduits, than those traversing the exterior structures of the body. This explains the difference of structure which exists between the systemic arteries (*sic*) and the *loose membranous channels* (fig. 2, *g, f, e*) opening into the auricles of the heart. The former belong to a distinct segment (the visceral) of the circulation, the latter to the integumentary or peri-

\* See article *Insecta*, Cyclop. Anat. and Phys.



pheral. In the Insect, as in the Myriapod and the Annelid, the circulatory current acknowledges two main directions; in *all* dorsal trunks, from the extreme tail to the antennæ, the movement of the blood is *forwards*, in all ventral trunks it assumes an opposite course.

In all branches connecting more or less transversely these two systems of longitudinal trunks, the blood travels from below upwards, from the ventral in the direction of the dorsal trunks. On the supposition that the "systemic arteries" are distributive neither in Insects nor in Myriapods, is it possible to solve the mechanical problem of the circulation? As now explained, the principle of the system is intelligible and consistent. It is asserted with great confidence by the physiologist, that in Insects no distinction into venous and arterial blood can prevail. The ubiquity of the tracheæ renders such a distinction impossible.

Such are the doctrines now taught; they are not necessarily true; at present neither the extreme peripheric parts of the blood-system, nor those of the tracheæ are known. New questions, to be presently propounded, will prove that the material conditions of the processes of nutrition and respiration in the air-breathing Articulata are as yet by no means clearly defined. But let the central parts of the circulation in Arachnids be first defined.

To Mr. Newport is due the credit of first solving the problem of the 'circulation' in the Arachnid; but his solution is neither clear nor complete\*. On his interpretation, conceding the merit of correctness to his descriptive anatomy, the circuit of the blood cannot be consistently described. Like that of the Myriapod and the Insect, the dorsal vessel (fig. 3, *p, a*) of the Arachnid extends from the tail to the head, along the dorsal median line. With its sides, along its entire course, there are connected two orders of branches; first, the pneumo- or branchocardiac canals (fig. 3, *k, k, k*), which return the blood from the pulmonary or branchial sacs (*g*); secondly, the systemic arteries (*n, n*) of Mr. Newport†. At its anterior extremity it breaks forth into a great number of branches destined for the supply of the appendages. To the dorsal vessel in the Arachnid Mr. Newport assigns an extraordinary duplicity of action. According

\* See his papers in the Phil. Trans. Part ii. 1843.

† I am very desirous in this place to invite the attention of the student in comparative anatomy to the beautiful work now being published by M. Emile Blanchard; it is entitled 'L'Organisation du Règne Animal,' à Paris, chez Victor Masson et J. B. Baillière. The delineations which adorn this work are executed in the first style of French art. M. Blanchard implicitly follows the interpretation of the circulatory system of the Arachnids, rendered by Mr. Newport.



to him, the same straight vessel (*p, a*), and furnished too with valves opening in *one* direction, sends the blood in two diametrically opposed currents! forwards towards the head, and directly backwards towards the tail at the same moment\*. He thus wantonly violates the unity of principle which presides over the distribution of the blood in the whole annulose and articulated series.

Directly contrary to the views of Mr. Newport, the blood in truth, in the *caudal artery* (fig. 3, *p*) of the Arachnid, moves *forwards*, not *backwards*. It follows therefore, that in the ventral trunk (*l*) of the tail of the Scorpion the direction of the current is backwards, not forwards as stated by Mr. Newport. The pneumo-cardiac channels (*k, k, k*) enter the auricles of the heart; the systemic arteries arise (Newport) from almost the same point in the walls of the chambers. The author has already argued in favour of the *venous* character of these vessels in Myriapods and Insects: if in the latter classes they be venous, they cannot be arterial in the Scorpion; they are the same vessels—they present the same relations—they are connected with the viscera in the same manner. They anastomose with the branches which proceed upwards from the supraspinal visceral arteries. Henceforth they will be called systemic *veins*.

At its cephalic extremity in the Scorpion, the dorsal vessel divides into three groups of secondary trunks (fig. 3, *b, c, d*),—those first which supply the brain, head and tentacles,—those secondly which proceed to the claws and legs,—and lastly those which form the great ventral longitudinal trunks of the body. In the Scorpion they consist of two orders, those first which Mr. Newport in this instance has called the visceral arteries (*b*), and secondly the *supraspinal artery* (*c*). If the visceral arteries exist as separate trunks in Arachnids, they must be present

\* This is his language:—"Having traced the distribution of the arterial vessels from the anterior extremity of the heart, it remains now to follow those of the posterior, which *afford some curious peculiarities*. The last two chambers of the heart, which are situated in the seventh segment of the abdomen, are greatly reduced in size, and constitute the *origin* of the caudal artery (fig. 3, *p*, of the author's plate), and seem to be the means by which part of the current of the blood is *directed backwards to the tail*." See page 292 of his paper on the Myriapods and Arachnids, in the Phil. Trans. 1843. There are eight valves to the heart. The anterior six act forwards. The two posterior act directly backwards (Newport)!—Is this probable, physiologically or mechanically? Does it not involve a hydraulic absurdity? Can the *same linear tube*, whose contractions *begin* behind and travel undulatorily *forwards*, drive the contained fluid simultaneously backwards and forwards? (!) *Why* should this reversal of the blood-current take place in the same homologous vessel in the Arachnid, and *not* in the Insect and the Myriapod? The mere addition of a *tail* to the Scorpion does not necessitate such a mechanical paradox.



under some form in the Myriapod and the Insect. They constitute a conspicuous class of distributive vessels in the Annelids. Mr. Newport does not suspect even their existence in the Myriapod and the Insect. He replaces them by his incomprehensible *systemic arteries*. In the pulmonary Arachnids a great *venous* abdominal trunk (fig. 3, *e, l*) is superadded to the system of the circulation. It conveys *forwards* the blood (according to Mr. Newport) from the caudal region. This again is undoubtedly an error. In this vessel in the Arachnid, as in the Insect, the course of the blood is *backwards*; it distributes it over the branchiæ, from which it is returned by the pneumo-cardiac channels to the heart again to repeat the same course.

The corresponding central parts of the *tracheary apparatus* require but few preparatory words:—

In the Myriapods the large tracheæ communicate externally with the spiracles. In the *Scolopendridæ*, *e. g.* the *Lithobius*, they exist on alternate rings to the number of eight or ten. The tracheæ proceed thence in longitudinal trunks to be distributed over every part of the body.

In Insects the *spiracles* are usually nine in number on each side; each spiracle consists of a horny ring of an oval form, within which is a valve formed of a series of converging fibres, and which opens perpendicularly on its long axis guarding the external entrance\*. In the perfect Insect the spiracles of the abdomen are small, those of the larva large. In the latter, abdominal respiration is most active; in the former, the thoracic is predominant. In Insects as in Myriapods, the tracheæ, arising at the spiracles, are distributed over every part of the body (Plate X. fig. 8). The tracheæ of *all* larvæ are simply tubular, those of all volant perfect insects are dilated at various parts into *vesicles*.

In some tribes, as in most of the Hymenoptera, Lepidoptera, and Diptera, these sacs are present in almost every species and occupy a large portion of the interior of the body, more especially of the abdominal region. They exist only in the volant species of the Coleoptera. They are present in the winged Carabidæ, but not in the apterous. The tracheæ, in those species of Orthoptera which are merely saltatorial in habits, never dilate into vesicles. M. Emile Blanchard declares that the *substance* of the walls of these vesicles is channelled into plexiform passages for the blood. This is most certainly incorrect. These sacs have no reference to the respiratory process; they subserve only a mechanical use; without them the insect could not fly. They exist in the male of the common Glow-worm, but not in the female (Newport).

\* Art. *Insecta*, Cyclop. Anat. and Phys.



The relation of the tracheæ to the blood-currents will be studied under the next head.

*Peripheral extremes of the respiratory and circulatory systems in Myriapoda, Insecta, and Arachnida.*

In their extreme distributions these two great systems will be most advantageously studied in connexion. There prevails between them an extensive parallelism; they are not, however, everywhere in coincidence. Though much has been accomplished by the ingenuity of minute anatomists during the last few years to dispel the difficulties of this subject, much still remains to be unravelled. Swammerdam, Malpighi, Lyonet, and Cuvier\*, did really no more than discover the existence of the dorsal vessel. It was at this time that Cuvier first made the felicitous observation, "Le fluide nourricier, ne pouvant aller chercher l'air, c'est l'air qui vient le chercher pour se combiner avec lui." Cuvier believed the fluids in the Insect to be stagnant, except in the dorsal vessel, in which they only oscillated to and fro. In the year 1827 Carus saw the movement of the blood in the transparent larvæ of the *Ephemeridæ* and *Agrionidæ*†. Carus could not trace the currents to their remote courses. Wagner in 1832‡ confirmed the observations of Carus. Straus added his authority upon the same point. Mr. Bowerbank§ has published admirable observations on the circulation of the blood in the wings of *Chrysopa perla* and *Phlogophora meticulosa* in the order Lepidoptera. Mr. Bowerbank has in no instance, however, followed the blood beyond the larger nervures of the wings, in which he saw the current (accompanied always by a trachea) turning back at certain points. He nowhere states that these currents followed the tracheæ to their extreme ramifications. Mr. Newport corroborates these observations in his article "Insecta," in the Cyclopædia of Anatomy and Physiology. In the year 1848, M. E. Blanchard|| published a celebrated essay, in which he first announced the ingenious experiments which led him to conclude that the blood travelled everywhere in the sheaths of the tracheæ:—"il est démontré que le fluide nourricier pénètre entre les deux membranes qui les constituent." M. Emile Blanchard does not attempt to show how the blood can describe a circuit in such a manner and in such a situa-

\* Sur la Nutrition dans les Insectes, Mém. de la Société d'Hist. Nat. de Paris, 1797.

† Nova Acta Physica, vol. xv. 1834.

‡ Beobachtungen über den Kreislauf des Blutes, &c. bei den Insecten, Isis, 1832.

§ Entomological Magazine, 1833.

|| Annales des Sciences Nat., 3<sup>me</sup> série, Sur la Circulation dans les Insectes, &c.



tion. But his conclusions have by no means received the undivided assent of subsequent observers\*. It is easy to prove that the coverings of the tracheæ are very unlike those implied in the inferences of M. Blanchard. This will be afterwards done.

Agassiz† declares that he has repeated the injections of M. Blanchard with confirmatory results. At this period M. Charles Bassi and M. Filippi‡ undertook especially to examine this question. They fed the *larvæ* of *Sphinx atropos* and *Bombyx mori* on indigo, cochineal and other coloured substances; they found on dissection that the tracheæ were everywhere coloured; they satisfied themselves that the colour was limited to the tunics of the aëriferous tubes; it never entered into the interior. Prof. Alessandrini§, varying the preceding observations, concludes from similar experiments that the coloured matter actually enters into the *interior* of the *tracheal tube*:—"Le Prof. Alessandrini crut remarquer que la matière colorée était contenue dans l'intérieur même des trachées, et que la coloration dépendait ainsi d'une véritable injection de vaisseaux trachéens." The famed observations of Mr. Bowerbank lend support to the views of the French and Italian observers just explained. He remarks, "the course of the blood is almost invariably in immediate connexion with that of the tracheæ." Mr. Newport, in his article "Insecta," teaches precisely the same doctrine. In a paper very recently|| read before the Linnæan Society on the *Ichneumon atropos*, Mr. Newport states, "that the ramifications of the tracheæ which penetrate the structure of the alimentary canal and of every other organ, *become denuded of their external covering*, and then seem to form only two tissues, the *spiral* and the *mucous*; if indeed there be not also, as he has some reason to think, an extremely delicate serous or basement, closely adherent to and uniting the coils of the fibrous tissue on its external surface. The *ultimate divisions of the tracheæ are always distri-*

\* With reference to the remarkable relation which, according to M. Blanchard, subsists between the tracheæ and the blood, it is important that his views should be clearly apprehended. He says again,—"*Mais n'est-ce pas plus encore sous le rapport de la nutrition que ces tubes respiratoires, dont nous connaissons la nature actuellement, doivent arrêter notre attention. En portant de l'air dans leur intérieur ils portent le sang dans leur périphérie. Ces trachées divisées et ramifiées à l'infini dans la profondeur de l'économie conduisent ainsi le fluide nourricier à tous les organes, à tous les muscles au moment même, où il vient de subir le contact de l'air. C'est le sang nouvellement artérialisé, le sang propre à vivifier, à nourrir tous les organes.*"—*Op. cit.* p. 380.

† *Annal. des Sc. Nat.* 1851, and *Proceedings of the American Association for the Advancement of Science*, Cambridge, U.S., &c.

‡ *Ann. des Sc. Nat.* 1851.

§ At the Scientific Congress held at Geneva, Sept. 1851.

|| See *Annals and Magazine of Nat. Hist.* for July 1853.



buted separately and do not anastomose, ending, as noticed by Mr. Bowerbank, in *extremely minute, filiform, blind extremities*, and this Mr. Newport finds to be their condition in all structures, in the nervous and integumentary, in the glandular and muscular\*." M. Blanchard† has very recently proved the existence in the Arachnids of a *true capillary network*? at the extremes of the circulation. "This network," he remarks, "which has not yet been pointed out in the Articulata, exists under the integuments and between the various layers of the muscles, in the connective tissue; it consists of *distinctly circumscribed canals lined with a thin epithelium*. Thence the blood is received by the venous canals‡." Thus is presented in bibliographic but faithful outline the sum of existing knowledge on the distribution of the air-tubes and the blood-channels in the air-breathing Articulata: who can say that it exhibits a consistent history? The physiologist rises from the scene confounded by its manifold contradictions. The assertions of one observer are opposed and outweighed by those of another. Mr. Newport, the most recent and laborious investigator, leaves the subject utterly unintelligible; his observations cannot be verified in nature.

The author does not, for one moment, pretend to affirm that his researches (now first published) have as yet destroyed the possibility of all controversy upon *every part* of this subject. He does, however, believe that he has *finally* settled *one part*,—that which relates to the extreme distribution of the tracheæ. He has not definitively established, by actual demonstration, the manner in which the blood is related to the *extreme* tracheæ. On this subject he will state at present only what he has clearly and confidently observed.

It should first be affirmed as an absolute principle, from which there can be no departure, that a tracheal tube is an *air-tube* in *every part* of its course. It is not, as supposed by Agassiz and M. Léon Dufour§, an air-tube in its proximal moiety, and a

\* I have given in the text at length the views of Mr. Newport, as reported in the abstract published in the 'Annals'; I have indicated the points in controversy by italics. They express the results of Mr. Newport's last and very recent observations. It will be afterwards seen by the text, that the conclusions at which I have arrived, from numerous and scrupulous examinations of the very same points, differ in a remarkable degree from those just communicated by Mr. Newport to the Linnæan Society.

† Comptes Rendus, June 20, 1853, p. 1079. See also the beautiful figures in his work 'Sur l'Organisation du Règne Animal.'

‡ See translated abstract in the Annals and Mag. of Nat. Hist. for Sept. 1853.

§ "Elles se divisent, comme dans les Insectes en général, en *trachées-artères* ou grand *canaux aérifères*, et en *trachées nutritives*, qui naissent des premières, et vont épanouir leurs subtiles ramifications dans tous les tissus."—Ann. des Sc. Nat. tome xv. no. 2. p. 76, 1852.



blood or circulatory conduit in its distal; the microscope everywhere proves such a view to be an unmitigated error. It is quite another and more rational supposition to maintain that the *passages* which bear the tracheæ may probably serve also to convey the nutritive fluids. Even this opinion requires the evidence of new demonstration. The author will now proceed to consider the results of his own recent investigation, distributed under the following heads:—1. The structure of the tracheæ. 2. Their distribution; (*a.*) in the adult and larval internal structures; (*b.*) in the branchiæ, in connexion with the question of insect aquatic respiration. 3. The anatomical relation in which the tracheæ stand to the nutritive fluids. 4. The mechanism of respiration in air-breathing Articulata.

#### *Structure of the Tracheæ.*

The air-tubes in Myriapods, Insects, and Arachnids, admit of division into two distinctly different parts: 1. the *spiral trachea*, and 2. its capillary continuation, the *membranous*. The former is a continuously tapering tube, branching arborescently, the branches never re-entering. It is always and everywhere furnished with an elastic spiral by which its bore is maintained in an open state. It is composed, as stated originally by Sprengel, of three anatomical elements (Pl. X. fig. 13); the outermost (*a*) consists of a dense membrane which swells under the agency of acetic acid, and *separates* from the spiral on which it normally rests and to which it forms a *close investment*. When raised by acetic acid it retains the impress of the spiral. This would not be the case if the membrane did not naturally *closely embrace the spiral*. And if it did closely embrace the spiral, it required no further persuasive to satisfy the physiologist that between it and the spiral there can by possibility travel no current of blood. This simple experiment is quite enough to effect the demolition of M. Blanchard's theory. All structures *external* to this membrane belong to the blood-channels (fig. 10, *b, c*) and not to the trachea. From the coverings of the latter they are quite dissimilar in anatomical structure; they are really the *loose* delicate membranes which constitute the walls-proper of the blood-channels. They are attached to the tracheæ only by loose adhesions. If now, while the tube is under the reagency of acetic acid, the eye search for the internal lining membrane (fig. 13, *c*), which lies on a plane to the inside of the spiral, it will appear with as perfect clearness as the external. It swells and separates from the *spiral* like the external. It is impossible to *prove* the existence of much difference of structure between this and the external membrane; it is more delicate and less refractive. The spiral lies in the space between these two membranes. On close inspection it



seems as if a membrane distinct from the two former united together tubularly the coils of the spiral, and that the spiral itself consisted of a *hollow tube* formed out of cells arranged spirally in the substance of this membrane. In a short time the *fibre* of the spiral, after immersion in acetic acid or turpentine, loses its dark, highly refractive *solid* character. It appears distinctly as though its substance were permeated by the fluid and that air was displaced. In this state the spiral looks like a pellucid diaphanous coil wound around the axis formed by the internal membrane. This description applies to every *spiral* trachea in the body. But there is a limit, different in different structures, at which the *spiral* ceases. It is at this point that the second division of these tubes or *membranous tracheae* begins. It is not the *external covering*, as stated by Mr. Newport, which ceases, but the *spiral* (Pl. IX. fig. 5, C, e). This fact admits of various and unquestionable proofs. The spiral grows less and less visible until it graduates insensibly into a *continuous* tube (f, g). It still however retains the peculiar optical character of a *trachea*. Its edges are faint *reddish*, from the iridescent decomposition of the light. This appearance was observed by MM. Alessandrini, Filippi and Bassi. The latter of these observers believed that the tint was due to the colour of the hollow cylinder of coloured blood which embraced the air-tube, corroborative of the views of M. Blanchard. It should rarely be ascribed first to the high refractive index of the air contained in the tube, and next to the density of the external fibrous membrane. It is a character by which a membranous air-tube, though of capillary diameter, can be distinguished with certainty from a blood-channel or a capillary blood-vessel. The direct continuity of the *bore*, as well as of the walls of this membranous capillary air-tube, with the larger and spiral trachea, can be proved in several modes beyond the possibility of dispute. By pressure, skilfully managed, while the specimen is under the microscope, air may be forced from the 'spiral' into the membranous tube; but the continuity of the walls of the latter with those of the former is so clear and convincing under the microscope, that no other evidence is required to prove that the capillary membranous tube is to the 'spiral' as a capillary is to an artery. The diameter of the 'spiral' trachea constantly decreases as it divides; that of the membranous observes throughout its entire course, whether it multiply into a network (Pl. X. fig. 9, d, e), or wavy brushes (fig. 12, c, d, f), or into the muriform plexus which exists in the substance of muscles (Pl. X. fig. 15), a uniformity which can compare only with that of true blood-capillaries of the vertebrated animal.

A tracheal tube, in many instances at the point of penetrating into the substance of a solid organ provided with a membranous



investment, will *appear*, from the close and tubular manner in which it is embraced by this membranous investment, to throw off, as supposed by Mr. Newport, its external coat at the point of entrance. Acetic acid however proves this appearance to be false. The tube still preserves its three constituent elements *after* entering the substance of the organ, whatever it be, and until it assumes the capillary or membranous character.

It is important to observe, because it reconciles the accurate observations of Mr. Bowerbank with those of the author, that on the *wings* (fig. 10, *f*), especially on the scaly intervals between the nervures, the *spiral* tracheæ, as correctly stated by Mr. Bowerbank, do *not* for the most part degenerate into the *membranous* tracheæ. In these situations the *spiral* continues to the extreme termination of the tube (fig. 11, *b*). There is something anatomically characteristic in the walls of the membranous tracheæ. They denote a difference between those 'parietes' through which a *gas* has to pass, and those (of the vessels) which *fluids* transude. The smallest trachea differs from the largest only in the absence of the spiral, just as the largest artery differs from the capillary only in the presence of a thick elastic coat. The tracheæ terminate differently, and form different plexuses, in different organs, according to the varying mechanical arrangements of the ultimate parts of the latter.

The conclusion must be emphatically reiterated, that however, wherever, and in whatever structure the tracheæ may peripherically terminate, they are *air-tubes* throughout all changes to their final extremes.

#### *Distribution and Subdivision of the Tracheæ.*

The primary, secondary and tertiary tubes divide and subdivide arborescently, the branches never reuniting (fig. 14). In the *spiral* tracheæ no plexiform union of the branches ever, anywhere, occurs; so far the observations of Mr. Bowerbank and Mr. Newport are exact to nature. It is because these distinguished observers could not succeed in tracing the air-tubes beyond this limit, and because they drew a general inference intended to be applied to *all* structures, from the distribution and termination observed by the tracheæ in the wings, that they were both seduced into the error of supposing first these points to be the distributive *ultima* of the tubes, and secondly, that the tracheæ nowhere inosculate. As already stated, this is true only of the scaly intervals which separate the nervures of the wings—*of no other structures*. In nearly *every other* structure in the body of the Insect the air-tubes divide and subdivide in the same profuse retiform manner as the blood-capillaries of the



vertebrated animal. In the *muscles* the ultimate membranous tracheæ divide and unite plexiformly (figs. 14, 15). The meshes are large and oblong (fig. 15). Some tubes run parallel with the ultimate muscle-fibre; others cross the latter at right angles, connecting the former. In the glands the capillary tubes *enclose* the space occupied by the gland-cells (fig. 9): they unquestionably *reticulate*, and in their ultimate form preserve a remarkable uniformity of diameter. In many parts of the mucous membranes they observe a peculiar *wavy* method of distribution (fig. 12). They elaborately reticulate in the loose structure beneath the integuments. It is by no means improbable that M. E. Blanchard has mistaken the plexus formed by the *tracheæ* in the integuments of the Arachnids for a *rete* consisting of true blood-vessels. In the nervous tissue they follow two modes of subdivision. The brain substance is actually *penetrated* by the plexiform capillary tubes. The nerves are accompanied by long undulating filaments.

In some of the voluntary muscles the tracheæ are profusely numerous. The larger spiral branches enter the sheaths of the muscle=fascicles at right angles (fig. 14); the *membranous* tracheæ into which in the substance of the muscle they subdivide, coincide generally in direction with the fibres of the muscles (fig. 15). In other muscles the primary entering tracheæ are few in number. As a rule it seems at present probable, that the volume of air (oxygen) which by means of the tracheæ enters into the substance of a *solid* organ in the tracheary Articulata is *directly* as the *vital importance* of that organ. The reticulation of the tracheæ is most dense and profuse in the glandular and nervous structures. The large spiral air-tubes which travel along the axes of the spacious blood-channels, detach from their sides here and there *minute wavy* branches (fig. 10, *j*, *b*) which *float in the fluid*, and which appear to be expressly intended to *aërate the fluids*. These floating air-tubes are everywhere seen where the blood-stream comes into contact with the main trachea. The main tracheæ are simply convective. It will afterwards appear that the function of these *floating tracheæ* is distinct from that of those plexiform extremes of the system which penetrate and traverse the substance of the solid organs. *These aërate immediately the solids, those the fluids.*

*The distribution and subdivision of the tracheæ in the branchiæ* of the aquatic larvæ of Insects involve the consideration of the mechanism and significance of aquatic respiration as it occurs in the young of the air-breathing Articulata. Is it *real* aquatic breathing, or is it only apparently so?

In the larvæ and pupæ of gnats, the branchiæ exist in the form of slender hair-like organs arranged in tufts. Each filament is



penetrated by a single trachea and an advancing and returning current of blood. In the *Agrionidæ* (fig. 5, *a*) they assume the character of lancet-shaped processes attached to the sides of the abdomen at the points of the future spiracles. Examined carefully as transparent objects, the tracheæ of these branchiæ divide and subdivide much more elaborately than is commonly supposed (fig. 5, B, *b*). It is only the *larger* tracheæ that are accompanied by a current of blood (fig. 9, *i*, *b*, fig. 12, *e*). The latter is much *less* profusely subdivided than the former. This fact seems incontestably to prove that the tracheæ, *not* the blood-channels, extract the air from the surrounding water. In the anal branchiæ of the *Libellulidæ*, M. Léon Dufour exhibits the tracheæ (fig. 7) as terminating in *bulged* extremities (fig. 7, B, *a*). The author will only state that he has never, in the course of his numerous researches, in any instance met with this mode of termination. In the filiform branchiæ of the larva of gnats each trachea tapers to the finest extreme.

In *Pteronarcys regalis* Mr. Newport describes the branchial filaments as consisting "each of a simple, unarticulated, uniform structure, slightly tapering and closed at its extremity, and in the interior of which there is an extremely minute tracheal vessel\* terminating in delicate cæca." In no one of his writings is it evident that Mr. Newport is aware to what an extreme degree of *capillary* subdivision the tracheæ are carried in the *flat branchiæ* (fig. 6, B, *c*), if not in the filiform, of the larvæ of Insects. In those of the *Agrionidæ*, cut off and examined separately under the microscope, they cannot be followed by the highest powers of the microscope. The blood-current turns back at the larger branches: it does not ramify in network streams. It is obviously not designed to fulfil the office of breathing: this function falls upon the tracheæ. This conclusion is opposed to the views of Mr. Newport. "The blood-corpuscles of the whole body circulate through the branchiæ for the purposes of respiration. The current of the blood is always in the vicinity of the tracheæ, absorbing oxygen by endosmose and giving out carbonic acid. *This takes place in every form of branchiæ* †." The author is fully satisfied that this is an erroneous interpretation of the respiratory process as it occurs in the branchiæ of Insects. The ramifications of the tracheæ in these organs are far more elaborate than Mr. Newport and other observers have ever yet supposed. They render the inference irresistible that the branchial respiration of the Insect is really atmospheric in type. The air does not, as in fish-breathing, enter immediately into the blood.

\* Linnæan Transactions, 1851.

† *Op. cit.* p. 432.



In the vessels of Insects in every phase of life, there seems to be some structural peculiarity which *unfits* them for the interchange of *gases*. There resides on the contrary in the walls of the tracheæ a marvellous endosmotic property, which enables them to give passage in any direction to *gaseous* elements with extraordinary facility. There occurs then in reality no example of true branchial breathing in the larvæ of Insects. It is only the extracting of air from the water instead of directly from the atmosphere\*. The aquatic life of the Insect therefore is only apparent, not real. The *principle* of the respiratory process is the same whether in or out of the water, whether in the larva or imago state, whether with internal tracheæ or external branchiæ. There is no example of *real* aquatic breathing.

What light then do these anatomical minutiae reflect on the question which involves the *mechanism of nutrition and respiration in the tracheary Articulata*? That is the question now to be considered. It is surpassingly interesting. If the conclusions which the author is about to present should prove to be exact, the physiologist will have approached nearer to a solution of the ultimate problem of respiration. He will see this function under a new phase—under strikingly novel conditions.

In all the transparent structures of Insects, such as the wings, antennæ, branchiæ, &c., every observer may prove for himself that the blood-currents travel in the same passages as the tracheæ (fig. 10, *b*, *k*, *c*). On closer scrutiny it will be seen that a channel, such as the nervure of the wings, bearing in its centre a large tracheal tube (*k*), exhibits on *one* side of this tube a current going in one direction (*b*); on the other, another bearing in an opposite course (*c*). These are afferent and efferent, arterial and venous blood-streams. They are bounded by separate walls. The afferent current is circumscribed by its own proper coats, the efferent by *its* own; and the trachea is placed intermediately, having parietes quite distinct from, though contiguous to, those of the blood-channels. This coincidence between the tracheæ and the blood-currents can be traced in the wings nowhere beyond the limits of the nervures into the scaly spaces which they circumscribe. The returning of the corpuscles at a certain point renders this fact quite unquestionable. Beyond this limit *only the fluid elements*, not the corpuscles of the blood, extend. In

\* M. Léon Dufour contends for the same principle: "Le dernier terme de la composition organique serait donc ici, comme dans les branchies des Poissons, une trame *vasculaire*, en ne donnant à ce dernier mot que sa valeur rigoureusement étymologique, c'est-à-dire anatomique. Seulement dans les Poissons c'est du *sang*, et dans les Insectes de l'*air*, qui est renfermé dans les vaisseaux de cette trame." Ann. des Sc. Nat. 1852, tom. xvii.



this extra-vascular region it is *cyclosis*, not circulation, which governs the movements of the nutritive fluid. If the same passages served everywhere for the blood and for the tracheæ, and if their parallelism was unexceptional and universal, wherever the tracheæ could be seen, there also should be observed the corpuscles of the blood. This is the case only in the primary and secondary, *never* in the capillary tracheæ (fig. 11, *b*). The blood-corpuscles (fig. 10, *g*) in the Myriapod, Insect, and Arachnid exceed by several times in diameter that of the extreme capillary membranous tracheæ. It is perfectly marvellous to what inconceivable minuteness the *air-current* is reduced in travelling along these tubes. It affords a captivating example of the illimitable divisibleness of matter.

If *everywhere* the blood and the air travelled together, branched together, *capillated* in concert,—if *everywhere* a *double* blood-current to *one* air-tube could meet the eye, the inference could not be resisted, that the sole, entire and exclusive design of the tracheal apparatus of the Insect consisted in *aërating the fluids*.

Since, however, the blood *returns far before* the tracheæ reach their remote *penetralia*;—since the comitance between the blood and the air is broken abruptly at a limit *proximal* to the extremes of the organism, *it is certain* that the tracheal system in the Insect fulfils some other function—answers some other end—than that merely of *aërating the fluids*. What can be the meaning of those incomparable *pneumatic plexuses*—veritable *retia mirabilia*—which embrace immediately the *very ultimate elements* of the *solid* organs of the body;—those microscopic air-tubes, which carry oxygen *in its gaseous form*, unfluidified by any intervening liquid, to the very seats of the fixed solids which constitute the fabric of the organism? There is an immeasurable difference between oxygen dissolved and oxygen free. In the former case, all the *forces* liberated during the moment of condensation from the elastic to the fluid form are expended upon the *blood*, and that, too, remote from the scene at which that blood is to be utilized; in the latter case, free, gaseous and uncombined, it is delivered immediately at the spot where the oxygen is to be employed; it electrizes by direct combination the last sedentary elements of the organism; by such an arrangement those forces attendant on chemical action vivify undissipated the very ultimate components of the body at the very moment of their disengagement. This then is the real difference between an insect and every other living animal. This is the unequalled mechanism which renders the insect a *multum in parvo*, the unsolved riddle of creation. In *all* other animals the quickening action of oxygen is first *exclusively* exhausted upon the *fluids*; in the insect, the fluids are only partially influenced as the vitalizing



element travels forwards to operate *immediately*, in its *unexhausted* form, on the final elements which conspire to maintain the nutrition of the living body.

The intense electrical and chemical effects developed by the immediate presence of oxygen, *in the gaseous form*, at the actual scene of *all* the nutritive operations of the body, fluid and solid, give to the insect its vivid and brilliant life, its matchless nervous activity, its extreme muscularity, its *voluntary* power to augment the animal heat; such contrivance, subtle and unexampled, reconciles the paradox of a being microscopic in corporeal dimensions and remarkable for the relative minuteness of the *bulk* of its blood, sustaining a frame graceful in its littleness, yet capable of prodigious mechanical results.

The epidermal skeleton of the Arthropoda is histologically peculiar. *Chitine* was first defined by Odier\*. In the year 1845 it was more fully investigated by C. Schmidt†. By Lassaigne it has been distinguished under the name of *Endomaderm*: it is a proximate principle which resembles *cellulose*. Both are insoluble in caustic potass. Nitrogen however is present in chitine and absent in cellulose: it is the animal basis of the integumentary structures of Insects and Crustacea. It is a principle of low vital properties. To the presence of this substance is probably to be ascribed the fact, already mentioned as extraordinary, of the universal absence of vibratile cilia from *all* the structures of Insects and Crustacea. And why is *vibratility* not a property of those organized parts of which *chitine* is the proximate basis? The very definedness of this question marks an advance in the real *science* of physiology. Effect is linked to its true cause, attribute to its right substratum, function to its immediate instrument. Chitine is produced under two distinct conditions: in Insects it occurs under the circumstances of atmospheric respiration, in Crustacea under those of the aquatic.

The *external* machinery of the process of breathing, however unlike the constituent parts, or different the principle of its action, does not therefore appear to involve any difference in the ultimate products of the nutritive actions of the organism.

The suppression of motive cilia in the Arthropoda is the signal of the saving of power. The economized force is diverted to other purposes. The nervous and vascular centres are raised in standard: the whole muscle-system is augmentedly developed, and the secernent organs are woven into more complex structures. The presence of chitine in the dermal skeleton of the Articulata entails a distinctive character upon the periphery of the circu-

\* Mém. de la Soc. d'Hist. Nat. de Paris, 1823, p. 29.

† Zur Vergleich. Physiol. d. Wirbellos. Thiere, p. 32.



latory system. Contractile vessels cannot exist in the substance of an incontractile solid. This segment of the circulation of Insects should be studied with special reference to this point. When the skeleton is very thick, it is composed of a series of superimposed laminæ, between which are tunnelled certain channels, as in bone, for the conveyance of the nutritive fluid. In the centre of the larger of these channels tracheæ may be demonstrated\*.

The true epidermis of Insects is always and universally composed of a tessellated hexagonally-celled epithelium. The anatomical characters of the ultimate blood-channels of Insects will be most successfully studied in the corresponding parts of the circulatory apparatus of the Crustacea. The same description essentially applies to both.

#### *Crustacea.*

Every Crustacean is a water-breathing, every Insect an air-breathing animal. To this rule there can be found no real, many apparent, exceptions. In the system of the Crustacean there exist no *water* tracheæ. Although the Crustacean is an insect breathing water, the mechanism contrived to accomplish the process is comparable in no single particular with that used in the instance of the Insect breathing air. In the former plan there is no wonder-striking singularity. The apparatus employed is common to every aquatic animal. The organs of breathing in every true crustacean conform essentially to the aquatic type. Though some species seem to enjoy the power of respiring on the atmospheric plan, the apparatus used fulfils the requirements of the branchial principle.

One typical form of blood-corpuscle prevails throughout all the species of this class. The fluid, in the embryonic state, as in the larvæ of Insects, and antecedently to the evolution of the branchiæ and the heart, presents a description of corpuscle different from that which afterwards in the same animal characterizes the adult fluid. The former is a real chylaqueous compound, is moved by means of the general muscles of the body, and undergoes the change of aëration without the intervention of any special organs.

#### *Central parts of the Circulatory System.*

In this class *the heart* occurs under the character either of a saccular vesiculiform viscus, or under that of the vasiform or tubular.

In the higher species, in which the organ is partly branchial

\* See Histological Catalogue by Prof. Quekett.



and partly systemic, it is the point of departure of an arterial system of distinctly walled pulsatile tubes which in the lower becomes abortive. It is placed in the axis of the body, directly under the shell, at the anterior part of the back, and is often attached to the internal surface of the dermal skeleton by muscular fibres: it is the chief propelling power of the blood. In the Siphonostoma and Lophyropoda it is a simple sac, either spheroidal or elongated in figure: it has only two orifices, a venous behind and an arterial in front. This organ in the Decapods, occupying the middle of the cephalothorax and star-shaped, passes off into arteries in front, behind and below, the returning venous blood entering through orifices at the upper and lateral portions. In the Pœcilopoda, Isopoda, Amphipoda and Læmodipoda it is tubular in form, and occupies the mid-region of the dorsum, sends off arteries before, behind and laterally, and receives the venous blood through lateral venous orifices. It is most highly developed in the Stomapoda. In the Phyllopoda it approaches the Myriapodal chambered type.

In the lower Crustacea the blood passes from the heart directly into intervisceral lacunæ: no defined vessels exist. In the higher, in which the organ is unarticulated and more centralized, arterial trunks occur; after a short course they are lost in the interstices of the tissues.

The *venous currents* converge from the lower part of the body into various intercommunicating sinuses, situated some upon the median line and others at the base of the appendages. From these sinuses the blood proceeds to the branchiæ and thence into the dorsal sinus, the walls of which are thin and non-contractile, and within which the heart is entirely enclosed.

This dorsal sinus is filled during the systole, and the arterialized blood which it contains is absorbed during the diastole through the venous orifices of the heart without any aid on the part of the walls of the sinus\*.

#### *General descriptive Anatomy of the Branchial Organs.*

The ultimate questions of structures will be more advantageously studied if preceded by a few general statements as to the more prominent characters of the organs dedicated to the office of respiration. The Siphonostoma, Lophyropoda, and many Stomapoda present no special branchial organs.

Those of the Læmodipoda and some Stomapoda are reduced to a few vesicular or cylindrical, sometimes wholly rudimentary

\* See Anatomy of the Invertebrata, by Siebold, translated by Burnett, for very copious bibliographic references on the literature of this and all other classes of Invertebrated animals.



appendages which hang freely from the base of some of the feet, or are inserted isolatedly at the sides of the body (Pl. XVIII. fig. 1). The Phyllopoda are provided at the base of each of their swimming feet with an ovoid or lanceolate branchial lamella: it is distinguished from the feet by the absence of bristles.

It is only the first and last pairs of feet in the Amphipoda which are modified into respiratory organs.

In the Isopoda the five pairs of post-abdominal feet are nearly always concerned exclusively in the office of breathing. The two multi-articulate cirri of each of these feet are changed into plates (Pl. XVII. figs. 4 & 5), which directed backwards, are imbricatedly arranged and applied against the under surface of the last caudal segment. In shape these plates differ according to the species. Intermediate between the Isopoda and Decapoda, the Pœcilopoda in their branchial organs partake of the characteristics of both. Inserted on the abdominal feet they resemble those of the first order; lamellar in figure they approach the branchiæ of the Decapods.

The respiratory organs of some Stomapoda (Pl. XVII. fig. 3) are evolved in the highest degree; they consist of tubular tufts arranged around a stalk, and float freely in the external medium. In anatomical structure they fall under the type of those of the Lobster (fig. 8). In *Squilla* these tufts exist on the ten anterior feet.

The branchiæ of the Decapods are attached to the bases of the anterior abdominal feet, lodged in a branchial chamber, and protected by the cephalothorax. The most developed form of the breathing apparatus in the Crustaceans occurs in the Decapods. In this order not only is the function thrown upon particular organs entirely set apart for the purpose, but these organs are lodged and protected within a special cavity; and the renewal of the water necessary to their operation is secured by the motion of distinct appendages or *flabellæ*. The thoracic cavity is formed by a reduplication of the external tegument, and is provided with two orifices, one for the introduction and the other for the expulsion of the fluid. Through these orifices a constantly renewed supply of water is made to pass by the agency of a large valve-like organ, placed in the efferent canal, which by its movements drives a continual current from behind forwards, or from within outwards, and thus occasions a constant ingress through the afferent opening: this organ is the flabellum. It is the modified appendage of the second pair of feet-jaws, specially developed to answer this purpose. The perfect contact of the water with the respiratory surface is further ensured by the actions of the flabelliform appendages of the other maxillary or ambulatory member, which in most Decapods penetrate into the



branchial cavity, and incessantly sweep and comb over the surface of the branchiæ. The membrane lining the branchial chamber in some land Crabs, which not only habitually live out of water, but are infallibly drowned if immersed in that fluid, is sometimes disposed in folds capable of acting as reservoirs for a considerable quantity of water, and sometimes presents a spongy texture equally well adapted for storing up the fluid which is necessary to keep the organs of respiration in the state of humidity required for the performance of their functions\*.

The preceding cursory account is offered only as an introduction to that narrative of original details which is now to follow.

An exact inquiry into the circumferential circulation of the Crustacea will serve to elucidate the apparatus of the blood-system as it exists in the Insect organism. It is only by a minute scrutiny into the last extreme of the blood-current, that the physiologist can penetrate the mystery of the nutrimental act and the ultimate mechanism of the respiratory process. No opportunity is more favourable than that offered in the example of the Crustacea;—the structures are transparent; the blood-current is obvious to the eye; every element of structure may be readily reduced to its last analysis.

*Minute Anatomy of the Peripheral Blood-channels and Branchial Organs.*

In nearly all species the *primary* blood-channels, both venous and arterial, are circumscribed by a special membrane which is a distinct and separable structure. The arterial trunks are contractile; they embrace closely the contained fluid. The muscle-tissue present in the parietes of the heart extends evidently to those of the arteries. The veins are non-contractile; their walls adhere externally to the solid parts, amid which they lie; they cannot therefore contract in transverse diameter; they are passive conduits, the arterial are active. The arterial and venous trunks are lined internally by an extremely fine hexagonally-celled epithelium (Pl. XVIII. figs. 2, 3, 4). The cells present remarkable regularity in size and outline. They are not detectable on the internal walls of the parenchymatous passages which coincide with the capillary segment. The blood-channels are *therefore* here imparietal. The epithelium ceases where the special boundary of the artery ceases; it begins again at the limit denoting the origin of the true veins. This hexagonally-celled epithelium is the prevailing envelope or lining of all organs and cavities in the Crustacea. It betrays no other diversities than those which depend upon the size and distinctness of the

\* See Carpenter's Principles of Comparative Physiology.



contained cell-granules. The cells are *never* furnished with a nucleus. The granules are in the interior of the cells, and adhere internally to the cell-wall. A different opinion is expressed however by Professor Quekett: he describes the granules as belonging to the underlying structures. The error of this description may be placed beyond doubt by the reagency of acetic acid. Dr. Carpenter denies the existence of cells in the epidermis. In the adult Crab, for some time after the moulting has taken place, that is, after the shell has become hard, it is, as this author states, impossible to detect the cellular arrangement of the membrane exterior to the calcareous layer. The cells seem to have been mechanically worn away. Soon after the moulting however, the presence of *cells* in the epidermis of the carapace, for instance, admits of easy demonstration.

The hexagonally-celled epithelium is an element of varied use and great importance in the crustacean organism; it constitutes real boundaries everywhere of the extreme or capillary circulation (Pl. XVIII. fig. 5). Plates (*a, b*) are formed by the apposition of its constituent cells laid accurately edge to edge: these plates are united by interposed islets or patches of parenchyma (Pl. XVIII. fig. 1, *a*). Between the latter are left large, irregularly and angularly bounded passages, traversed by the extreme blood-currents (fig. 1, *b*). The islets of parenchyma consist of a variable number of nucleated cells, filled obviously with the *fluid* elements of the blood. The groups differ in size and outline in different organs. They are sometimes embraced by a common capsule: in such a case the latter would constitute the real boundary of the blood-channel. As such a capsule is the independent envelope of a detached group of cells, rather than the continuous boundary of a conduit, however irregular in form and outline, it cannot with any anatomical propriety be defined as the *wall* of the latter. The epidermal plates, between which the blood-passages are disposed, are inflexible, firm, non-contractile. "Membranous parietes" of blood-vessels adherent internally to these plates could not contract upon the contained fluid without approximating the plates. Such an effect would imply a strong muscular effort. No muscles exist in these extreme situations. No separate vascular membranes bound the peripheric blood-currents; therefore no "*capillaries*" exist in the Crustacea. The fact then is now susceptible of general expression, that in the articulated animals, most certainly in Insects and Crustacea, the *peripheral circulation* in consequence of the presence of a firm unbending epidermal skeleton, cannot by mechanical possibility be any other than it is, namely a profusion of irregularly subdivided streams, traversing angularly bounded passages in fixed non-contractile



inflexible solids. An exception to this axiom may exist in the example of some of the internal organs—probably in the musculo-glandular walls of the alimentary canal, certainly not in the liver of the Crustacea, as will be afterwards shown.

Let now these general anatomical facts be applied to the analysis of the branchial organs in their several varieties in this class, or to the mechanism of the respiratory act, where there exists to this end no separate provision.

The *araneiform* Crustaceans are furnished with no separate respiratory organs. Almost every English systematic writer describes the Pycnogonidæ as destitute of a true circulating system\*. This is an error. In *Pycnogonum* the existence of a dorsal vessel lying on the dorsal aspect of the stomach may be readily demonstrated. The blood follows the cæcal diverticula of the stomach into the legs; it returns by separate channels along the ventral aspect of the cæca into an auricular division of the heart. The peripheral blood-currents do not subdivide. The solids are not permeated by subdivided capillary currents. Everything beyond the main stream is *cyclosis*—that is, *non-corpuscular* fluid passes by endosmose from cell to cell. This extra-vascular movement of fluid plays a part in the nutrition of the solid structures of Invertebrata, of which the frequency and the extent are by no means yet rightly estimated by the physiologist. The floating corpuscles of the blood never pass beyond the walls of the proper vessels: they never reappear *de novo* in the fluid, beyond the vessels. In the latter region the fixed cells impress upon the blood required changes. But this extra-vascular fluid *after leaving the vessel*, may unquestionably undergo the process of aëration. This is exemplified in the Pycnogonidæ, in which the blood-current is so little subdivided. In this group the floating corpuscles are relatively to the size of the animal very large. They conform to the crustacean type; they are granular and nucleated, suspended in a clear, colourless fluid. They move in a definite orbit. This fact alone proves the presence of a heart—if the fluid constituted a chylaqueous system its movements would be oscillatory.

The Entomostracous Crustacea present few diversities as regards the number and disposition of the parts dedicated to the office of breathing. In every species the feet are found to be modified parts. The circulating system is crustacean, not insect-like, in type. The dorsal vessel is a simple tube; it is in no instance moniliform; it is *not* multiplied by valves into indepen-

\* "In one of the most degraded forms of the class, we revert to the simplest possible type of the circulating apparatus; even the dorsal vessel, which is so characteristic of the Articulata, being apparently deficient in the Pycnogonidæ."—Dr. Carpenter's Principles, &c., p. 695.



dent contractile chambers. The peripheral circulation is *lacunar*, not capillary\*. In the Branchiopodidæ the articulations of the feet expand foliaceously. An augmented surface is thus created. It is utilized respiratorily. By the ceaseless action of the legs a current in the surrounding element is maintained, which is applied to the purposes of respiration. In every order of Entomostracous Crustacea the extreme circulation coincides precisely in every particular with that afterwards to be described in the higher Crustacea. Every appendage of the body is subservient to the function of breathing.

In the families Nebaliadæ and Branchiopodidæ, the abdominal appendages of which are foliaceous, currents of blood can be traced by aid of the corpuscles, traversing irregular passages which coincide with great exactness with those so easily seen in the corresponding appendages of the Macrourous Decapods.

In several genera of the familiar Daphniadæ, and Lynceidæ, the extreme blood-currents in almost every part of the body can be clearly defined by the eye. In every foot, in every foliaceous appendage, in the very bristles, the act of aëration is accomplished. The blood-corpuscles in all Entomostraca are crustacean in type and structure. They are small in number relatively to the bulk of the blood.

In *Caprella linearis* (Pl. XVII. fig. 6), a filiform crustacean, common in the Bay of Swansea, two membranous processes (*a*) depend from the under surface of the abdomen. By Milne-Edwards they are said to be vesicular. They are really flat. A *single* current of blood courses round the circumference (*b' b*). The centre of the lamina is parenchymatous. These organs exemplify a principle in the organization of the Crustacea. They prove how little is the measure of the respiratory function in the Crustacea, compared with the high nervous development and active muscularity of these animals.

No setæ or bristles of any description are added to these simple organs. They are enveloped in an exquisitely-attenuated tessellated epithelium. It preserves its tenuity without a sacrifice of stiffness. These organs are very readily converted into *vesicles* by compressing the body of the animal. The force of the fluids separates the parallel laminae, and converts a plane into a sac. They are moved by muscles at the base; they are attached to the second and third segments of the thorax. The action of the water upon them is auxiliated by flabellæ. They exhibit the

\* The general facts stated in the text may be verified most readily by the examination of any of the numerous Entomostraca which inhabit our freshwater pools. Microscopic in size, they admit of being easily submitted to inspection.



apparatus of breathing under the characters of the greatest simplicity.

The common *Talitrus* will serve to illustrate the anatomy of the branchial parts in the Amphipodan family. The thoracic limbs are commonly said to be transformed into branchiæ at their bases. The depending edges of the dorsal plates (the epimeral pieces of the tergal arc) are however much more suitably organized than the proximal articulations of the legs (Pl. XVIII. fig. 1, c). They are penetrated by a very dense system of canals (b, c). The epidermis is reduced to an extremely thin and transparent lamina. The component hexagonal cells may be readily observed (fig. 2). The outer or epidermal lamina is united to the opposite parallel lamina by dots of parenchyma (a). The blood streams in the intermediate passages (b). These parts therefore correspond in ultimate structure in the most exact manner with leaves of the branchiæ of the Crab. The bases of the legs are filled with muscle fasciculi. In *Talitrus*, as in all Crustacea, the blood-currents are large and few in number. No setæ or bristles of any sort belong to these lateral branchial plates. The respiratory current is maintained by the action, which is ceaseless, of the three pairs of abdominal prolegs. In several orders of this family the flabellæ of the abdominal appendages are converted into branchiæ (Pl. XVII. figs. 4 & 5). In minute structure they coincide with the lateral respiratory plates of *Talitrus*. From these parts, when thus specialized for breathing, bristles are absent. The associated *palp* excites the aërating current.

In the family of Stomapoda, the species of which are rarely found in the British seas, each segment of the abdomen is furnished with a pair of broad natatory feet, the basilar joint being quadrilateral (Pl. XVII. fig. 3, a), each bearing two lamellar branches (d), the exterior of which gives attachment on its posterior face, and close to the peduncle, to a *tufted branchia* (b). The minute structure of the branchial tubuli conforms in every respect with those of the Lobster, afterwards to be described. Each tubule is traversed in its centre by an afferent column of blood, which breaks out into a network along the circumference on its return to the proximal extremity. They are admirably fitted for the intended purpose.

The respiratory organs in the *Decapod* Crustaceans manifest the highest specialization. They are fixed to the sides of the thorax, and lodged artfully in expressly provided thoracic chambers.

Two types of structure prevail among this class, the tubular or cylindrical, and the laminar. Both forms are exemplified in the Macrourous decapods. The tubular is less common than



the laminar. *Scyllarus*, *Palinurus*, *Gebia*, and *Homarus* are genera which afford examples of the cylindrical or tubular; in *Astacus* the tubules of the branchiæ are less numerous, and are disposed only on two of the sides of the branchial shaft, having a pinnate appearance; those tubules which are inserted on the coxæ are terminated by a thin, multiplicate, lamelliform dilatation, and resemble in structure an ordinary branchial lamella.

The coxæ in *Homarus* and *Palinurus* are provided with a plate-like process inserted at the side of the coxal branchia. It is of a leathery consistence, and covered with numerous hairs. The presence of these bristles proves that it cannot participate in the process of respiration. It is probably only a septum of separation between the branchiæ. In *Aristeus*, in which the branchiæ are sixteen in number on either side, they are penniform. They are composed of a shaft, from which pass off right and left numerous curled filaments, whose convex borders are covered by tufts of very delicate, densely packed, branchial cylinders.

The second or *lamellar type* of branchia occurs in all the *Brachyura* and *Anomura*, and in the genus *Galathea* among the *Macroura*. This type prevails also in the genera *Palæmon*, *Hippolyte*, *Alphæus*, *Penæus*, *Crangon*\*.

The familiar Lobster affords the best example of the first or cylindrical type of branchiæ. They consist of plumose pyramidal processes, enclosed in a thoracic cavity, and provided with peculiar *flabellæ*. The latter subserve the twofold use of agitating the water and cleansing, and separating the minute tubercles of which the organs are composed. In number the branchiæ vary in different species. They amount to 20 in *Astacus*, and in the most nearly allied species. In other *Macroura* the number falls. In the *Palinuri*, *Scyllari* and *Penæus* it is 18; in *Pandalus*, 12; in the *Calianassæ*, 10; in the *Palæmons*, 8; 7 only in the *Crangons*, *Hippolytes*, and *Sergestes*. In the Lobster, the Crawfish, in *Nethrops*, *Palinurus*, and the *Scuyllarus*, the branchiæ are subdivided most elaborately into minute tubular or cylindrical processes, which diverge at right angles from the axis of support, in which the main afferent and efferent channels of the blood are lodged. The gill of the Lobster (Pl. XVII. fig. 8) expresses, typically, the general and minute structure of the branchial organs of *all* the above-enumerated genera. They consist of fourteen separate organs, disposed in two alternate series, and lodged in a thoracic cavity. Each gill, conical in general figure, resolves itself into a multitude of small tubes (fig. 8, *a'''*), proceeding from the sides of the axis. In a transverse section, it

\* Ann. d. Sc. Nat. xi. 1827, pl. 26, and xi. 1839, pl. 3. fig. 1, pl. 4. figs. 1-4.



will be seen that the large afferent trunk (*a*), running up one side of the axis of the whole gill, sends off a minute branch to *each* lateral tubule (*a'''*). A single tubule (*B*) has then its afferent vessel, which runs along its central axis (*B, b*). The sides of this afferent vessel are cribriform, so that the blood readily escapes at *every* point of its course into the loose lacunose tissue (*C*) and (*B, c*) which forms the *circumference* of the tubule, and through which the blood returns to the efferent or venous trunk (*B, c*). The blood-corpuscle thus runs round the circumference of a cylinder. This latter represents the area and period of aëration. It corresponds with a plane surface equal in length to such circumference. There is not, therefore, either functionally or structurally, any real difference between the cylindrical branchial filament and the leafy variety of this organ. The walls of the tubule are perfectly smooth. The hexagonal cells of the epidermis are detectable at the extreme outermost coat. These cells differ from those of the ordinary epidermis in nothing but in the fact of their greater tenuity. The islets of the included parenchyma are composed of nucleated cells. They are nourished by the branchial blood. The presence of these masses of living solids in the midst of the blood-current, at the very point at which the latter is undergoing aëration, concludes the controversy as to the capacity of the fluid in such place and time, at one and the same period to receive oxygen and to nourish the parenchymatous tissue. Here it is accomplished. The question *why*, in the Lobster and its kindred, nature should resort to this curious method of multiplying and subdividing the branchiæ, illustrates the unsearchableness of ultimate causes.

In the Lobster, as in the Crab, two orders of *flabellæ* exist. The first consists of a whip-like process, moved by powerful muscles, and guarding the *outlet* of the branchial chamber (Pl. XVIII. fig. 9. shows the minute structure of extreme end). By its regular movements, a determinate current of water flows outward. The edges and flat surfaces of this marvellous instrument are profusely armed with secondary instruments (Pl. XVIII. fig. 9), matchless for their beauty, surprising as means to an intended end. The external or horizontal *flabellum* is sufficiently long to sweep vertically over the whole group of gills. From its position and structure, it can affect only the outermost surfaces of these organs. If this instrument were a simple, flat, smooth-edged process, it is easy to conceive, that during its motion over the branchiæ from above downwards, the component tubuli of the latter could not by mechanical possibility be separated so as to favour the rush between them of the aërating element. This difficult purpose is accomplished by an inimitable contrivance. The flabellum is covered in rich profusion with minute, flexible, mop-like



threads (fig. 8, E). At the distal extremity of each seta or bristle, a group of minute flexible processes are added. A structure of so great singularity cannot be misinterpreted. The purpose which they are designed to fulfil cannot be mistaken. They constitute artfully-adapted provisions for cleansing, mopping, separating, agitating the constituent filaments of the branchiæ. No other description of instruments would answer the same ends. They are not merely substitutes for *cilia*. *Cilia* would simply effect the rapid renewal of the aërating element. *They* answer the manifold uses enumerated. Another variety of seta is intermixed with the former on the same flabellum. It consists of a sword-shaped process (fig. 8, f), less flexible than the former, from the edges of which secondary, acute, minutely-delicate points arise at an obtuse angle. They are designed only to act in one direction. They are situated chiefly on the margins of the flabellum (D). They exist on those placed vertically between the gills, as well as on that long whip-like flabellum which acts horizontally in the branchial cavity. They are less fitted to wipe the surface of the tubules than to catch at their edges when swiftly drawn over or between them. Thus they separate and momentarily hold apart the slender filaments of the branchiæ. Nearer to the root of each of these setæ, and only on one side, a second system of angular teeth occurs, which are turned backwards towards the root (Pl. XVII. fig. 9, C, E, D). They are thus capable of acting in a direction the reverse of the serrations placed on the extremity of the same seta. The *mop-like* variety of setæ does not exist on the flabella of those Crustacea the branchiæ of which are leafy or laminar.

Under the latter circumstances they would prove ineffective as cleansing utensils. They could perform no mechanical work on passing between smooth parallel laminæ. Between cylindrical filaments they act far otherwise. Nothing can surpass the efficiency of the contrivance. There exists such an evidently suitable relation between the structure and form not only of the flabella, but of their minutest hairs, and the shape and figure of the branchiæ in the same subject, that the incomparable ingenuity with which these little implements are adapted to the exact office to be discharged can only be appreciated by studying them in their connexions.

The *flabellum*, examined in its *general structure*, is a machinery no less remarkable. It consists of two horny parallel plates (Plate XVIII. fig. 9, b, c). Between these plates there travel with great regularity radiating currents of blood (f). The currents are separated by muscular fascicles (e), observing a similar disposition. The latter are levers of great power. Along the margins of the flabella the blood returns in large obvious channels. It



is worthy of the special attention of the physiologist, that from these currents there proceed outwards at right angles minute streams traversing the axis of each microscopic seta (*a*). The fluid in these exists as a *single* column, sometimes as a flux and reflux stream moving in lacunæ (fig. 7, *a*). It does not advance and return along different conduits. In other words, the hollow axis of the seta is not divided by a longitudinal partition into two channels. It is a single tube. The blood in these parts moves in a flux and reflux manner. These little appendages, the structure of which is so accessible to the eye, express with great clearness the method in which constantly, in *all invertebrated animals*, the nutritive fluids reach the collateral recesses, the by-parts of the solids. In the Lobster, the biliary tubules (Pl. XVIII. fig. 10) resemble strikingly in structure the branchial. To establish further the manner in which, in the crustacean organism, the blood is related to the organized parts, it were at this place not inappropriate to allude incidentally to the minute anatomy of the liver-follicle of the Crustacea. It is a simple tube (fig. 10), having two coats embracing one another concentrically (*f*). Between these coats the blood flows in irregularly-bounded channels, forwards on one side, or half, and reversely on the other.

The hollow axis is filled by the secreted product (*c, g, h*). It is the commencement of the excretory duct. The epithelial cells of the outer coat are the same at every stage of the tubule (*a*). Those of the inner (*e*) begin to change in character as the extreme cæcal end of the tubule is approached. At first they are hexagonal and flat; by degrees they bulge; they become filled more and more with fluid, until at length they become spheroidal (*b*). They form a layer of several series deep. This end of the follicle, as supposed by Mr. Goodsir, is really the producing or secretive centre. The blood pervades irregular passages tunnelled between the spheroidal cells (*b*). The *fluid* elements of the blood pass from the blood-channels *into* the interior of the *modified* epithelial cells. From the latter it exudes into the *hollow axis* of the tubule (*c*). *This is the act of secretion!* The fixed cells impress upon the fluid by which they are traversed a *tendency to change*, a *disposition* to combine its elements anew. This change continues after the fluid escapes from the cells, *beyond the pale of the living* solids. The oil-cells (*c*) in the axis of the follicle are not organized cells, as represented by Dr. Leidy. They are mechanically-formed oil- and albumen-cells (*g*). The chemical change proceeds in the secreted product, *without the direct agency of cells*, as it flows from the distal to the proximal end of the tubule\*. The *yellow colour* (*h, d*) is not

\* I have not attempted in the text, because it would be out of place, to compare the results of my own investigations on the structure of the liver-



developed until the product reaches nearly the middle of the tubule. The process of respiration can only be resolved to its last analysis by first determining with exactness the manner in which *other* vital nutritive acts are accomplished. The endosmose of gases requires that the partition should be thin (Pl. XVIII. fig. 5, *a, b*), the epithelial cells compressed and attenuated, and all unnecessary contents withdrawn; the act of *fluid* secretion demands the presence of the reverse conditions (fig. 10, *b*): such contrasted reasoning must prove directive to the thoughtful reader. Induction founded on contrasts serves often best to establish the *principia* of a science.

The branchiæ of the *Anomourous Crustacea* are arranged in the thoracic chamber in alternate series of fourteen in number. The chamber is open along the whole extent of its inferior boundary. To this circumstance is to be ascribed the *absence* in these Crustaceans of the flabella. They are not required. The influx and efflux of the water into the respiratory cavity are without such assistance unimpededly rapid. Propelling and guiding instruments would here prove a useless incumbrance. The gills in the Paguridæ are composed of laminae. They are four-sided pyramids in shape. The respiratory leaflets are arranged however in a bipyramidal manner (Pl. XVII. fig. 7, B); that is, a wide channel (between *f* and *g*, fig. 7, B), coinciding with the length of the gill and with the primary blood-vessels, lies between the rows of leaflets which are built up on each side of the axis. Along this groove (fig. 9, *a*, fig. 7, *d*) rushes a current of water, descending along the gill on one side and ascending on the other. The ascent occurs on the inner side. The minutely-divided streams of water, which directly operate on the respiratory laminae (or cylinders, as the case may be), connect these two main vertical currents by horizontally passing between the branchial leaves. If these laminae were to become adherent through the absence of moisture, the respiratory process could no longer proceed. Thus the Crustacean dies rapidly in perfectly dry air; but if, in the branchial chamber, a sufficient proportion of humid vapour exist, the gaseous oxygen of the *air* (when the animal is out of water) is dissolved, and the breathing proceeds as efficiently as if the animal were still revelling in its native element. This mechanism explains the capacity with which many Crustacea are gifted, of living almost as well in air as in water. This apparent amphibious power does not prove that when in air they really breathe on the *atmospheric* plan, but that the oxygen of the *air* which is admitted into the branchial chamber is *fluidi-*

follicle of the Crustacea with those of Mr. Goodsir and Dr. Leidy. Such comparison must be made by the future student. I venture to think that neither the structure of the hepatic follicle nor the process of secretion has ever before been placed in so clear a light.



fied by the moisture which still remains in this cavity. The mechanism of the respiratory process, even under such circumstances, is really aquatic in type.

In ultimate structure the branchial laminae in the gills of the Hermit Crab (Pl. XVII. fig. 7, B), conform exactly with those of the Brachyurous orders, subsequently to be explained. The coats of the axial branchial vessel in the Hermit Crab are smooth, and destitute of those hooks which are distributed so systematically over those of the common edible Crab (Pl. XVIII. fig. 6). The hooks are not required because there are no flabella. The setae (Pl. XVII. fig. 7, M) which depend from the roof of the branchial cavity of the former present the mop-like character of those already described in the Lobster.

In the Brachyurous orders, exemplified by the vulgar edible Crab, the gills are constructed on the leafy or laminar principle (Pl. XVII. fig. 9, A). They stand vertically in the containing chamber. The leaves on each gill are arranged in two series (*a*), one on either side of the longitudinal blood-channels. The shape of the ultimate leaves differs in different species. In some they are semilunar; in others they are reniform, in others pointed, &c.; in all they leave deep grooves for the free play of the branchial current from the root to the apex of the gill, and from the apex to the root on the other side. The streams passing horizontally between the leaflets connect the two main longitudinal currents. Thus the water-currents on the outside of the branchiae observe the same distribution and division as the blood in the interior. The structure of the branchial laminae admits of resolution to the very last elements of organic structure. They are inconceivably slender and delicate. The most cautious attempt to inject the gills converts the leaf into a bag, the lamina into a sac, so delicately are the plates held together; but though thus attenuated in the extremest degree, each lamina consists of two opposed plates.

These plates are composed exclusively of a single layer of epithelial cells, hexagonal in outline, and adjusted edge to edge. Under the highest power of the microscope they exhibit minute granules (Pl. XVIII. fig. 4). Neither tubercles, nor setae, nor hooks, nor teeth such as those of the cells of the epidermis of insects, occur on any part of their surfaces or edges. The flat surfaces and edges are perfectly smooth. The laminae are slightly thicker immediately around the vessels than near the margins. In the former situation the intermediate parenchyma is slightly thicker than in the latter.

The microscope readily resolves these patches of solid tissue to their last elements (Pl. XVIII. fig. 5). They are cells, generally but not always bearing nuclei, and frequently oil-globules.

They are enveloped by a common capsule, but not always so.



They are filled with a colourless fluid, which reaches them immediately from the contiguous blood-current.

Their office is simply and purely mechanical. They connect together the parallel epithelial laminæ. They divide the blood-stream. They exhibit every possible variety of size and figure. They are undoubtedly penetrated and surrounded by a plexiform arrangement of *nerve-tubules* (Pl. XVIII. fig. 13, *b*). These nerves play no part in the *physical act* of respiration. Nerve-force is here introduced only for the maintenance of the organic structural integrity of the elements. From this condition their right function is inseparable. Oxygen does not therefore *really* enter and mix with the blood independently of nerve-power.

In the Brachyurous Crustaceans the flabella (Pl. XVII. fig. 9, B) constitute important instruments in the machinery of breathing. They are indispensable in consequence of the closed character of the branchial chamber. They amount to three in number: two small ones which move between the anterior gills, and one external horizontal flabellum, which in its arc of motion sweeps over the external surface of the whole row of branchiæ.

Like those of the Lobster, the flabella of the Crab are profusely studded with appropriate hairs (C, D, E) for agitating and separating the branchial laminæ. During the moment of separation a rush of water takes place between these laminæ. So admirably adapted are the setæ of the flabella to the purpose intended, that they must be regarded as express provisions. No other sort of instrument would subserve the end in view. How graceful are the contrivances of nature! how perfect her adaptations!

The ultimate setæ are multiplied at their distal extremities by several parallel rows of acutely-pointed teeth (C, D, E). Those on the base of the stalk point differently from the former. By this inimitable disposition these exquisite organules are fitted to do double work. They also obtain a better leverage by hooking to the corresponding teeth, which in these orders are distributed over the exterior of the vessels of the gills (Pl. XVIII. fig. 6).

The part enacted by the adipose element in the physiological act of respiration, replete with novel interest, belongs to the physiological bearing of the question of respiration\*.

In the preceding review of the mechanical condition of the respiratory process as it occurs in the higher Articulata, the physiologist must have observed the comparative fewness of the corpuscles of the blood (Pl. XVIII. fig. 11), the smallness of the bulk of the blood relatively to the dynamical capabilities of the articulated animal, the small proportion of blood which in a

\* See *ante*, "Process of Respiration."



given time traverses the branchial organs, the *breadth* of the ultimate blood-stream measured by the size of the pulmonary capillary of the vertebrate animal. These facts seem certainly to prove that there can exist no direct proportionality between the amount of respiratory process and the general dynamical capabilities of the Crustacea\*.

### *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 vertebrate 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

\* I have understood that some years ago a paper was read by Prof. Quekett, before the Microscopic Society of London, "On the structure of the *flabella* in the Crustacea." It has never been my good fortune to see that paper. The description given in the text is founded upon a very extensive series of original examinations. I am desirous here to pay the tribute of my gratitude and admiration to Prof. Milne-Edwards, for the assistance and instruction which I have received from the study of his numerous splendid contributions to this branch of comparative anatomy.



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 constitutently 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



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.

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.



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 configured 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 excréments," &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

\* 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.



is that tubular extension (Pl. I. fig. 7, *a, a'*) of the mantle by which the surrounding element is admitted into the "branchial 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



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

are lucidly affirmed:—1st. That the water concerned in breathing *permeates the branchial lamellæ*, and thus traverses the partition which divides 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 *ex-current* 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, *palman 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 (*b*). 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 pha-



ryngeal 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 Clavelinidæ: 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 régulièrement en travers par les vaisseaux; la bouche est à une extrémité, 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 Acephean, 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<sup>2</sup>, *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 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 ejection, 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<sup>2</sup>). 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, dorsally 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 Lamellibranchiata. 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<sup>2</sup>). 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<sup>2</sup>, *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<sup>2</sup>, *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*, *Macra*, *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

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



in a coat of mail, is rendered unequivocally clear to the understanding.

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 laminae, 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 laminae (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.



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



act no part either in the alimentary or respiratory process. It cannot reach the mouth without permeating the branchial foramina. It can do this only by overcoming the opposing force exerted by the branchial cilia. If the water which occasionally enters at the exhalent siphon were normally designed for respiration, like that flowing in at the inhalent siphon, as supposed by Mr. Clark, the former could not reach the branchial lamellæ without meeting and mingling with the counter impure current driven by cilia, coming from the branchiæ. The principle is absolute in the mechanism of the respiratory process in all Tunicate and Lamellibranchiate mollusks, that the aërating element *must pass through the gill*. The function of breathing cannot be accomplished if the water merely passes in a stream whose direction is parallel with the planes of the gill-laminæ. The ultimate and true respiratory currents are those which permeate the laminæ at right angles to their planes. It results of logical necessity, therefore, that if the water did *not* traverse the branchial partition (Pl. II. fig. 12, *g*) which divides the extra- from the intra-branchial chambers, the great and imperious function of respiration could not be accomplished.

The preceding postulates, supported only by theoretical reasoning, will on a future occasion be rendered incontrovertible by the demonstrations of minute anatomy.

*Structure of the Branchiæ in the Lamellibranchiate Mollusks.*

The *mist* upon this branch of natural history which has survived the brightening science of a bright century may indeed refuse to be dissipated even by the achromatic microscope—the potent wand of the modern observer. That which the calm eye discerns with clearness, and the understanding interprets with confidence, though amplified many hundred diameters, is as likely to be an immutable objective truth as any “instance” within the sphere of the unassisted vision. Faith in the verity of microscopic facts is a fundamental article in the scientific creed of every living philosopher. The sphere of the naked vision is exhausted: another is opened by the microscope. Minute descriptions of subtle and complex structures, rendered possible only through its instrumentality, will prove of as great service in the hands of the future lawgivers of science, as the grosser narratives of the fathers of anatomy have already proved in the founding of the temple in which the high priests of natural theology now chant her service.

The branchial structures of the Mollusca have never yet been unravelled. The problem, though not impracticable, still awaits solution. The system of the gills is a conspicuous element in the molluscan organism. In apparent size they are considerable.



If function were expressed in numeric amount by the dimensions of the organs, the physiologist would assign to this class of animals a high degree of respiration. Minute structure is a factor in the estimate. The gills of the Lamellibranchiate mollusk are singularly and peculiarly formed: they admit of comparison in structural characters with no other organ found amongst Invertebrate animals. The *meaning* of a part is an inference of the intellect. When exact, it is founded upon a correct appreciation of structure. A 'law' is upraised upon the basis of particulars. Let the following difficult inquiry be conducted in rigid compliance with this *regulus philosophandi*. Though abundant, the elder literature upon this subject has bequeathed little that is accurate and true. Baer\* alludes in a special manner to the pectinated character of the branchiæ in the Lamellibranchiata; he illustrates his description by the gills of *Mytilus*. Meckel† depicts and describes in general terms a comb-like structure in the gills of *Spondylus*, *Pecten*, and *Arca*. Cuvier's figures and descriptions‡ delineate the same formation. In his valuable notes, Siebold§ describes the branchiæ in *Pectunculus*, *Mytilus*, *Arca*, *Pecten*, *Avicula*, and *Lithodomus* as consisting of a system of parallel vessels. In the text of his work, however, Siebold, like Mr. Hancock, speaks of the trellis-like network of the branchial structures. Among the older authors by whom allusion is made to the pectinated arrangement of the branchial vessels, the names of Bojanus, Treviranus, and Poli may be enumerated.

The contributions of Mr. Hancock upon this subject are the most recent, special, and distinguished ||. By this observer three types of structure are recognized. They are thus defined in his own language:—"There appear to be *three distinct modifications* of gill-structure in the Lamellibranchiata. In the first the laminae forming the gill-plate are composed of filaments either free or only slightly united at distant intervals, as in *Anomia* and *Mytilus*; in the second they are formed by a *simple vascular network*, as in *Mya*, *Pholas*, &c.; and in the third the laminae of the gill-plate are complicated by the *addition of transverse plicae composed of minute reticulations of vessels*, as in *Chamostrea*, *Myochama*, *Cochlodesma*, &c. Other modifications may exist,

\* Meckel, Arch. 1830, p. 340.

† Syst. der Vergleich. Anat. vi. p. 60.

‡ Règne Animal, nouvelle edit., Mollusques, pl. 74. fig. 2 a.

§ Anatomy of the Invertebrata, translated by Burnett, p. 211.

|| The excellent papers of Messrs. Alder and Hancock, to which repeated reference is made in the text, will be found in various Numbers of the 'Annals and Magazine of Natural History' for the years 1852 and 1853. To the attentive perusal of these valuable essays the student of the subject is earnestly advised.



but these are all that have come under my observation\*." In each of these "modifications" one common character is said to prevail—the vessels *reticulate*—in the first only "slightly," in the others more "minutely." Such is the structural law of the branchiæ of the Lamellibranchiata as expounded by Mr. Hancock. It is at direct variance with the prevalent and accepted definition. Dr. Sharpey says—"Each gill (of *Mytilus*) or leaf consists of two layers, which are made up of vessels set very close to one another like the teeth of a comb or like parallel bars, &c.†" "These bars are connected laterally with the adjacent ones of the same layer at short intervals by round projections on their sides," &c.‡

Here this accurate observer conspicuously indicates the difference between the solid projections interposed between the vascular bands, tying them together into a horizontal lamina, and the "transverse plicæ" of Mr. Hancock, which transform a matchless system of parallel bars into one of "minute reticulation" (Hancock), which neither the eye nor the understanding can unravel. M. Deshayes§ stands in this anomalous position:—he has figured accurately what he has interpreted wrongly. Albeit to this author merit is due. He has pointed out clearly by the pencil—what really exists in nature; what he himself misunderstood; what neither Dr. Sharpey nor Mr. Hancock seem at any time to have recognized—a structure without which the gill of the Lamellibranch could not architecturally be what it is; a marvellously woven fabric, refined in the utmost degree in its mechanism, adapted with incomparable skill to the purpose in view—a structure which no observer either anterior or posterior to the time of M. Deshayes has even suspected to exist—that apparatus of transverse scaffolding (Pl. VI. fig. 1 *c, c, d*) situated between the lamellæ of the gill, crossing at right angles the axes of the interlamellar water-tubes, *j, j* (of the existence of which M. Deshayes had not the slightest knowledge), and doubtfully described by him as the true *blood-channels* of the branchiæ! M. Deshayes mistook the laminæ formed by the real branchial vessels for "*membranous layers or laminæ, within the substance of which the branchial vessels are arranged with great regularity.*" His eye caught with correctness nearly *all the parts* of this exquisite apparatus; his reasoning then enveloped them in

\* Annals and Magazine of Natural History for April 1853.

† Art. "Cilia," Cyclop. of Anat. and Phys.

‡ This concise description is rendered still clearer by the original figures which accompany the famed article of Dr. Sharpey, to which I have adverted in the text.

§ See art. "Conchifera," Cyclop. of Anat. and Phys.



confusion\*. Nothing less than a *rediscovery* of these skeletal parts, by which the branchial vessels are maintained *in situ* and the whole tubular system preserved in shape, could suffice to render complete and consistent the demonstration of the anatomy of the Lamellibranchiate gills.

With the eye stedfastly fixed on these parts, it is surprising that M. Deshayes could see in them no meaning, could read in them no purpose. In defining the outline and office of the inter-lamellar water-tubes, it is matter of wonder that Mr. Hancock did not suspect the mechanical *necessity* for a supporting apparatus such as this, without which the water-tubes could not sustain their patency or their form. Such is the history of progress in all the manifold paths of scientific observation. Discovery must literally be *prefigured* in the intellect of the thinking observer. In the absence of the foreshadowing conception, wondrous things in nature rendered manifest by accident are vacantly gazed at, left unfathomed, and then forgotten, or mentioned only as incidents or episodes in the drama. The merit which belongs to rediscovery is too often withheld from its author. It is morally, in equity, not less worthy of honour than the first discovery.

The law was formerly stated that the blood-channels in the gills of the Lamellibranchiate mollusks occur always in every species in form of straight, parallel, independent, non-communicating tubes, supported on the two opposite sides by hyaline cartilages, generally membraniform and semicylindrically curved (Pl. VI. figs. 6 & 6<sup>2</sup>; and Pl. VII. fig. 15). These blood-channels never reticulate. At the free border of the gill the afferent channel returns into the efferent in a looping manner (Pl. VI. fig. 1 *e, f*). The efferent like the afferent channel preserves its individuality from one border of the lamella to the other (*m, e*). The blood-current, therefore, preserves unmixedly its singularity and independence from the beginning to the end of its branchial orbit (Pl. VIII. figs. 23 & 24). This is a striking and remarkable characteristic. It is a molluscan peculiarity. Its prevalence in this class is universal. It stands in contrast with the crustacean. The network plan is here the type. In some species of Annelids the branchial vessels observe a straight, parallel, looping mode of division. In the Annelid the blood is coloured and non-corpuseular. In the mollusk it is replete with globules. The blood-globules travel through the branchial 'bars' in a single series, or two abreast. In the crustacean the blood-channels are imparietal sinuses. In the mollusk each

\* The reader is requested to refer to fig. 352, article "Conchifera," in the first volume of the 'Cyclopædia of Anatomy and Physiology.'



vessel is elaborately carved and wonderfully protected (Pl. VI. figs. 6 & 6<sup>2</sup>). The difference is as essential in kind as it is conspicuous: it may serve hereafter to establish the true direction of equivocal affinities. Subtle analogies, like deeply hidden differences concealed amid the profoundest recesses of the organism, are often more conclusive in disputative questions of specific and generic relationships, than diversities or resemblances graven prominently in the manner of the outward form.

In now entering upon the narrative of the minute structure of the gills in the conchiferous mollusks, it must be premised that illustrative types only can be comprehended in the story. Specific varieties and modifications must be left to the specific inquiries of individual observers. There prevails, however, such a remarkable uniformity in the architectural principle on which the breathing organs in all Lamellibranchiate mollusks are constructed, that departures from the central plan never involve a change of type. Such variations are apparent, not radical. Though a concise description, aided by illustrations, may enable the author to convey a readily intelligible statement of these parts, the reader must not infer that his task has been easy or his labour light. He has traversed dark and tangled controversies. For long he could pilot his course by the magnetism of no clearly-defined principle. Evidence conflicted, assertions bewildered; the subject was intricate, the clue of *principle* was wanting. He would fain trust that the history which he is about to write will transform a pre-existing chaos into the cultivated scene of exact demonstration.

The minute structure of the gills in the Conchifera may be conveniently described under the heads severally of the constituent parts of which they are formed.

1. The parallel bars or vessels forming the lamellæ.
2. The borders of the lamellæ, (*a*) attached, (*b*) free.
3. The transverse connective parts—intervascular, or inter-  
vactal.
4. The interlamellar water-tubes and the *intra-tubular frame-  
work* of support.
5. The ciliary system of the gills.

1. In the Acephalous mollusk the branchial vessel is sculptured upon one essential plan. All deviations from this plan are inessential varieties. So singularly do these blood-canals differ from ordinary blood-vessels, that they will be henceforth described under the name of "*branchial bars*." The word 'bar' implies, first, straightness, and secondly, rigidity, two properties which belong to the branchial bars. The word 'bar' involves the idea of separateness, individuality and independence—characters which apply to the branchial bars. Rigid bars arranged



in parallel directions on the same horizontal plane would form a *stratum of bars*—such is the branchial lamella. Disposed on two coincident planes, one above the other, two parallel lamellæ would result. Between parallelly-arranged rigid bars the *interspaces* would be parallel and equal—such are the *intervectoral*\* water-passages of the branchiæ. If traversed by cross threads at frequent intervals, a long fissure would assume the form of oblong foramina (Pl. VI. fig. 1 *g*, fig. 2 *e*). Such sometimes are the varieties which occur in the intervectoral passages. If the parallel lamellæ be tied together at regular points by bands running with the bars, the space between the lamellæ would be divided into tubes. Thus are formed the interlamellar water-tubes (figs. 7, 9). The picture is faithful to nature. It mirrors the reality of a complex apparatus. It represents in simple outline the machinery of the branchiæ in the bivalve mollusk.

The details are now neither intricate nor unintelligible, because the *constructive idea* is clear to the intellect. In all investigations a tangibly-grasped *mental* picture must forerun the clear perception of the outward reality.

A branchial bar is a *tube* whose sides are comparatively rigid, and whose diameter is uniform (Pl. VI. fig. 6 *a, a*). It is clothed externally by a membrane, the continuation of the mantle, of which the epithelium is evolved at certain regular lines into cilia-bearing scales (*b*). The opposed sides of each bar are formed of, and supported by, cartilages (*a, a*). If these two cartilages were far removed apart, the blood-channel would be broad and flat (Pl. VII. fig. 15 *b, b, b*). These cartilages are slender in the extreme in texture; they are membraniform and exquisitely hyaline; curved at the edges, they assume the figure of a hollow semicylinder; they possess just enough rigidity to preserve the straightness of the bar; they are *continuous* throughout the whole length of the bar (Pl. VIII. fig. 17). Being placed on the opposed horizontal sides of the bars (not on the upper and under aspects), they must necessarily circumscribe a tubular channel of unbroken continuity. The sides are not perforated by openings of any description. If the transverse structures (Pl. VIII. fig. 22 *a*), afterwards to be described, be *vessels* or blood-channels, as conceived by Mr. Hancock and some of the elder anatomists, the bore of such channels cannot communicate with that of the parallel bars. The transverse parts must therefore, if they be blood-channels at all, constitute an independent system. But they are *not* so. They are con-

\* From the Latin *vectoris*, a bar. Since it is proposed to distinguish the branchial blood-channels under the name of bars, it is only consistent to mark the spaces between them as *intervectoral*, rather than as *intervascular*.



nective fibrous structures (Pl. VIII. fig. 19). In almost all species of bivalve mollusks, the branchial bars more or less closely approach the cylindrical in figure. To this rule of structure those of the common Mussel form a remarkable exception: they are here blade-shaped (figs. 17 & 20). The section of the bar is frequently oval. In the genera *Cardium*, *Unio*, *Ostrea*, &c. this form is exemplified. The subcylindrical canal, circumscribed by the hyaline cartilages just described, is the true blood-channel\*. All naturalists have conjectured this fact; the existence is now only for the first time *proved*. The cartilages bounding these channels are now first announced. They do not enclose the whole circumference of the vessel: they form a third of the opposite halves (Pl. VI. fig. 6<sup>2</sup>). The rows of cilia correspond with their edges: the intervals between these edges are membranous. The real osmotic movement of the gases concerned in respiration is limited to these intervals. Along these intervals, extending with beautiful regularity from one end of the bar to the other, there travels a cilia-driven current. In *Mytilus* the bars appear to swell (Pl. VIII. fig. 17 *o, o, o*) at the points at which they are joined together by the transverse structures. The real blood-channel does not bulge. The cartilages of the bars at the base of the lamella are lost in and identified with that embracing the trunk common to the whole series (*c, c*). Traced carefully to the proximal border, they will be observed to have this disposition: the cartilages of contiguous sides of *adjoining* bars form one piece, being so bent as to become continuous at the proximal border of the lamella. The bars are thus held firmly *in situ* and in relative connexion.

At this point it becomes extremely interesting to inquire, whether the *lamella* is composed of a single series (Pl. VI. fig. 4), laid side by side, of parallel bars, or of a double series arranged in two separate planes? (fig. 5). The answer to this question will implicate an important point of function. It is difficult to convey clearly the idea of a double series of bars constituting a *single* lamella. This undoubtedly is the disposi-

\* A very recent study of the minute structure of the gills in the Tunicates and Ascidians has enabled me to resolve completely the homology of the *branchial bars* in the bivalve mollusks, to explain demonstratively why it is that in the gills of some Acephalans the blood-conduits are placed like membranous channels between *alternate bars* (as is shown in Pl. VII. fig. 15, *b, b, b*), and that in others the blood-canal (as in Pl. VIII. fig. 22) occupies the *axis* of each bar. Though there exist in the gills of the Tunicata a system of large *transverse* trunks, with which the *parallel* ultimate blood-channels (the homologues of the "bars" in the Acephala) openly communicate, in a *supplementary note on this subject* in the next paper, it will be shown that the ultimate elements of the branchiæ in Tunicata and Acephala are really arranged on the same type.



tion of the branchial bars in some species of Acepala. If a "bar" be bent once upon itself (fig. 3), and if then one limb only be rested upon a flat surface, the other limb will be on the same vertical plane, but on a different horizontal plane. If a second, then a third bar, and so on, be placed in coincident directions, the limbs will form two horizontal series or laminæ, between which a free undivided horizontal space will exist (*e, f*); but there will also exist vertical spaces between each two adjoining bars having the same vertical planes. In words this arrangement is complex, in illustration simple. Now it may at first be supposed that of mechanical necessity this must be the order in which the bars are arranged in all the examples of double gills\* (Pl. VI. figs. 1 & 7), as it is really that in which the afferent and efferent limbs of the same looped bar are disposed in all instances, without exception, of *single* (Pl. VI. fig. 2) gills. But it is truly the case only in a very few genera. It is so in the Mytilidæ (Pl. VIII. fig. 24). It follows that under the latter circumstances the interlamellar water-tubes must be bounded by two concentric walls (Pl. VI. fig. 5), each wall being composed of a single horizontal series of bars. Of this disposition another apparent example is afforded in the Ostreadæ; if the disposition of the loops at the free margin *only* be considered. In nearly *all* other genera, known to the author, the limbs of the same looped bar are placed on the same horizontal plane (Pl. VI. fig. 7 *f*). The plane of the loop notwithstanding at the distal border of the lamella is not horizontal, but vertical. It results that each lamella is composed of a single series of bars, though the contiguous limbs alternate in function, one conveying a centripetal, the other a centrifugal current (Pl. VII. figs. 9 & 11). But it must be remembered that a single lamella (*a* or *b*, Pl. VII. fig. 11) of a double gill is not the exact equivalent of an entire single gill (fig. 14). In *all* single gills the limbs of the same bar rest on vertical planes; those of a single lamella of a double gill are placed on the same horizontal plane (fig. 12). In the single gill the physical conditions are more favourable to the complete aëration of the blood. The water-currents are different, not the same. It will greatly facilitate the comprehension of the preceding history if now *the minute anatomy of the free or distal borders of the branchial lamella be carefully and accurately studied*.

The structure of the extreme free edge of the lamella furnishes a ready key which unlocks at once the whole mystery of the branchial apparatus; and yet this wondrous part of the organ

\* The meaning attached in these papers to the *double* as opposed to the *single* gill is afterwards explained.



has never arrested the curiosity of the anatomist. In *Mytilus*, and in *Mytilus* only, Dr. Sharpey figures correctly the manner in which, at the distal margin of the lamella, the bars of the upper become continuous with those of the lower lamella. In *Mytilus* the structure of the gill is almost unique (Pl. VIII. fig. 17). The order which obtains in nearly all other genera could not be deduced from the anatomy of the Mytilidan gill. It is a singular exception. It is the rare exception only that Dr. Sharpey has pictured. The rule of structure remained really to be discovered. If the blunt and acute edges of the penknife-shaped branchial bar (fig. 20) carry each a blood-channel, then each gill in *Mytilus* will be a double gill, for the upper and lower are identically formed. If, on the contrary, the blood-channel exists only at the blunt edge (*a*) of the blade, the current travelling peripherally along the bars of the upper lamella (A, fig. 17) must turn round (as shown in fig. 24 *d, d*) at the free margin through the loop and move centrally along the bars of the lower lamella (B, fig. 17). In the latter case the gill would be single, in the former double. The bars of the upper lamella when the gill is single carry currents moving in the same direction (Pl. VI. fig. 2; Pl. VII. fig. 14) from one border of the gill-plate to the other; those of the lower, oppositely tending currents (Pl. VIII. fig. 23 *e, f*). This point is the wonder-striking feature of the branchial enginery. No writer has ever given to it a single thought. It deserves to be further elucidated. In *Pholas* (Pl. VI. figs. 1 & 2), *Gastrochaena*, *Mya*, *Tellina*, *Mactra*, *Cypraea*, *Cardium* (Pl. VII. figs. 13 & 14), *Ostrea* (Pl. VIII. fig. 21), and probably in many other genera, the inner gill is *double* and the outer is *single*. The Pandoridæ and Lucinidæ are families in which the outer gill is altogether suppressed. In *Solen*, *Pecten*, *Unio*, *Venus*, *Kellia*, *Arca*, &c., the two gills on both sides are equal in size and *double* in structure.

Every gill-plate, whether single or double, is composed of two lamellæ, between which the excurrent water-tubes (see large arrows in Pl. VII. fig. 13, Pl. VI. fig. 1, and figs. 7 & 8) are situated. In the example of the double gill *each lamella* is the scene of a double system of opposed currents of blood, since the two limbs of the same looped bar lie on the same horizontal plane in the same lamella (Pl. VII. fig. 9 *c*). The adjoining limbs are thus alternately afferent and efferent, or venous and arterial. *Each lamella* then of every double gill is a complete and independent gill. Its system of circulation is distinct, and totally unconnected with that of the other lamella. Nevertheless, a single lamella of a double gill is not identical in anatomical characters, or structurally, or perhaps officially, equi-



valent to an entire single gill. As formerly intimated in the example of a single gill, the limbs of the same looped bar, respectively venous and arterial, are placed on different horizontal planes (Pl. VII. fig. 14), the planes of the *loops* (*a*) at the free margin being vertical, and not horizontal as they are in general in the double gill (Pl. VI. fig. 1 ; Pl. VII. figs. 9 & 11). The single gill, like the double, is composed of two lamellar planes (fig. 14 *b, c*) bounding intermediate water-tubes. But in the single gill each lamella is single in function, since it consists of the afferent or efferent limbs separately and exclusively of the looped bars. In either lamella therefore the adjacent bars belong to separate and independent loops. The component bars of the lamellæ in all single gills are separated from one another by intervectal water-fissures (Pl. VII. fig. 15 *c, c, c*). In the double gills in which the two limbs of the same loop lie adjoined on the same horizontal plane, such limbs are united together by a *continuous membrane* (Pl. VI. fig. 5). In such case the intervectal water-fissures exist only between the limbs of different contiguous loops, not between those of the same looped bar. By this arrangement the volume of water which traverses the gill at any given time is reduced by exactly one-half. The functional value of the organ therefore sinks in the same degree. A *double* gill (Pl. VII. figs. 13, 9 & 11 ; Pl. VI. fig. 1) in structure is not necessarily twofold in physiological import. In official activity it exceeds little the single gill. In the latter the blood is more intimately brought into contact with the respiratory medium, and this medium is more readily and rapidly renewed. To the single gill (Pl. VI. fig. 2 ; Pl. VII. fig. 14) conchologists have applied the term *supplementary*. It is difficult to understand in what sense this term should be received. In *structure* the single gill is *not* supplementary. It is a perfect and complete organ. No constituent element is deficient or suppressed. In *function* it is complete. It is not a supernumerary organ. Both these designations are significant of what is untrue. It is as much an integer of the organism as the upper or inner gill. A *law* hitherto undiscovered does, however, affect the presence and dimensions of the outer or single gill which does not influence the inner or double gill. If, as in the Pandoridæ, Lucinidæ, and some other families, there exist only one gill, it is invariably the single or out-gill that is wanting. The principle of suppression or non-development affects exclusively the latter. When only one gill exists, that is, one on either side of the foot and body, it is always *double* in structure. It contains the same number of bars and loops as any other double gill. It is quite erroneous to conceive that in such a case the absent or suppressed gill has been fused into and iden-



tified with the present solitary gill. The latter is the same in essential structure as if the single gill were present.

In *Pholadomya* and *Anatina*, Professor Owen describes the two branchial lamellæ of either side as having been united to form a single gill\*. Valenciennes states that the solitary gill of the family Lucinidæ resembles that of *Anodonta*; it is larger, and formed of thicker and more prominent pectinations. *Lucina Jamaicensis*, *L. tigrina*, *L. columbella*, and *L. lactea*, are examples in which only a single branchial organ exists on either side. The solitary gill differs from the ordinary double gill only in *apparent* characters. The free border is composed only of two rows of loops; but these loops are soldered together by an obvious longitudinal band or cord, running in shape of a deep water-groove from one end to the other of the free margin (Pl. VI. fig. 3 *b*). It is this character which occasions the appearance of doubleness and fusion. In the solitary gill of the Pandoridæ and Lucinidæ, the pectinations† of the lamellæ are coarse and large to the naked eye. This circumstance is due to the greater size in these cases of the interlamellar water-tubes. It is repeated, that the vascular elements, in the solitary gills, are the same in number and disposition with those of any other double gill. If, in the example of the solitary gill, the outer single gill were really organically united to the inner double gill, an organ should result consisting at the free border of *three* rows of vascular loops, *two* distinct systems of parallel interlamellar water-tubes, *four* separate lamellæ, *three* layers of afferent and *three* of efferent bars! Such, of mechanical necessity, should be the anatomical characters of a gill which owed its formation to the union of one already double to another struck on the single plan. Such a monstrosity is not illustrated in nature. It is a fabulous branchia, born of hypothesis. But it *may appear* quite reasonable to explain the anomaly of a solitary gill, on the supposition that it is the natural and necessary product of the fusion of two *single* gills. A glance at the illustrations depictive of the type of the latter, will at once convince the mechanician that two single gills could not in any manner be fused in order to make a double gill,—such a double gill, that is, duplex in mechanism, twofold in function, as actually exists in the real animal. Let two single gills be brought together (Pl. VI. figs. 7 & 8),—the water-movement and the ciliary action would cease at once on the two adjoined, apposed faces. Thus the power of each would be reduced by one-half. Two singles united make a single! Such is the clumsiness of human handi-

\* Forbes and Hanley, British Mollusca, vol. ii. p. 42.

† It should be distinctly understood, that the word '*pectinations*' is not synonymous with an ultimate branchial bar, but with that *set* of bars which form an interlamellar water-tube.



craft: attempting to mimic nature, it is lost in caricature. Nature does not reach her ends by the "fusion" of organs. An existing organ is *modified* to fulfil a collateral purpose. A solitary gill has its own peculiar characters. The component vessels remaining unchanged in number and arrangement, a solitary organ is rendered equivalent to a double one, by augmenting the dimensions of the passages and tubes in such a manner, that the aërating element brought into relation with the blood can be increased almost to any amount. *Function* is thus intensified, while structure remains unaltered.

The *loops of the vascular bars*, as they project at the free margin of the lamellæ, are differently joined and variously figured and sculptured in different genera, and frequently in different species of the same genus. In *Pholas* (Pl. VI. figs. 1 & 4), the free border of the double or inner gill presents two rows of loops (*e, f*). The plane on which the loops of the upper lamella rest is horizontal, coinciding with the *length*, as opposed to the *breadth*, of the gill. Those belonging to the lower lamella of the same gill, form a row on a plane an eighth of an inch below the former. Between these two projecting scalloped edges, a groove (fig. 3 *b*) runs from one end of the gill to the other. The cilia which fringe this groove (Pl. VIII. fig. 24 *h*; Pl. VII. fig. 10, *a, b*) are very much larger in all species than those which are distributed over the bars at the plane faces of the gills. They excite a vigorous current, bearing towards the mouth. Those of the flat surface (Pl. VIII. fig. 20; Pl. VI. fig. 6 *b, b*) raise streams, tending towards the free border of the gill. Both are subservient to alimentation and respiration. In *Pholas*, then, the double gill (Pl. VI. fig. 1) is composed only of two lamellæ, like the single gill (Pl. VI. fig. 2); but in the former, each lamella is composed of two orders of bars, in the latter of one order only. The two limbs (fig. 4 *b, b, c, c*) of each looped bar in the former are placed on the *same* side of the intermediate water-tube: the afferent and efferent limbs of the same bars (fig. 2 *h, f*), in the instance of the single gill, are so *opened* or separated at the free margin as to form respectively the *opposite* walls of the included water-tube. The vascular *loops* at the margin of the double gill in nearly all genera are disposed flatwise (Pl. VI. fig. 1 *e, f*; Pl. VIII. fig. 21 *c, b*; Pl. VII. fig. 9 *a, b*, fig. 11 *a, b*), so that all the loops of the same lamella form one horizontal plane. Those of the single gill (Pl. VII. fig. 14 *a*; Pl. VI. fig. 2) are placed vertically, so that the plane of each loop is separated from, though parallel with, that of the adjoining loops. In the double gills of the *Cardiadae* an exception occurs, and probably in other families. The loops at the distal margin are disposed here on vertical planes (Pl. VII. fig. 14 *a*); but though standing verti-



cally, they do not enclose two systems of interlamellar water-tubes, but only *one*. The *mechanical* problem presented by the gills of *Cardium* proved extremely difficult of solution. *When understood*, it challenged any living mechanism for beauty and perfection. In *Mytilus* the loops of the two lamellæ are soldered into union at the free borders: they stand vertically (Pl. VIII. figs. 17 & 24): they circumscribe a deep intermediate gutter. In *Solen* (Pl. VIII. fig. 23) the loops expand. In *Venus* they also somewhat exceed in diameter that of the bars, of which they are *the bend*. In *Mytilus*, the inner and outer gills exhibit the same formation. In the *Ostreadæ* (Pl. VIII. fig. 21), the loops at the margins of the gills are so closely packed together horizontally, as to appear like a continuous membrane bounding an angular groove. Numerous other varieties in the mere shape and size of the loops occur in different families of Bivalves—the *type* of structure never changes.

*The proximal or attached border* (Pl. VI. figs. 1 & 2 *a, b*) of the gills occurs under many varieties of anatomical plan. *Pholas* exemplifies one type. The two lamellæ\* are attached to the pallial tunic. All the vascular bars terminate in a common trunk (Pl. VI. fig. 2 *a, b*) which runs at right angles to their axes, and parallel with the length of the entire gill. There are two of these trunks, one afferent, the other efferent. They occupy respectively the proximal margins (Pl. VI. fig. 1 *a, b*) of the two lamellæ of which each gill is composed. In *Pholas* these trunks are supported by the framework of *solid* structure (*c c* and *d d*) which occupies the interlamellar spaces. In *Solen* (Pl. VIII. fig. 23 *a*) and *Mytilus* (fig. 17 *A*) another plan of formation is observed. Here the proximal border of the superior lamella of the upper gill, and inferior lamella of the under gill, are *unattached*, floating in the mantual cavity. In such instances the interlamellar framework is wanting. The vascular bars at this border, for some distance up the breadth of the gill, are tied together by means of a *continuous* membrane (*e, e*). Here the interlamellar scaffolding, and the water-tubes which the former assist to form, exist only where the two lamellæ are adherent; viz. over the two-thirds of the breadth of the gill nearest the free border.

\* It should be clearly explained that the word *lamella*, as applied to the gill of the Acephalan Mollusk, should signify, *one* of the two plates of which the gill, whether double or single, is composed. The gill is the whole organ. In those instances in which (as shown in fig. 5, Pl. VI.) the bars stand vertically on the same lamella, then of course each lamella would be composed of two plates, or finer lamellæ. I am not quite certain that such an arrangement exists in nature. In several genera—in *Cardium* especially—when care is taken to avoid *pressure* upon the margin, such is the true position of the loops, if not of the bars proceeding backwards from them.



*Intervectoral and Interlamellar Framework of Connective Structures.*

These structures constitute the true skeleton by which is sustained the vascular fabric of the gill. Of the latter, they determine the shape and the form. They preserve the blood-carrying bars in position. They hold apart the component lamellæ of the gills. They thus form the interlamellar tubes, since without these structures the lamellæ would fall together into contact and obliterate the tubes. Messrs. Alder and Hancock recognized the tubes, but overlooked the framework system by which they were constructed\*. M. Deshayes has figured this framework (Pl. VI. fig. 1 *c, c, c* & *d*, fig. 2 *i*, and fig. 8 *d, d*) apparatus in a conchiferous (*Pecten* or *Arca*?) mollusk. Not a sentence is written descriptive of its characters, or interpretative of its meaning†. Attention was drawn to it by no allusion whatever, direct or incidental. Philippi‡ has this observation with respect to the branchiæ of *Solenomya*, which probably refers to the interlamellar structures in question:—"Branchiæ duo non quatuor, non lamelliformes, sed pectinatæ vel potius pennam exacte referentes, lamellis transversis perpendicularibus, carina media corpori per totam longitudinem adnatæ, versus apicem ope ligamenti." Ill-defined reference to the same parts is made by Carus, Blainville, Garner, and others. To be known descriptively, and comprehended physiologically, they remained really to be rediscovered,—to be read by a new eye, from

\* It is very probable, from the following passage, that Messrs. Alder and Hancock have mistaken the thick solid cords which at short intervals cross the tubes, for real blood-channels: "The laminæ forming the walls of these tubes were now examined through the microscope, when the whole was observed to present a regularly reticulated structure composed of blood-vessels; those passing transversely being the stronger and more prominent."—Annals and Magazine of Natural History, paper on Currents in *Pholas* and *Mya*, 1852.

† The following is the only passage which occurs in the excellent article (Conchifera, Cyclop. Anat. Phys.) of M. Deshayes having reference to the structure of the gills:—"In the greater number of genera, the branchiæ are formed of two membranous layers or laminæ (*a, b*, fig. 352), within the substance of which the branchial vessels descend with great regularity. In several genera, as the *Archidæ* and *Pecten*, the branchial vessels, instead of being connected parallel to one another within the thickness of a common membrane, continue unconnected their entire length, and they are thus formed of a great number of extremely delicate filaments, attached by the base within the membranous pedicle on which the branchial veins pursue their way towards the auricle." Nothing is said of the distinct and independent structures which separate the laminæ. The condition, namely the separation of the laminæ—upon which depends the existence of the interlamellar water-tubes—is here accidentally stated; but neither the existence nor the meaning of such parts seem in the slightest degree to have been imagined by M. Deshayes.

‡ Moll. Sicil. i. p. 16.



a new point of view. The author believes that the following is the first systematic exposition on record of the anatomy and significance of the *non-vascular* elements of the lamellibranchiate gill.

They are classifiable under two heads. Those parts which are placed between (Pl. VI. fig. 1 *g*, fig. 2 *e*, fig. 8 *d*; Pl. VIII. fig. 19 *c, c, c*) the parallel bars (*the intervectal*), uniting them into the form of a leaf, constitute a separate order. Those, *secondly*, stronger, coarser, in some genera very conspicuous, in others very concealed, which separate the lamellæ, forming and bounding the excurrent interlamellar water-tubes, to which in many species the ova adhere, the basis of the whole gill, the wonder of the whole enginery, the last of the branchial constituents to be described and understood, are really a distinct and unknown class of structures.

The first class vary the apparent anatomy of the gill more than the second. They cut the fissural spaces (Pl. VI. fig. 7 *d*) between the individual bars, or individual loops, into oval stigmata (fig. 5 *d*), elliptical perforations, or lengthened parallelograms (Pl. VII. fig. 12 *d*). In the absence of them, as in *Thracia* (Pl. VII. fig. 15), the intervectal water-fissures are continuous from the free margin of the gill to the proximal. In *Mytilus* (Pl. VIII. fig. 17 *o, o, o*) they appear under the character of fleshy nodules; in *Cardium* (Pl. VII. fig. 12 *c, c, c*) they are almost invisible; in the Veneridæ they consist of a flattened bundle of slender threads, running from bar to bar at equal intervals; in *Pholas* they assume almost a membranous form (Pl. VI. fig. 4 *e*), perforated at regular distances by oval holes; they exist only between alternate loops. In a physiological sense, the highest value attaches to these intervectal parts. They determine the dimensions of the water-stigmata. If they are small, the water of respiration is very much subdivided; if large, the lamella is readily traversed by the aërating element. In calculating the quantum of respiration in the Conchifera, *two factors* demand to be estimated: first, the amount of blood entering the breathing organ; secondly, the volume of water by which, in a given time, it is capable of being traversed. The latter will depend upon the dimensions of the water-passages.

The intervectal connective structures have been mistaken for half a century by the best observers for *vessels, blood-canals crossing the bars*,—deceiving the observers into the idea that each lamella in the lamellibranchiate gill is really composed of a *network of blood-vessels*. This idea as regards the Acephala involves a fundamental error; it envelopes everything in unresolvable confusion. The orbit of the branchial circulation cannot be explained. It contradicts the anatomical arrangement conspicuous in other parts. A consistent sentiment cannot be shaped of this



most perfect mechanism. They are *not* blood-channels. They are elastic, fibrous structures, enacting a purely ligamentous part. They derive their supply of blood from that of the branchial bars. Their office is mechanical, not chemical.

The *intra-tubular structures* (Pl. VI. fig. 1 *k, k, k*, fig. 8 *d, d*; Pl. VIII. fig. 21 *f*, &c.) are neither less remarkable nor less important. Upon this interlamellar framework depend the whole characters of the gill. They hold the lamellæ apart at *definite* distances. They unite closely together the loops of these lamellæ at the free margin (Pl. VI. fig. 7 *a, b*); thus they *close up* cæcally the tubes at this border of the gill\*. This single point of structure is the pivot whereon turns the action of the gill. If the tubes at this extremity were open (as suppositionally at Pl. VII. figs. 9 & 11), it is hydraulically certain that the water would take this course to pass from the extra- to the intra-branchial cavity; none would pass between the bars which contain the blood; the function of respiration could not proceed; and this calamity, further, would ensue—no food could be carried to the mouth. Men do not value health until it is lost! Spectators see not, *feel* not, the perfection, the unimprovableness of organic mechanism until an element is ideally removed—until some deviation from nature's method of working is *supposed*! The *argumentum ad absurdum* startles by the bungle and foolery which it is sure to introduce; *then* philosophers realize the inimitableness of her certainty and refinement.

As the proximal borders of the lamellæ (Pl. VI. fig. 1 *a, b*) are separated by the whole diameter of the water-tubes, and as the distal margins are fused together, it follows that these tubes, like rivers, are small and shallow at their commencement, deep and broad at their termination. This arrangement favours their *suctorial* action. The water, as first explained by Mr. Hancock, is undoubtedly *drawn into* (properly *pushed* into) these tubes through the lamellar stigmata (Pl. VIII. fig. 17 *f, f, f*) from the pallial cavity. The water is discharged from the tubes by ciliary agency, which is constant (arrows in Pl. VII. figs. 9, 11, 13 & 14). They are thus constantly being emptied. If they were not refilled from without, they would become *vacuous*. During the action of the gill, there is momentarily generated a tendency to a *vacuum*. The pressure that is on the tubular side of the

\* In the accompanying illustrations, in several instances (Pl. VII. fig. 9 & 11, Pl. VIII. fig. 21), these tubes are represented as if they were *open* at this margin of the gill. This method of illustration was adopted only for the sake of clearness, and in order that the disposition of the loops and bars of each lamella may be readily understood. In all cases, without a single exception, the tubes are *closed* at this border of the gill by the apposition of the loops of the two constituent lamellæ.



lamella is diminished; on the other it remains the same as long as the animal continues in the water. It is hydraulically inevitable, even *without* the assisting agency of cilia, that the water must transude the lamella by way of its intervectal fissures and perforations. This mechanism could neither be conceived nor explained before the nature and office of the interlamellar framework were brought under clear demonstration. It is important to understand, that that surface of the lamellæ which faces the intermediate tubes, namely the *internal* walls (Pl. VI. fig. 8 *e*) of the water-tubes themselves, is far less richly ciliated than the external surface. The excurrent movement of the respiratory water is much aided by the action of the connective structures of the bars and tubes. The intervectal pieces—those which pass crosswise from bar to bar by approximating the latter—are capable of stopping up the intervectal stigmata,—of suspending, therefore, the act of respiration. Thus is prevented the passage of irritating substances through the branchial lamella. The alternate movements of the shutting and opening of the bars are as important to the sieving operation of the gill, its prehensile function, as the cilia themselves. The transverse intervectal pieces (Pl. VII. fig. 12 *c, c, c*; Pl. VIII. fig. 19 *c, c, c*) consist of irritable and contractile tissue. They are capable, in part, of voluntary contraction. Thus, although the chemical act of breathing is in itself uncontrollable, it may be interrupted by the exercise of those connected parts which are subject to the will.

The skeleton of *solid* pieces (Pl. VI. fig. 8 *d, d*, fig. 1 *c, d*, fig. 2 *i, j*, &c.) by which the *tubes* and the *lamellæ* are supported and held apart, exists probably in the branchiæ of *every lamelli-branchiate mollusk*. It constitutes a framework system, though anatomically distinct from, having a mechanical action concurrent with, the intervectal. At the free border this interlamellar substance is thin, slender, and difficultly detected by the eye, admitting of the falling together of the lamellæ and of the closing of the tubes. At the opposite attached border, the interlamellar substance is much thicker, coarser, and more conspicuous (Pl. VI. fig. 1 *k, k, k*); the parts being quite apparent *through* the lamellæ. Here, therefore, the lamellæ are further separated, and the tubes of the greatest diameter. This framework consists of two distinct pieces,—those, first, which run parallel with the vascular bars (Pl. VI. fig. 1 *c*, fig. 2 *i*); and, secondly, those which transversely connect these longitudinal pieces (fig. 1 *d*, fig. 2 *j, j*). The former limit the breadth of the interlamellar water-tubes. The tubes are capacious when the lamellæ are far apart, small when they are near each other. As the exterior appearance of “pectinations” in the gill is due to



the presence of these tubes, the pectinations are obvious, as in *Cardium*, *Solen*, *Pecten*, *Thracia*, &c., when the tubes are large, invisible to the naked eye when they are small. The *cross pieces* tie together the longitudinal at regular intervals. The latter run with the tubes, and *divide them* from one another, the former cross them. If the transverse pieces were so thick and large as to fill up the tube, and interrupt its continuity, the excurrents of water of course would be arrested, and the function of the gill would be suspended. It is far otherwise. They traverse the tubes in form of cords. Their extremities are attached to the opposed points on the horizontal sides,—to those very lines along the sides of the tubes at which the chemical act of breathing is passive. From this arrangement there flows this most beautiful result: the water, having permeated the lamella and gained the *interior* of the tubes, in its course towards the excurrent siphon, is *made to keep continually in contact with the branchial bars*. By this simple arrangement, the *two* sides, in fact the four sides, of each individual blood-carrying bar are *persistently* embraced by a moving current of the respiratory element! If the cross cords did not exist, every drop of water which entered the tube would collect at the most depending side, and flow out as *a useless and unused stream*. In the œconomics of nature, the subtlest œconomist may well marvel at her care!

The long pieces of this interlamellar framework are capable of shortening the length of the water-tubes, the cross pieces of diminishing their diameters. These actions impel, interrupt, facilitate, &c. the breath-giving currents. While they complicate the branchial machinery, they double the certainty of the process; they provide against accidents; they preserve in the required position the slender, tender, beautiful parts of which the apparatus is composed.

Endless diversities occur, in different species and genera, in the size, the figure, the visibleness, &c. of this interlamellar framework. In no single instance is there observable the slightest departure in *principle* of structure, in intention, in purpose, from the typical plan unfolded in the preceding description.

The *cilia-bearing epithelium* (Pl. VI. fig. 6 *b*) of the branchial lamellæ in the conchiferous bivalves is well known. It has been well described by trustworthy observers, from Leeuwenhoek to Quekett. The cilia in all cases are distributed in rows on the bars (Pl. VII. fig. 15; Pl. VIII. figs. 20 & 22). There are two rows on each external hemi-cylinder of each bar. On the *external* aspect of each bar, therefore, there are four lines of cilia (Pl. VII. fig. 10 *b*, *a*). They drive two currents in intersecting directions. On the internal aspect of each bar, that namely which faces the



interlamellar water-tubes, these rows of cilia are single on the opposite sides. The excurrent streams are consequently driven by a power which is one-half in amount of that by which the water is propelled through the lamellæ into the tubes. No cilia are detectable on the supporting framework between the lamellæ. The current raised by the cilia which are distributed on the external surface of the lamellæ tends in the direction of the free border; that excited by the internally-placed cilia bears towards the proximal border, coinciding with the outlet of the interlamellar tubes. It is a true ciliary current; but it is reinforced, quickened from time to time, by the contractile, voluntary action of the musculo-fibrous parts which constitute the intervectal and interlamellar framework. The cilia which fringe the free border of the gill propel the water in the direction of the mouth, at right angles, consequently, with that raised by those covering the flat surfaces of the gill. It is an alimentary, not a respiratory current. It is powerful enough to bear on its waves pellets of food for the mouth. The true aërating currents travel along the *naked* lines between the rows of cilia. These are the ultimate scene of the respiratory process.

Thus ends an imperfect sketch. It is but a rude outline of a beautiful picture. Much is left to the industry of observers coming after the author. Magnetic thoughts, indicating the pole of truth, have been but hastily projected. May they stimulate others to a truth-admiring repetition of his labours!

#### *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 fulcrum 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 *Haliotis* 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, 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



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

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 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-



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 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 be-

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 *Firolöides* and *Atlanta*, the space between the integuments and the viscera is described by some observers as forming a constituent arc of the fluid-system.



tween 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

\* Comptes Rendus, 1843.



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 through 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 variations 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 laminæ 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 ingoing 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 *pinnae* 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.

*General and Minute Anatomy of Branchial Organs in the  
Gasteropod Mollusks.*

The author is not acquainted with any English or continental researches on the subject of the present paper. While the organs and the process of breathing in the Lamellibranchiate classes have engaged the study of various able observers, no special attention has at any time been given to the minute and ultimate anatomy of these parts in the higher Mollusca. General views can only securely rest on correctly ascertained particulars. The laws which govern the structure and functions of individual organs of animals may be discovered with far greater certainty by tracing the advancing phases of their histological elements throughout the zoological series, than by following the mutations which occur in the progress of their embryonic development in one class. Comparative anatomy is still very deficient in such information. The general anatomy of organs has been ably written: their histological anatomy remains untold. The information to be drawn from the serial history of any given structural element of any given complex organ is more calculated to illustrate the homology of that organ and the architectural design under which it has been built, than any knowledge which can be attained by a descriptive account of its mere general conformation. The inmost constituent of structure may display greater invariableness of character than external outlines and the gross configuration. It is only by such a serial history that that which is essential to an organ can be eliminated from those superadded and accessory parts which are separable and non-essential. For instance, it is quite certain (see a memoir on the Serial Histology of the Liver (under the title of the Physiology of Cells) by the author, in Guy's Hospital Reports for 1848), that the same idea of the liver cannot be acquired by tracing the stages through which the organ passes in the embryo of the mammal, as that which is obtained by exhibiting consecutive pictures of the form under which it occurs in the successive links of the animal chain. There is much that is deceptive and fallacious in general resemblances and leading



analogies. The ultimate and the particular must be seized before the comparison of general conditions can become correct and complete. How far-sought and really worthless it were to assert, that a single cell of the mammalian lung finds its counterpart, its prototype, in the membranous vesicle on the dermal surface of an *Asterias*, in which the process of respiration is carried on! In such an alleged analogy how many real deep differences are ignored! What a wide space is overleaped by simplicity and ignorance! How unsafe are generalities in science when unsupported by *ultimate* knowledge, by facts and details! On the other hand, how utterly valueless are figures, facts, and particulars, unless they form the substratum of *some* generality! To apply them to the maintenance of *any* theory invests them with life, renders them mutually coherent. Abandoned to themselves they may be likened to grains of sand, between which there is no cohesion. These few preliminary remarks are made, at once, in apology and explanation of the plan of investigation which the author has adopted in these papers. He has sought at the expense of great labour, and heavy cost in several senses, to amass such a store of minute facts as will constitute at another time the ground of an appeal in support of a wide generalization. With this explanation he will now proceed to complete the serial history of the organs of respiration in Invertebrate animals.

In a former paper it was stated, in relation to the gills of the Lamellibranchiata, that from the Tunicata to the highest mollusk of this class, there prevailed a unity of structure which acknowledged no single real exception. In every form of branchia the blood-channels were straight, parallel, and non-communicating; that at the free border of the gill they returned upon themselves in form of loops, and that thus the afferent layers of vessels became separate and distinct from the efferent; that whether these layers were two or four in number, the real architecture of the organ remained unchanged\*.

These fundamental facts will be found to pervade every variety

\* In the paper to which I refer, I promised to show that the apparently rectangularly-arranged blood-channels of the branchiæ of the Tunicata were not *real* exceptions to the rule stated. In a subsequent part of these memoirs, it will be proved beyond doubt that the ultimate vessels in the pharyngeal gills of these inferior mollusks are disposed in "parallel, straight, non-communicating order," and that the crossing which takes place between the larger and the smaller blood-channels is a mere appearance depending upon the mode in which the gill is folded in the cavity. It will then also be shown that the ultimate blood-vessels in the branchiæ of the Tunicata are bounded by hyaline cartilages which also define the channels, precisely in the same manner as is done by the corresponding cartilages in the gills of the higher Lamellibranchs.



of gill to be found among the higher class of the Gasteropod and Cephalopod Mollusca. In fact, wherever there is a separately developed branchia within the range of the Molluscan subkingdom, these principles of organic construction will receive an illustration. But between the Lamellibranchiate and Gasteropod gill, several important and striking differences exist. In the former the blood-channels are of large bore; they are capable of carrying a voluminous column of fluid: such a fact implies that in the organ of respiration in this class the fluids are not minutely multiplied and subdivided, and that consequently the contact between them and the external aërating medium is less intimate and complete. Another interesting fact to be noted is, that the corpuscles of the blood of the Lamellibranchiata are considerably larger\* than those of the blood of the Gasteropod and Cephalopod mollusks. This difference flows naturally from the greater diameter which the blood-vessels of the former present as compared with those of the latter. On another occasion and in another place, the author will show that the same differences of size distinguish the blood-corpuscles of the lower Crustacea from those of the higher. This is either the consequence or the cause of the disparities of calibre in the branchial vessels which occur in these two sections of the same classes. They are visible facts which bear most explanatively upon not only the morphyic, but upon the subtler organic and chemical differences which mark the nutritive fluids of a less highly organized animal from those of another of higher standard; for it scarcely admits of doubt that the *vital standard*, the nutritive value of any given animal fluid, bears a direct ratio to the numerical amount of its floating corpuscles. As in the animal scale followed upwards, the floating globules of the blood become smaller and smaller and more and more numerous, correlatively the circulating channels gradually decrease in sectional area, become more and more subdivided and multiplied, until at length in the higher mammals the bore of the ultimate capillary exceeds little the diameter of the individual blood-corpuscle. These general views will serve to impart meaning to the minute anatomical details which are now to follow.

The *Tubulibranchiate* genera, *Vermetus*, *Dentalium*, and *Magilus*, are commonly placed at the bottom of the Gasteropod scale. For this disposition no reason can be drawn from the position and general anatomy of the branchial cavity or from the structure of the gills. M. Philippi† gives a figure which the

\* The measurements upon which this general statement is based will be published in the next paper on the Blood in the 'British and Foreign Med.-Chir. Review.'

† Enumeratio Molluscorum Siciliæ; and Règne Animal, pl. 62.



author has copied (Pl. XI. fig. 1), in which the organs (*a* & *b*) contained in the respiratory chamber are clearly exhibited. The gills (*a*) are as perfectly pectinated, that is, they conform in figure and structure with those organs in the higher Gasteropods which are described as 'pectinate' gills\*. They occupy the same position in the branchial sac, that is, on the roof, and distant from the rectum (*b*). One border of the leaf is strengthened by a penknife-shaped cartilage, such as that which will be defined in the Pectinibranchiates. The breathing crypt in *Siliquaria anguina* is depicted by Philippi as having the same configuration. The branchiæ differ but triflingly from those of the former genus. By this observer, these parts are sufficiently clearly delineated in the two preceding Tubulibranchs to justify the inference that the branchiæ are formed precisely on the plan of those of the Pectinibranchiata. So similar to that of the latter order is the general cavity, so analogous the contained parts, so identical in structure the branchiæ, that it is difficult to conceive why *Vermetus* should be called a Tubulibranch, and *Buccinum* a Pectinibranch. In minute anatomy, the description which at another time will be given of the branchiæ of the latter will apply also to those of *Vermetus*. When species, whose vital organs are so similarly constructed, are placed at opposite extremes of an extended scale, the anatomist may well exclaim,—how artificial, partial, and arbitrary is the classification of the mere naturalist!

#### *The Branchiæ of the Chitonidæ.*

A *Chiton* has a carapace like an isopod Crustacean, a dorsal vessel like an Annelid, bilateral symmetrical reproductive viscera like an acephalous Mollusk, a head and foot like a patelloid Gasteropod, a posterior anus like the Fissurellidæ, and branchiæ like those of the brachyurous Crustacea! Such manifold affinities at once unite and sever this odd group from several most dissimilar classes. Measured by the standard of its branchial

\* The word 'pectinate,' as will be subsequently shown, is anything but descriptive of the real figure of the branchial laminæ of the Pectinibranchiata. To describe them as comb-like is to suggest a very false comparison. If the naturalist who first coined the word had isolated a *single* leaflet from the gill of a Pectinibranch and defined its *outline*, such a word never could have suggested itself. The same ridiculous disparity between the thing and the name will be found to occur in other designations of Orders. False titles like these—terms indeed constructed upon imperfect knowledge—illustrate the difficulty which must ever attend the attempt to establish a true and natural terminological system in zoology before the real structure of animals is made known. The mere naturalist can never find himself in a position to construct a consistent "terminology." This task, so important to the progress of knowledge, must be jointly undertaken by the philosophic anatomist and the descriptive naturalist.



organs alone, it deserves a higher rank than that accorded to it by the side of the Patellidæ. The anatomical position of these organs nevertheless allies the Chiton to the Patella. In both, they are placed in the furrow between the border of the foot and the edge of the mantle. But in structure they are totally unlike. Imagination may indeed construct ideal analogies. If a branchial cone (fig. 2) were placed on either side of the anal debouchure in *Chiton* and then simply enlarged without change of figure, the branchiæ of *Fissurella* (fig. 10) would be simulated. They are organically different from those of *Emarginula* (fig. 9) and *Patella* (fig. 5). In structural characters the gills of the last two genera bear the same relation to each other as that which subsists between those of *Chiton* and *Fissurella*. The ultimate respiratory laminæ in the last two are bilateral, resting, that is, on either surface of a common axial plane. In *Emarginula* and *Patella* they rise from one surface only of a common basis. In *Patella* that basis is fixed, in *Emarginula* it is free. The branchial system of *Chiton* is distributed and subdivided, that of *Fissurella* is centralized in place and united in structure. In anatomical arrangement they are precisely the same. It should however be remembered, while discussing the generic affinities of the Chitonidæ, that, according to Cuvier's\* dissections, the branchiæ in *Chiton spinulosus* (Linn.) are only one-sidedly laminated, resembling the arrangement of the teeth of a comb. By Forbes and Hanley† the branchiæ in the British families are defined as "forming a series of *lamellæ* between the mantle and the foot on each side." By Mr. Clark those of *Chiton fascicularis* are described as consisting of "a cordon between the mantle and the foot, composed of fifteen oblique cord-like, short, close-set, pale brown *filaments* on each side ‡." This description is calculated to mislead. The branchiæ in the Chitons are neither 'lamellæ' nor 'filaments.' They are complexly constructed organs (Pl. XI. figs. 2 & 3). Each 'filament' or 'lamella' (Forbes) is a separate and distinct fabric. Not less so than *one* of the cones of the gill in the Crab, or one of the penknife-shaped processes of the branchia of the Fish. In number these conules differ according to the species. A row of fifteen occurs in *Chiton fascicularis*, of seventeen in *C. cinereus*, of only ten in *C. asellus*, on each side of the body. They amount to eighteen in *Chiton discrepans*, to twelve only in *C. ruber*, to eighteen in *C. quinquevalvis* (Brown), and even to twenty-four on either side of the body in *C. marmoreus*. Several other spe-

\* Mém. sur les Mollusques; and Règne Animal, pl. 68. vol. sur les Mollusques.

† British Mollusca, vol. ii. p. 391.

‡ British Marine Testaceous Mollusca, p. 249.



cies of Chitons are described in works on British Mollusca. In all, the branchiæ are overlooked. Numerous comparisons of the young with the old would be necessary to prove that in the adult state of each species these organules are *constant* characters. If they are, in descriptions of species a correct account of them, as regards number, size and position, should be included. They are well known to vary in size, apparent form, and in situation, relatively to the transverse median line of the body in different species, but in *plan* of formation or design they present no diversities. A branchia (figs. 2 & 3) in the genus *Chiton* may be typically described as a process of the mantle, consisting of a wedge-shaped axis (*b*), from whose opposite plane surfaces project at right angles secondary laminae (*a, a, a*), laid flatwise the one upon the other from the base to the apex of the process. The laminae (fig. 4 *d*; figs. 2 & 3 *a, a, a*) are largest at the root, smallest and tapering at the further free end. Each leaf (fig. 4 *d*) being attached only at one border, is capable of floating freely in the water. This is a point of immense functional advantage. The aërating current, however, is otherwise brought under muscular control. The row of gills, being disposed in an angular groove between two strongly contractile and extensile parts, namely the edges of the foot and mantle, are mechanically operated on by the current thus muscularly set in motion. Thus the laminae are separated from one another.

The gills of *Chiton* are much more parenchymatous or fleshy than those of *Patella*. They possess an obvious power of collapsing and expanding. Muscular fibres are disposed variously throughout the entire gill. Even the borders of the leaflets are contractile (fig. 4 *d*). But the axial plane, in which the two large vessels (fig. 4 *a* & *b*) are lodged, is conspicuously fleshy and muscular. By the fibres situated in this axis the whole process may be shortened, and drawn strongly up towards the base. This power may be given in order to protect the part, or to quicken the circulation, or effectually to cleanse the gill of effete water. Each branchial process carries in its central plane two large vessels (*a, b*). They are connected with two main trunks which run along the edge of the mantle. They are respectively afferent and efferent. Thus far the apparatus is simple. The circulation in the laminae is infinitely more complex (fig. 4). From the main afferent vessel (*a*, arrow) of the branchial process secondary branches (*e*) proceed. These latter run along the attached border or root of each leaflet. A similar secondary efferent vessel runs parallel to it on the other side of the same border (*e'*). The two vessels are connected together by means of the looped, parallel, ultimate blood-channels of the laminae (*c, c'*). These latter are the true respiratory capillaries. They



form in the substance of the leaflet *two layers* of vessels. The upper loops into the lower layer at the free border (*d*) of the lamina. Thus then the vital fluid flows, in horizontally parallel streamlets, of extreme minuteness, along the upper aspect of a sheet, itself flattened in the highest degree; following the direction of the loops, it curves round at the distal margin, returns in a similarly distributed stratum along the inferior face of the lamina, and reaches in the form of an arterial fluid the efferent vessel at the fixed base. Although these ultimate blood-channels are *unquestionably* separately walled conduits, they branch here and there and unite with those in the neighbourhood. This branching however so seldom occurs, that each vessel may really be defined as maintaining its individuality from the beginning to the end of its course. This fact identifies the branchiæ of the Chitonidæ with the Molluscan type, and severs them from the Crustacean. This is an anatomical character of essential importance\*.

Although an ultimate leaflet from the gill of the Chiton has precisely the same *figure* as the corresponding part of the gill of a brachyurous Crustacean, its real structure is demonstratively Molluscan. The microscope is thus enabled to prove, that beneath an exterior general resemblance there lies hidden an essential identity of organization. In the Chiton, as in *all mollusks*, the *branchial* vessels are individualized channels bounded by distinct walls. In the Crustacea the blood traverses wall-less lacunose passages, and forms invariably only a single stratum in its course. These facts are beyond question. They prove that the Chitonidæ are far more intimately allied to the Mollusk than

\* I would here confess to the naturalist who may perchance repeat these observations, that no researches in which I have ever engaged have required so much *training of the eye*, and *familiarizing of the mind* with the appearances under study, as the ultimate characters of the vascular apparatus of the gills in the Cephaloporous Mollusca. Numerous difficulties occur. The same doubtful point must be tested in very different modes, in the recent and preserved specimens, and by aid of various chemical agents. In the Acephalous Mollusks, as in the Crustacea, the ultimate blood-channels become unquestionable at the first glance. Not so in the branchiferous Gasteropods. The vessels are smaller and covered with a denser epithelium; the tissue is contractile and softer, the parts of difficult access, &c.; but notwithstanding these difficulties, I believe that the real and true anatomy of these parts is faithfully given in the present memoir. It is the first occasion in comparative anatomy on which an attempt has been made to unravel the *ultimate character* of any part of the circulating system of the Mollusca. I am disposed to attach importance to what is true of the branchiæ in this sense, since it may hereafter prove of service in deciphering the last vessels of other tissues and organs. I would only in this place and at present venture to observe, that the *lacunar* theory of Milne-Edwards is incontestably in every sense more applicable to the Crustacea than to the Mollusca.



to the Crustacean. They establish a new principle in homology. They prove that conformity in the last elements of structure signifies more than the superficial analogies of outward form.

Another striking point of dissimilitude between the gill of the Chiton and that of the Crab, is that in the former the *whole lamina*, but most conspicuously the borders, is covered by a comparatively dense *ciliated epithelium*. Cilia do not exist in the Crustacea. It is possible that these vibratile appendages may exist on the branchiæ of Gasteropod Mollusks, and not on those of Crustacea, because in the former the blood moving in the ultimate vessels can be exposed to the agency of the aërating element *only on one side*; whereas, as formerly explained, in almost every Crustacean the extreme blood-passages are equally exposed on both sides of a single current to the action of the surrounding medium. Thus the area of exposure being the same, the functional value of a Crustacean gill may be equal to that of a Molluscan, albeit the circulatory system of the latter may be incomparably more perfect and elaborate than that of the former. A curious fact may here be mentioned, as connecting the branchial operations with the position of the cloaca: that in the Chitonidæ the effete current of water flowing in the respiratory groove between the edge of the mantle and that of the foot sets *backwards* towards the anus—in the Patellidæ it sets forwards, towards the common position of the mouth and anus.

To recapitulate: it may be stated that in figure the gill of the Chiton is the counterpart of that of the Crab; in the ultimate arrangement of its vessels it conforms with the type prevalent throughout the branchiferous Gasteropods; in its fleshiness, the denseness of its epithelium, and in the presence of minute follicles on its surface, it allies itself with the branchiæ of the Nudibranchs. Nothing is more easy than to *prove* the presence of epithelium over the entire surfaces of the laminae. The waving of the cilia is visible throughout the whole extent of the surface. The cilia which are situated on the free margins (fig. 4 *d*) are much larger,—supported by correspondingly larger cells than those distributed over the flat face. Opportunities will afterwards occur for considering the question, *why*, in the organs of branchial breathing, *ciliary* epithelium should almost always clothe even the *ultimate* vessels, and *why* they should be as constantly wanting on the corresponding parts of the pulmonary or air-breathing series.

#### *Branchial System of the Patellidæ.*

It is proposed here to take the branchiæ of the genus *Patella* as the type of those of the remaining genera of this order. But



it will be shown that the Fissurellidæ, Emarginulidæ, and Haliotidæ, &c., differ strikingly both in the special and in the general characters of the branchial system from the Patellidæ. Though there may exist *other* features which in the judgement of the malacologist may justify the marshalling of these several genera under one and the same order, estimated by the branchial apparatus, the Patellidæ ought unquestionably to stand apart and alone. The author is deeply persuaded that minute *ultimate* histological questions will *some day* in the history of science exercise a far more potent sway over the minds of classifiers than they have hitherto done. Unity and uniformity reign with greater constancy in the small than in the great productions of nature. The cell or the fibre, which the wondrous microscope only can reveal to human ken, is no less fixed and invariable in its structure than the huge bone or the stupendous brain.

In the *Patella* the heart stands in the geometrical centre of the body. It is situated above and behind the head. It is not perforated by the intestines as it is in the Bivalves. It is an elongated sac dividing in front into two main pallial trunks. These latter distribute arterial blood throughout the mantle\*. From the mantle and the viscera it returns into the branchiæ and thence into the heart, to be redistributed over the body. This apparatus can be detected with perfect clearness in the uninjected subject.

In *Patella* the branchiæ (fig. 5 *a, a*) form a *circle*, which is interrupted only by a small notch for the admission of water. That is, the lamellæ are neither deficient behind nor before. The "cordon" is continued over that portion of the margin of the mantle which is situated in advance of the head. Thus, in *Patella* the branchiæ neither arise from, nor are in any way attached to, the neck of the animal. They are developments of the mantle alone. This point is one of specific importance. It proves that the *figure* used by the late Prof. E. Forbes was unphilosophical, because unsupported by anatomy. He said that the branchiæ of *Patella* were really only those of *Fissurella* and *Haliotis*, *fixed* to the mantle and extended all round, instead of being *free* plumes as in the latter. But it is at once obvious, that not only the branchiæ themselves, but the anatomical relations of them are radically different in *Patella* and *Fissurella* and

\* So clear and water-like are the fluid contents of these vessels in a fresh specimen, while expanding itself in the struggle to get out of its shell, that they may most readily, but most erroneously, be mistaken for *aquiferous canals*. As on a future occasion I shall have a great deal to say on the ill-understood subject of the aquiferous system of Mollusks, at present I only desire to indicate a source of misconception which has led many an acute naturalist into error.



*Haliotis* for example. If, indeed, the latter genera have no better title to a rank in the Patellidan group than that which is furnished by the branchiæ, they should receive at once a summary sentence of exclusion.

The branchial organ of *Patella* consists of a *double* row of leaves (fig. 5 *a, e*) oblong in shape (fig. 8), standing vertically on, and at right angles with the plane of, the mantle (fig. 5 *c, c*). They constitute a special apparatus distinct from that papillose, ciliated fringe (*d*) with which the extreme edge of the mantle is ornamented. They extend over the entire circumference of the pallial border. They are not attached to any part of the body of the animal. The outermost row of leaflets (*a*) is a little larger than the innermost (*e*). By a poetical stretch of fancy it might be said that, being composed of two sets of laminæ, though situated on the same side of the same base, they may justly be likened to the oppositely-placed laminæ of the plumose free gills of the other Patelloid orders. But such a comparison would be indeed far-sought.

The branchiæ of the vulgar Limpet, to the careless looker-on on Nature's marvels, appear so contemptibly familiar, that to subject such objects to a grave and minute philosophical examination must prove a severe trial to his patience and common sense. Alas! how short is the range of human sight! Beneath the familiar exterior of these common objects there lies an undiscovered machinery of startling beauty and perfection! These little organs will serve to unite the branchial systems of the two great groups of Mollusks, the Acephalous and Encephalous. Through their aid it will prove practicable to establish a *unity of branchial type* coextensive with the entire Molluscan series. They will convince the zoologist that Nature never changes either the plan of her action, or the design of her architecture, by senseless and ludicrous transitions. Her incomparable, unequalled skill lies in adapting a single principle to the most varied ends.

Of the two rows of laminæ in *Patella* as just stated, the inner is composed of smaller leaflets than the more external. The smaller and larger leaves occur alternately in the series. Both are precisely the same in minute structure. Expert manipulation is required in order to obtain a complete view of the gill-processes *in situ*. The whole ring of the mantle to which they are attached should be removed. Every portion of the loose edge and fringe should then be cut away, leaving only so much as will hold the laminæ in position. A small segment of this circle should be then placed in the cell of an object-glass, floated with water and covered with a slip of thin glass. The position of the laminæ may now be changed at will, by slackening or extending the portion beyond the edge of the glass.



It will now be remarked, that each lamina (fig. 8) is a separate and distinct process, resting on, or proceeding from, a distinct base; that it is *not* a simple vertical sheet like the leaf of a book, of equal thickness at every part, at the edge and at the base; that it is not, what seemed certain to the naked eye, a compactly-structured *single* sheet. A far more intricate arrangement discovers itself. First, each lamina, as it stands in its place and *unstretched*, forms a concavo-convex outline (fig. 8). It bulges out (*a*) like a sail in the wind on one side; it is hollow on the other (*b*). This figure is due to the fact that the free border (*c*) is denser and less extensile than the intermediate membranous portion. Many advantages are secured by such an arrangement. The individual laminæ of the series mutually support one another by a more exact and rapid adaptation of the *vis-à-vis* surfaces. They are less liable to fold and wrinkle by the rapidly varying degrees of distension to which they are exposed by the action of the margin-muscles of the mantle. But the free border of each leaflet is further so constructed as to realize a great degree of elasticity (figs. 7, 6). On looking sideways, that is, directly down upon the edge of the leaflet, the eye discovers with perfect clearness an arched or vaulted outline (fig. 7 *c*; fig. 6 *e*) formed by the *curving* round of the blood-channels of one half or layer of the sheet, in order to run into those of the other half (fig. 7 *a, e, b*). It is by this method of viewing the object that the anatomist may convince himself that each gill-plate is really composed of two distinct and separated layers (figs. 6 & 7 *a, b-a, b*), united only at the margin (*c, c*), in exact accordance with the pattern of the *single* gills of the Lamelibranchiate Acephala.

The satisfactory determination of this point of structure is of great importance in this inquiry. It possesses all the power of a key as regards the after-stages of the investigation. So extraordinary is the uniformity of the *plan* on which the respiratory organs of the branchiferous Gasteropods are formed, that it may be inferred with perfect certainty that what is clearly proved to be true of one grade in the series will apply with essential accuracy to all the others. Extremely difficult therefore though it may be to unravel the minute structure of the gill-laminæ of *Patella*, from the key-like power of the information thus only to be acquired, it is worthy of all the patience which the student can command.

Two facts of structure are then determined:—1st. That the plate is composed of two layers; 2nd. That those two layers are united by a looped arrangement at the margin. Now it may be proved with exact certainty, that each layer is composed of straight or waveling parallel channels (figs. 6 *a, b*, and 7 *a, b*) laid



on the same horizontal plane (fig. 6 *a*, as far as *i*), such that a *membrane* is formed. Although these channels are far less individually distinct than those of the gills of the Lamellibranchs, they are unquestionably blood-vessels, united together into a membrane-like series by delicate intervening fibres or membrane. Various kinds of proofs might be adduced in support of this interpretation.

The cilia follow the outline of each vessel (fig. 7 *a*, *b*) in a line-like manner. The vessels present a linear bulge like a tube. They can be seen to be filled with rows of corpuscles, clearly distinguishable from the fixed cells and epithelia which form the solid substance of their walls. Traced carefully in the direction of the distal margin, they become more and more separated from one another (fig. 6 *d*). The interposed substance becomes more and more pellucid, until at length at the margin the vascular loops (*c*, *c*) stand out in unmistakeable eminence. So microscopic is the mechanism however, that it is impossible by *direct* view to state whether these vessels are separated by a water-fissure, such as that which exists in the gills of the Lamellibranchs, or whether they are joined by an intervascular membrane. In the former case, water would penetrate into the space (fig. 7 *e*) between the two constituent layers of the lamina; in the latter this space would be entirely closed from the external element. On a superficial view this point may appear very insignificant. On a deeper insight it becomes pregnant with functional and homological meaning. If the water could find a ready entrance into the interlaminar space (fig. 6 *e*, *g*), the column of blood flowing in each afferent and efferent blood-vessel (*a*, *b*), that is, in the trunks bounding that space, would be aerated on both sides, and the respiratory value of the organ would at once be doubled. It is almost certain that it does not and cannot. If the external water cannot and does not penetrate into this interlaminar space, then it must be filled by the vital fluid of the animal; for the space exists beyond doubt. If this latter supposition be true, it is quite certain that this fluid must be distinct from that which circulates in the laminar or proper branchial vessels. This doubt must for the present be left undetermined. Whether it be soluble or not, enough of the essential structure of the gasteropodan gill has been demonstrated to establish between it and the branchiæ of the Lamellibranchs an extraordinary resemblance; not a mere outline-similarity, but a closeness, almost amounting to an *identity* of constructive plan. If everything else in the patelloid organism exhibited the same degree of similitude to the system of the Lamellibranch as that which obtains in the branchial apparatus, the naturalist would not hesitate to define the *Patella* at once as



the highest Acephalan and the lowest Encephalan. It must however be admitted, that the judgement of the classifier should not be swayed exclusively by special affinities. The question now arises, if these minute branchial leaflets of *Patella* really consist each of two layers, how are these layers tied together? They are fixed to one another by an intermediate system of threads (*trabeculae*) crossing each other in such a manner as to afford the most effectual mutual support (fig. 6 *h*; fig. 7 *g*). The points (fig. 6 *f*; fig. 7 *d*) to which these connecting fibres or bands (fig. 7 *f*; fig. 6 *h*) are attached to the vessels are swelled into nodules (fig. 7 *d*), which present a singular resemblance to the fleshy nodules on the branchial bars of the Mussel. Of course they are much less visible than they are in the latter case, but in anatomical characters and relations they are in both cases most remarkably analogous. Now the interval between the two layers which is crossed by the threads just described, is indubitably filled with *some* fluid. What that fluid is, it is impossible at present to say.

The water-currents excited by cilia on the flat surfaces of the branchial laminae set, from the fixed, in the direction of the free border. The cilia which are distributed over the flat faces of the leaflets are very much smaller than those which fringe the margins. The exact position to which the former are attached in relation to the lines of the blood-channels cannot therefore be clearly defined. This, however, is an unimportant point, since the *aggregate* action of the cilia, as indicated by the setting of the current, may be easily proved.

The epithelium which lines the flat surfaces of the laminae forms undoubtedly a *continuous membrane*. It is consequently impossible that there can take place any water-currents between the individual blood-channels, such as those which figure so prominently in the mechanism of the Lamellibranchiate gills. The water-passages being wanting, it results that, in *this* Gastropod, the branchia is *not penetrated by the aërating medium*. This fact should be regarded rather as a criterion of superior than of inferior organization. It signifies an increasing subdivision of the blood-streams. The blood-vessels being smaller, and the parietes being less dense and cartilaginous, exposure to the oxygenating medium *on one side only* suffices for the purposes of respiration. It is important in this place to remark, that if the *interlaminar* space of the branchial leaves of *Patella* could be *proved* to be filled with water and not with blood, *some* ground would be afforded, as will again be shown, for supposing that in these Mollusca the *external* water is actually admitted into the *penetralia* of the organism, forming an *aquiferous system*, and that it circulates like a nutritive fluid throughout the entire



body. This, however, is a *fancy* as yet at all events totally unsupported by fact.

It is difficult to leave this part of the present inquiry without once more drawing attention to the homologous significance of the branchiæ of *Patella*. They are composed of two layers of vessels, opposed face to face, and joined at the margin. They are invested by a ciliated epithelium which is restricted to the *exterior* aspect of the organ. The constituent layers are separated by an intermediate space. In these several items of mechanism these branchiæ approximate most wonderfully closely to the type which is normal to the Acephala. If there be no meaning in this approximation, there can be no *unity* in the organic system of nature, and the philosophic anatomist may indeed well abandon his studies in despair. In conclusion it should be remembered, that between a single leaflet of the gill of *Patella* and a single lamina of the *same form and figure*, taken from any small brachyurous Crustacean, the extremest difference exists. The Crustacean gill is far less perfect, more rude in every sense, as a purposive machinery. Carrying a single stream of blood, whose corpuscles are considerably larger than those of *Patella*, and which runs in irregular passages lying between two sheets of epithelium tied together only by means of accidentally distributed islets of fleshy tissue, it contrasts strikingly with the double-vessel system with the contractile and highly ciliated elements of which the Patellan gill is woven.

For reasons derived from other sources than those of the branchiæ, the genera *Emarginula*, *Fissurella* and *Haliotis* are placed by malacologists in the Patelloid group. The branchiæ of *Emarginula* (fig. 9 *a, a*) approach much nearer than those of *Fissurella* (fig. 10 *a, a*) to the type of these organs as they exist in *Patella*. The gills of *Emarginula* are attached to the base of the cervical cavity (fig. 9 *d*) on either side of the outlet of the intestine. They project *forwards* in form of tapering processes (*a, a*) on either side of the head of the animal. They are chiefly fixed at the base, but a slender membranous *frenum*, proceeding from the median line of each, connects them to that portion of the mantle which covers the roof of the cavity of the shell in which the head and rectum are situated. They are thus held in one position. They possess notwithstanding a slight power of expanding and collapsing. They are foliated only on *one* side (*a, a*) of a base. They are more comb-like than plume-like. In this particular of configuration they approach closely to the branchiæ of *Patella*. If the latter were seated on a free instead of a fixed base, the resemblance would be very near. Occupying a position on either side of the notch (*b*) in the shell, the latter should be regarded as playing as important a part in providing



a fresh current of water for the branchiæ, as in conveying away the excreta.

The ciliary movements observable in this region both in *Emarginula* and *Fissurella* point to the same inference. Examined separately under the microscope, a single leaf taken from the gill of *Emarginula reticulata* presents an outline not unlike that of *Patella*. It is, however, more lancet-shaped. In ultimate minute structure it corresponds exactly with the patellidan model already figured. Its vessels run in parallel columns, looping at the free margin and covered by a ciliated epithelium. The interlaminar space, so unquestionable in the gill-leaf of *Patella* (fig. 6 e), is here however much more contracted and less distinguishable. In other words, the layers are so intimately soldered together as almost to obliterate the intervening space. The layers nevertheless carry separate and distinct planes of blood-channels. In *Fissurella* the organs of breathing (fig. 10 a, a) consist of two plumose tapering processes (a, a), projecting forwards (when fully expanded) to a considerable distance under the anterior vault of the shell. They are capable, like the arms of a Brachiopod, of being coiled up on themselves. They are distinguished from those of *Emarginula* in having a double system of leaves. These gills therefore present rather a pinnate than a pectinate figure. They stand at the sides of the chamber, the roof of which is perforated by the opening at the apex of the shell. This orifice admits fresh water into this space; it also conveys externally all refuse excretions. In the disposition of the vessels, in the character of the ciliary epithelium, in the fact of two planes of vessels, the branchiæ of *Fissurella* conform to the standard of the Patellan gill.

The branchial plume of *Acmaea testudinalis* extends to a great distance beyond the limits of the shell. It is fixed to the neck of the animal at the root of the right tentacle. It is bisymmetrically foliated; each lamina in its ultimate anatomy follows the Patelloid type. The gills of *Propilidium ancyloide* consist of two small feathery processes attached to the dorsal surface of the neck of the animal. They incline in a parallel direction to the right side of the cloacal cavity. They are free processes, and furnished with a double series of leaves, supported by an axial base, in which the afferent and efferent branchial vessels are lodged.

In *Puncturella noachina* the gill is non-symmetrical. It occupies a special and spacious chamber on the left side of the neck and foot. It is a pinnate structure highly ciliated, the lamina being large.

Judged by the structure and relations of the branchial system exclusively, the Fissurellidæ are undoubtedly placed in their true



serial position by Forbes and Hanley, namely intermedially between the Limpets and Haliotidæ. They are Scutibranchiate. This cannot be said of *Acmæa* and *Propilidium*. The branchia here is not shielded by a fold of the mantle. Nor are they Cyclobranchiate, for the branchial processes are free plumes. If affinity is to be decided by structure rather than position, both *Acmæa* and *Propilidium* should be classed with the Scutibranchs.

The branchiæ in *Haliotis* (fig. 11) are sufficiently large to enable us to trace satisfactorily the distribution of the larger blood-channels. They will suffice to illustrate the circulatory apparatus of the gills in all the other Scutibranchs. The author's account is drawn from an examination of a specimen preserved in spirit, aided by the successful injections of Milne-Edwards.\* *Haliotis tuberculata* is a typical Scutibranch. The branchiæ (fig. 11 *a, a*) are lodged in a spacious enclosure of the mantle on the left side of the body. They are attached at the base by means of the vascular trunks; on the inferior surface to some extent of their length, by means of a membranous *frenum*. They are doubly laminose; that is, between two parallel trunks (*b, b* & *c, c*), a vein and an artery, which run from the base to the apex of each gill, there lie transversely two series of leaves (*a, a', a, a'*) which are traversed by the blood of the afferent vessel (*b*) on its path to the efferent vessel (*c*). Here again, as in all the Gasteropod Mollusks, the gills are observed to conform in *general* structure to those leafy piles which fill the thoracic cavity of the Crab; but how totally different in the minute parts of their organization! In *Haliotis* the heart (*e*) is *systemic*. The blood, freshly arterialized, returns directly from the branchiæ into the auricles (*d, d*); from the ventricle (*e*) it is driven into the systemic aorta (*f*). At the roots of the branchiæ the venous blood converges into capacious, but not lacunose, afferent trunks (*b, b*), along which it is conducted to the branchial laminae. The vascular system of the laminae (fig. 12) is the same in every respect as that already described and figured in *Chiton* and *Patella*.

Each lamina carries two layers of horizontally stratified, uniformly diametered tubes, united to one another laterally, and to those of the opposite venous stratum by transverse threads. Each leaflet consequently consists of two layers or planes of blood-channels, joined together at the free margin, and covered on their external surfaces by a ciliated epithelium. A thin film of water moves wavingly from the fixed to the free borders: it is sustained in motion by the vibration of the cilia. Such an arrangement proves that not only the blood to be aërated, but the water

\* Annales des Sciences Naturelles, tom. viii. 1847.



which aërates, is required in the act of respiration to be divided to the utmost degree. As far as this inquiry has proceeded, it must have been observed, that although the plumose or pinnate form of gill is constantly adopted as the most convenient figure in accordance with which to construct the respiratory organs both in Mollusca and Crustacea, the resemblance never proceeds beyond the exterior conformation and the disposition of the larger vessels. Beyond and deeper than this limit the microscope establishes an irreconcilable difference between the Crustacean and Molluscan gill. It exemplifies the supreme value of this instrument in zoological research. But apart from these physical considerations, a chemical ground of dissimilarity between the branchiæ of these two classes exists. The horny chitinous epithelium of the Crustacean contrasts obviously with the fleshy, soft, and ciliated covering with which the Molluscan structure is invested. In the latter the blood-movement is aided by muscular and vascular contractions. In the Crustacean the flow of the blood is due almost exclusively to the action of the heart, whose beats can be clearly read by the eye at the farthest periphery of the circulation in the saltatory motion of the floating corpuscles. In the *walled* contractile vessel of the Mollusk no such evidence is discoverable.

#### *Pectinibranchiata.*

This order comprehends a considerable number of families and genera. It is the largest and most important group of the Gasteropod Mollusks. In this summary it will be impossible to present a correct analysis, derived from personal observation, of the respiratory organs of every genus. If that were possible indeed to a single observer, an acquisition of great value would accrue to science. The author is deeply persuaded that even in such minute constituents of the organism as a *single* leaflet from the branchial apparatus, the microscope may reveal the presence of differences of shape, size, structure, &c., which may serve to establish the distinctness of species quite as clearly and convincingly as the grosser characters of the outward appendages. The branchial plates of two separate species, in general position, in form and size, &c., may to the casual eye of the descriptive naturalist, appear absolutely identical. Guided by the microscope, the minute anatomist, however, detects *organic* dissimilarities which enable him at once to assign the objects under view to two distinct animals. A thousand illustrations of this kind may be readily adduced to prove the importance of minute investigations of structure. False analogies suggested by general external resemblances of organs can be



authoritatively corrected only by an appeal to the facts of ultimate structure. How utterly confused, how deeply deficient are the views of the comparative physiologists even of these advanced times, as to the history of the renal and urinary systems of the Invertebrate animals! How difficult, in any given instance of doubt, to state whether an organ is a kidney or not! The ultimate elements, those last factors which constitute the essence of the organ, are utterly unknown. For it is not even now determined what is and what is not *essential* to the kidney of an Invertebrate animal. This opprobrium applied but a short time since to the fluid systems and to the respiratory organs. How great are the honours yet in store in this field of research for the clear thinker and fruitful observer!

The general affinities of the Pectinibranchiate order of Mollusks are familiar to all. In all the genera, a spacious branchial chamber exists (Pl. V. figs. 1 & 2). It is a recess over-vaulted by the anterior termination of the mantle. It occupies the last turn of the spire. It is open in front. This arrangement will be afterwards contrasted with the closed character which it exhibits in the Pulmonifera. The Pectinibranchs admit of division into two sub-orders—the Holostomata and the Siphonostomata. In the former, the margin of the shell and mantle is entire; in the latter, it is either notched or produced into a canal or siphon (*f*). Through this prolongation of the mantle the water enters the chamber. In the Holostomata it penetrates at the same point in the fissure between the dorsum of the animal and the edge of the mantle. The machinery by which the ingress and egress of the water are effected resides in the branchial hood of the mantle. It performs regular respiratory movements. These movements, however, are aided by the invisible agency of cilia. The Pectinibranchs are prosobranchiate. The heart in all affects a position immediately behind the branchial organ. The aerated blood returning from the latter is received directly by the auricle of the former.

What is designated the branchial vault in the Pectinibranchs is not exclusively a respiratory chamber. It serves to lodge other organs. It contains the heart, the termination of the intestine, the excretory ducts of the reproductive system, and several varieties of glands (Pl. V. figs. 1 & 2). It is therefore by no means an unimportant part of the body of the mollusk. Between the position of the rectum and that of the branchiæ there obtains in this, as in the Pulmonifera, a constant relationship: one reason for this relationship is a mechanical necessity. The egressing current from the gills is thus adapted collaterally to convey away from the body the fæcal excreta. This current connects itself also with the functions of the generative system.



It forms a vehicle for the mucus supplied by the glands of this chamber. By its aid the latter is enabled to invest the ova as they escape from the body—constituting thus a cocoon in which they are temporarily cradled. It is by skilfully subordinating the office of one organ to that of another, that Nature's contrivance surpasses man's. In her machinery a force is nowhere allowed to transpire unutilized. It is always deflected to a purpose; though sometimes to one whose significance may prove illegible to her observers.

As the details to which the reader's attention is now solicited are novel, and now for the first time published, it is desirable that a clear and concise method of presenting them should be adopted. The author proposes in the first place to describe the branchiæ in those genera especially of this order in which he has subjected these organs to a special examination. He will then return to a consideration of the glandular apparatus of this important cavity, and finally deduce such inferences with respect to their purpose and function, as their chemistry and the facts of their minute structure may appear to warrant.

The branchiæ of the Pectinibranchs (Pl. V. figs. 1 & 2 *a' a'*) are almost always fixed to the *roof* of the cavity in which they are lodged. They occupy an intermediate position between the "gland of the mucosity" (fig. 1 *b*) and the colour-gland (fig. 1 *a*, fig. 2 *b*), which lies invariably to the extreme left. In some genera the gill is placed at the extreme left of the chamber—at a point, that is, which is the direct opposite of that of the rectum (fig. 1 *c*). This position is significant of the care with which Nature locates the breathing organ in order that it may receive the most direct influence of the aërating current as the latter enters the cavity. In the following account few differences in the relative anatomy of this organ will demand attention. The most striking diversities will be found to affect the figure or outline-form and ultimate structure of the individual laminae or pectinations of the gill. These objects are entirely and exclusively microscopic (Pl. V. figs. 3, 4, 9, 13, 14): they are removed in structure far beyond the sphere of naked vision. Since however the individual parts of a pectinibranchiate gill constitute under all circumstances *sheets* whose opposite faces are more or less smooth, or more or less corrugated and folded, a little manipulative skill will be required to enable the student to put to the test of personal observation the particulars comprised in the following description.

The language commonly used by malacologists in describing the gills of this order of Mollusks is calculated to lead to many very false conceptions. They are first said to be "plumes." A 'plume' or feather is *bi*-pectinate, that is, it consists of a stem



bearing 'barbs' on either side. Such a word, therefore, conveys to the mind an untrue image of the real object. The word "pectinate" is nearer, but still very erroneous, and very inadequate as an illustrative analogue. A leaf of the gill of a pectinibranchiate mollusk resembles in figure much more nearly a 'fan' than the tooth of a comb. A gill would be a series of fans laid side by side. It should accordingly be defined rather as flabelliform (fig. 4) than pecteniform. The laminae of this gill are comparable to a 'fan' moreover in this remarkable particular—they are capable of being closed and opened under the action of muscles. In fact, in other respects they constitute an apparatus immeasurably more beautiful and complex than it has hitherto entered into the dreams of naturalists to conceive.

The branchia (fig. 1 *a, a*) of every genus of this order is seated on a fixed base which forms a part of the roof of the respiratory chamber (*e, e*). In this respect it differs from the breathing organ of the Tectinibranchs, and resembles that of the Cyclobranchs. But the pectinibranchiate gill is distinguished from that of every branchiferous Gasteropod, and is brought near to that of a Lamellibranch by a curious incident of structural mechanism. Each and every leaf of the gill is stiffened and strengthened at one of its free borders by the insertion into its substance of a whalebone-like process of rigid cartilage (fig. 4 *a, a*, & fig. 7). The presence of this process imparts to this edge of the organule a thick straight appearance which stands in obvious opposition to the floating and flexible character of the other margin (fig. 4 *b*). As this process of cartilage is concealed in the substance of the dorsal border of the leaf, and embraced by a dense ciliated membrane, it can only be detected by tearing up the whole leaf into pieces by means of needles. Viewed on its flat surface the lamina presents a triangular outline (*a, b, c, d*). This is more or less the figure of the branchial laminae throughout the entire Pectinibranchiate group. The terminology applicable in one genus will serve to designate the homologous parts in all others. That border which lodges the cartilage may be called the dorsal or cartilaginous (fig. 4 *a-f*); that which stretches from the distal point of the cartilage to the extreme end of the base, the free or flexible border (*a, b, g*) formed of the vascular loops; and thirdly, that may be called the fixed side (*c, c*) which is attached to the vault of the cavity throughout its entire extent, and is the mathematical base of the triangle. In some genera a portion of the gill is described as pendent and floating in the cavity. The power to exert the gill is enjoyed by *Valvata*. It is, however, so exceptional a character, that the branchia in nearly every Pectinibranch may be stated to be



sessile on a fixed base. But in describing the gills of this order, systematic naturalists without exception commit another error. In the Siphonostomata, embracing the carnivorous Gasteropods, the "branchial plumes are stated to be double, or to be two in number." In the Holostomata they are said on the contrary to be "single," that is, that there is but one branchial plume. If this error did not originate with, it certainly has been perpetuated by Dr. Sharpey. In his article "Cilia," in the 'Cyclopædia of Anatomy and Physiology,' he states that in reflecting the roof of the branchial chamber in *Buccinum*, two sets of gills are seen, one of which consists of two rows of laminae (fig. 2 b), the other of one row (a, a). That structure which Dr. Sharpey describes as a "gill with two rows of laminae," which is attached to the extreme left of the vault, is a gland (fig. 2 b; fig. 1 d). The details of this point will be given on another occasion. In external characters it looks like a gill. No one but the microscopic anatomist could note a difference. A deep difference however does exist. Here again is exemplified the service which minute special anatomy may render to the cause of general physiology.

His researches enable the author to affirm with confidence, that in all the Pectinibranchiata the gill is a *single organ*. Though in some of the Cyclobranchiata the organ is double, and may exhibit a bilateral symmetry, in the Pectinibranchs it is single. To this rule there is no exception. Since the constituent parts of every pectinibranchiate gill consist of triangular or fan-shaped leaves, strengthened at the dorsal border by a comb's tooth-like process of cartilage, the terms for the construction of an accurate and consistent general definition of the branchiæ in this family of Mollusks are established. A subdivision of these organs into two leading classes becomes essential, however, with a view to a more accurate description of structural minutiae. In the genera *Buccinum* and *Littorina* the extreme representatives of these two classes occur. The branchial leaf of the former (fig. 4) is distinguished by smooth sides—that is, it is an unPLICATED lamina having the same minute structure in every part of its extent. In the latter (fig. 3) complex plications (c, c-b, b) occur which multiply to a considerable degree the area of the active surface. This is so remarkable a character, that if the plicæ were a little more prominent, each leaf of the gill of the Periwinkle might be correctly described as a bipinnate structure (fig. 3 B). The plicæ are however mere folds of the smooth surface of the lamina, as will be afterwards explained. These parts are so minute, that the malacologist, using merely the unassisted eye, would pronounce the gill-leaf of *Buccinum* and that of *Littorina* to be one and the same thing,—to be identically or-



ganized. But how *essentially* unlike! The evidence furnished by the ultimate anatomy of the *branchiæ* would require that the family of the Littorinidæ should be placed in juxtaposition with the Tectinibranchiata.

The pectinibranchiate gill (fig. 1 *a, a*; fig. 2 *a, a*) may be defined then as a series of parallel blood-vessels-bearing leaflets, decreasing in size from the centre of the series to either end, projecting at right angles and vertically depending from the walls of the containing chamber. The long axis of the entire organ is parallel with the line of the rectum and that of the glands peculiar to this cavity (fig. 1 *d, b*). Though only two main varieties of anatomical structure occur among the branchiæ of this order, the diversities observable in the *size* and *shape* of the laminæ in intermediate examples are as numerous not only as the genera but really as the species. In the genus *Trochus* (figs. 13 & 14) they are more or less similar in all the species. In every species, however, some peculiarity is distinguishable in the contour of the laminæ, which suffices to establish specific independence. Those of *Trochus magus* (fig. 13) are triangular, the dorsal border (*a, d*) being slightly convex, the free or flexible border (*b*) being gently concave, while the distal apex is rounded (*a*). The base (*c*) of the longest lamina, which occupies always a position in the centre of the gill, measures about  $\frac{1}{10}$ th of an inch in full-grown specimens.

In *Trochus cinerarius* (fig. 14), a closely allied species, the distal angle (*a*) is elongated into an acute apex, the free border (*b*) is at first convex and then sweeps into a very prolonged base (*e, c*), giving to the attached border twice as great a length as in that of the former species. Other varieties of figure occur in the gill-leaves of *Trochus umbilicatus*, and *T. tumidus*\*. The cartilage which occupies the dorsal edge is curved at its point in some species (fig. 12), so that it acquires, its root being the fulcral point, all the resilient qualities of a bow. In others it is blade-shaped (fig. 7). It tends always to straighten itself. This tendency is expended upon the flat surface and the free margin

\* In arriving at a knowledge of the exact figure of the branchial laminæ I have invariably adopted one method of examination. It has consisted in cutting out a few leaves or a small portion of the centre of the gill; the section being coincident with the plane of the laminæ, and at right angles with the long axis of the entire organ. This portion is then carefully placed on the glass slip, floated in *salt* water if the specimen be marine in habits, in fresh water if from a freshwater habitat, and then lightly covered with a plate of thin glass. A few laminæ at the same time are detached by means of needles and torn up, in order that the objects may be examined under different points of view. Various reagents are used in the examination of the vessels, cartilages, muscles and fibres, &c. of the organ.



of the laminae, which are thus maintained in a tightened state, like outstretched or expanded sheets. This is undoubtedly the true purpose which this peculiar cartilage is intended to fulfil in the gills of this order of Mollusks. Its existence has never yet been suspected by anatomists. From the mechanical, lever-like character of its office, it is evident that upon its duly regulated action must depend the function of the entire leaflet. Without it, a sheet of such surpassing delicacy as an individual branchial lamina could not sustain the required vertical position. Without some such contrivance the leaflets would be driven, crushed and folded confusedly by every current and pressure. An elastic apparatus, of inconceivable beauty and perfection, is realized in these hyaline invisible and hidden parts. They hold, with a force of immeasurable gentleness, the respiratory laminae at such a degree of tenseness as best favours the transit of the water between them, and of the blood throughout the extent of their plane superficies. No crumpling or folding or confusion of any kind can happen even in the relative position of structures of such extreme tenuity and slenderness. And yet it has never occurred to the curiosity of any one of the thousand observers by whom these organs have been witnessed, to catechise Nature as to the mechanism by which such wonders, though minute, are accomplished! In organic workmanship, minuteness and perfection are often twin qualities of the same machinery! These cartilages are peculiar to the gills of the Pectinibranchiata, and as the unfolding of details proceeds, it will be seen that they undergo variations of size and shape, but never of relative position, according to the differences of families, genera, and even of species. Into the branchial system of this large and important order they are special importations, fulfilling purposes of a special nature.

But the office of the border-cartilages is not restricted to the end which has just been defined. They conduct and protect the larger afferent and efferent blood-channels of the laminae (fig. 3 *e*). It is by thus transmitting a primary column of blood from the fixed border to the apex of the leaflet, that every single spot of the flat surface of the latter is rendered available in the active operation of breathing.

When a single lamina is detached and placed singly, floating in salt water, under the microscope, and viewed as a transparent object, it may be supposed that the spectacle must be one of extreme definedness, every one of whose constituent elements may be readily singled out and read by the eye. This is an *à-priori*, and therefore as usual an erroneous fancy. Nothing is so difficult to the unpractised observer as to read clearly and accurately the spectacle under view. It demands an exercised eye even to



distinguish an epithelial particle from a blood-corpuscle, a blood-channel from the crease or fold of the lamina, a near object from one placed at a greater focal distance. Practice and perseverance will however enable the student to interpret with confidence and accuracy all the subtle elements of this inconceivably beautiful structure.

A little experience in the art of viewing the branchial organs of the Gasteropod Mollusks will suffice to assure the least interested observer, that the blood-channels traverse the plane extent of the laminae in parallel vessels, of uniform diameter, separated from each other by appreciable intervals, and bounded by individual and independent walls (fig. 4 *d, d*). In *Trochus* they appear to run (fig. 13 *e*) from the dorsal edge (*a*) to the free border (*b*) along one face of the leaf, and back again along the other surface, looping round the edge. On both surfaces they are invested in a similar manner by ciliated epithelium, the cilia being large at the edges and small over the flat face of the lamina.

Although the preceding account conveys an exact illustrative image of the type which prevails throughout the branchial system of this multitudinous order, yet as this occasion is the first on which these particulars have been published, it is desirable to enter into an examination of some few other examples of the pectinibranchiate gill.

In *Phasianella* the branchia is said to be partially detached and free in its cavity, but in other relations it imitates the type of the Trochidan organ.

The Paludinidae are prosobranchiate gasteropod mollusks which inhabit fresh water. It is curious to observe, that this marked contrariety of habitat should occasion no variation of place or structure in the organ of breathing. The branchia of this family, like those of all other Pectinibranchs, affects a position on the vault of the thoracic chamber, having the rectum and generative ducts parallel to it on the right side, and the mucous glands on the other. A siphon exists on the left of the breathing cavity, while on the right the rectum, as in Lymneadae, is prolonged in form of a tube beyond the edge of the mantle on the right. In a large specimen of *Paludina vivipara*, it is easy to extract the animal out of its shell by cracking the latter at different points. The position of the organs contained in the branchial vault may be now seen through the mantle. The whole cavity, as in all Pectinibranchs, is ciliated. On the exterior it is also ciliated to a short distance beyond the edge of the mantle. It lies obliquely in the cavity extending from the posterior left corner to the right anterior end. The gill is constructed in exact conformity with the pectinibranchiate model. The leaves of which it is composed are triangular in



shape, the base of the triangle being the free border. They rest on a fixed base, and carry a rigid process of cartilage in the substance of the dorsal margin. The blood-channels and the vibratile cilia exhibit the same disposition as those of *Buccinum*, which will be presently explained at length. The heart is situated at the extreme posterior boundary of the cavity near the point at which the rectum joins the branchia. The ovary, filled with young, is seen on the right side of the rectum. The specimen from which the preceding account has been drawn had been for some time preserved in spirit; but the author believes that near the dorsal edge of each branchial lamina in *Paludina*, slight traces of secondary pinnæ, or plications, will be discovered, such as those, far more prominently developed, which are now to be figured and described in the Littorinidæ. If this feature of structure should, on a further examination of fresh examples, be proved to exist, a new point of relationship between the genera *Paludina* and *Littorina* will have been established. In describing their respiratory system, it was once intended to place the Littorinidæ apart as a separate group, in order that contrast of position might attract towards them immediately the attention of malacologists. The author, however, thinks that, for the present—that is, until, by further search, other examples of the same formation shall have been collected,—it is better to place the Littorinidæ here, between the Paludinidæ and Turritellidæ (British Mollusca), rather than dislocate the arrangement of systematists, even at the inconvenience of returning afterwards to the description of the smooth or unplicated variety of branchiæ. A singular abnormality occurs in the gills of the genus *Valvata*. It is protruded for a considerable distance beyond the shell, at the left side of the body of the animal. It consists of a long straight axis, from the opposite sides of which filiform pinnæ or secondary processes project. These again bear minuter pinnulæ, which are the ultimate processes. This gill may be regarded as a transitional variety between the plain, or smooth, type of the lamina in the Paludinidæ and the plicated form of the organ which prevails probably throughout the Littorinidan family. An opportunity of examining minutely a recent specimen of *Valvata* has not yet occurred to the author.

In the genus *Littorina*, the last turn of the shell is very large relatively to the second and the third. By this criterion, the capacity of the respiratory chamber may be estimated. It presents a considerable size in these mollusks compared with the bulk of the entire body. The augmented dimensions of the cavity are due to the increased volume of the contained organs (fig. 1). The branchia (fig. 1 *a*, *a*) is highly developed, and occupies a large share of the cavity. It extends from the hind-



most boundary to the root of the siphon. It lies obliquely from left to right along the roof of the chamber. Viewed as a whole, it will be observed to consist of two halves (fig. 2 *a, a*), which are divided by a clearly marked line extending from one extreme of the organ to the other. One of these halves (fig. 3 *a, a*) corresponds with the dorsal or cartilaginous borders of the leaves, and consists of a series of parallel unbending rigid lines or filaments; the other half (fig. 3 *g*), more wavy, flocculent, soft and flexible, coincides with the membranous portion of the laminæ. To the left of the gill is situated a peculiar gland (fig. 1 *d*) having a bipectinate appearance, less developed in this mollusk than in *Buccinum*, and which Dr. Sharpey, and after him all systematic malacologists, has described as a *double*, though rudimentary gill. It will be shown that it is a true gland. To the left of the branchia there lies a large glandular mass, which is always enveloped in viscid mucus, and which exhibits a leafy or laminose structure. On the reflected roof (as shown in fig. 1), still further to the left, is observed another glandular mass (*e*), which some anatomists have described as the renal organ; and, lastly, a duct which belongs to the reproductive system (*j*). The structure of these glands will be discussed on another occasion: the branchia only will be at present described. Powdered Lycopodium strewn lightly over the fresh organ will move in one definite direction; namely from the right, or cartilaginous border, to the left, or membranous (arrows, fig. 1 *a, a*). This current, examined more closely, will be found to be subdivided into as many rivulets as there are spaces between the leaves of the entire organ. Of course these superficially indicated currents are but the edges of vertical sheets of water which are in the act of traversing the spaces between the laminæ. These currents are impelled by two forces, one of which is due to the action of the numerous minute muscles fixed to the cartilaginous margins of the laminæ (fig. 14 *c, d*), whose office it is to furl and unfurl, approximate and separate the individual leaves. By this contrivance a mechanical power is capable of being exerted on the strata of water interposed between the leaves, under which it is driven forwards at a speed regulated by the necessities of the breathing function. The second force is the ciliary. The large cilia which occupy the edges, and which are arranged in rows (fig. 3 *a, a*), are capable of raising a sensible current. The minute cilia which are distributed over the flat surfaces of the laminæ drive along only microscopic streams.

By means of a thin sharp scalpel, a section may be easily made through the gill, parallel with the plane of the laminæ, and through the substance of the vault. If this section be made



about the middle of the gill, one of the largest laminæ may be readily detached and placed as an individual object under the microscope. Such an object is represented in Pl. V. fig. 3. The dorsal margin curves like a reaping-hook (*a, a*). It is stiffened by a large sickle-shaped cartilage (*a, e*) which extends from the root to the apex: it supports the whole organ *in situ*. Within this border, running along the side of the cartilage, are also concealed two large vessels, with which many of the ultimate blood-channels of the lamina are connected. Along this dorsal edge are disposed two rows of large cilia, which propel currents in two opposite directions, downwards along one side, and upwards along the other. Every part of the leaf beyond this cartilaginous border consists of a soft membranous substance (*h*), thickly vascular, composed, in fact, of little more than vessels. The next feature to be noticed in the structure of this branchial lamina is a series of duplicatures (*c, c* and *b, b*) of this surface, and is singularly distinctive of the branchial organ of this family of Mollusks. At first they look like accidental folds of a delicate membrane; but as they occur in every single leaf throughout the organ, it follows that they are organic formations. If the leaflet is laid carefully on the glass slip, floating in water, and gently covered, *without pressure*, the true character of these parts may be most clearly determined. They consist undoubtedly of a *bifid* fold (*B*) of only one half of the lamina, for a similar fold exists on the opposite surface. Each fold is made up of two parts, which are united gradually at either end, and separated by an interval in the middle. The long axis of each fold is at right angles with the line of the dorsal margin; but the row is parallel with the latter. Slightly beyond this row of plicæ, and nearer to the centre of the leaflet, is to be observed a second and smaller system (*c, c*). The folds are formed in the latter case precisely as in the former. These two systems of plications are separated from each other by a narrow space of smooth membrane. All that portion of the lamina which intervenes between the second row of folds and the extreme apex (*j*) of the lamina is a plain unplicated surface, sustaining a double series of parallel blood-channels. The anatomy of the folded portion of the leaf may be better understood on a transverse section (such section is represented at fig. B). It will be seen that the duplications of the surface are the same on both sides (*f, f*), and that the opposite folds are formed upon the same transverse axis.

The next problem to be solved in the analysis of this most beautiful mechanism relates to the disposition of the blood-vessels (*h, h*). This question could never be determined by injections, however fine or successful. The practised eye, reading



the same structure throughout an extended series of varieties and modifications, may infallibly decipher the blood-system even of these subtle and delicate laminae. The leaf tapers away into a slender point at the extreme membranous end (*j*). If the same blood-channel, or the same drop of blood, travelled from the dorsal border (*a, a*) across the entire length of the laminae, as far as the tapering point (*j*), it is evident that such a portion of blood would undergo an excessive degree of aëration, while that which traversed the space at either apex (*i, h*) would fall short of the required amount of oxygenation. This inconvenience is obviated by giving to the vessels a *generally* oblique direction across the plane of the lamina (*d, b*). The vessels as they traverse the folds (*c, c* and *b, b*) maintain the same character and direction as they exhibit on the smooth portions. This fact proves that these folds are really none other than duplications of the surface. They serve, notwithstanding, to multiply the active superficies of the little organ, and the vessels which they carry, although unaltered in direction, are smaller in diameter and more closely arranged. The ciliary action over these portions is also more active and vigorous than on other parts. The vessels are most distinct in outline and disposition about the central region of the leaf (*h, h*, fig. 4 *d*). That the channels are conduits, distinct and individualized, separately walled, running side by side, and seldom inosculating, may be unquestionably proved by the steady examination of this part. That the channels loop around the free edge (figs. 5 & 6) to gain the other side, along which they return, the observer may convince himself by focusing the microscope at this border. The appearance is then such as is shown in fig. 5, and fig. 9 *b*. The cilia of the flat surface are seated on a pavement epithelium, those of the borders stand out like filaments from a larger description of cell (fig. 8).

The author has proved, that in all the species of the genus *Littorina* discoverable on the coast around Swansea, the branchial laminae are constructed on the model (fig. 3) of that just described. The duplications are not of the same precise size and character in all; but in all they exist. He would propose this incident of structural type as a criterion of relationship between the several genera of the family of the Littorinidae. He has not examined the branchiae of *Lacuna*, *Assiminia*, *Jeffreysia* and *Skenea*; but those of the genus *Rissoa* discover a marked tendency towards this peculiarity of formation.

Several families must now be passed over as hitherto unexamined. The branchiae of the Muricidae may probably, however, be considered as typically representative of those groups which intervene between them and the Littorinidae.



The whole of this extensive family is said by systematic authors to be characterized by the possession of *two gills*; one described as doubly pectinated, and the other as singly pectinated. As formerly stated, Dr. Sharpey has adopted this definition in his article "Cilia," in the 'Cyclopædia of Anatomy and Physiology.' The branchial chamber in this family (fig. 2) is constructed on the same principle as that of other Pectinibranchs. It is a capacious vault, open in front from one side to the other by a fissure. On the left side the edge of the mantle is prolonged into an extended recurved siphon. The glands (*c, b*) of the cavity, as will be explained afterwards, are highly developed; one of them so much so as to have led to the idea that it was a second branchia. The true gill (*a, a*), which is a single organ, stands between this supposed supplementary gill and the large mucous gland (*c*), to the left of which is observed the rectum (*e*). In the Muricidæ, the third gland (fig. 1 *g*), called by some authors the renal gland, is not visible within the boundary of this cavity. The whole of the interior of the chamber is actively ciliated; the exterior is *not* so. The epithelium here is smooth. Little peculiarity exists in the branchial system of this family (fig. 4). The organ is large (fig. 2 *a, a*); it has the shape of two cones laid base to base. The broadest laminae are therefore in the middle, the smallest at either end. It is so situated as to receive directly the column of water as it enters by the siphon (*f*). The course of this water, as indicated by the arrows (fig. 1), is from left to right; it thus passes first, and in the most pure state, over the branchiæ, then over the mucous gland, and lastly over the rectum. The planes of the branchial laminae (fig. 4) are coincident in direction with the main water-current in passing from the left to the right side of the branchial cavity. Nothing is so easy as to determine the figure of the gill-leaves in any of the larger genera of this family. *Buccinum* is a familiar example.

The gill of *Buccinum undatum* is composed of many hundreds of leaves. These leaves, towards the centre of the organ, are regularly triangular in figure (fig. 4 *a, a*). At the extremities, each lamina loses more rapidly in vertical depth than in length, so that at last they become scarcely visible creases of the pallial membrane. The membranous border is drawn out to a considerable length (*g*) beyond that part of the gill which is apparent to the naked eye. By this extension of the active branchial surface, the action of the aërating current on the blood is prolonged. In no single instance of the pectinibranchiate gill are the cartilages of the laminae so developed as in this family. It is here that the true structure and office of these singular elements of the branchial mechanism may be most advantageously studied. In the



branchia of *Buccinum* they are straight, sword-shaped blades (fig. 7); they are skilfully fitted into the dorsal or thick edge of the lamina (fig. 4 *a, f*); they act the part of beams, or arms, whereon is hung the sheet of the leaflet (*a, g*). Without them, the latter could not by any means be held *in situ*; that is, could not be maintained at that degree of expansion essential to the proper and adequate contact of the blood with the water. To the bases of these cartilaginous beams, muscles (fig. 14 *c, d*) are attached, which are capable of influencing the entire leaf. Under their action it may be either stretched lightly or folded together like a closed fan. The flat surface of the branchial lamina in *Buccinum* is always unplicated.

In the fresh specimen it may be seen, with perfect clearness, that it is traversed by waving parallel blood-channels (fig. 4 *d, d*). In no instance among the Pectinibranchs is it more easy to convince oneself that these vessels loop at the free flexible margin (*c*) of the leaf than in *Buccinum* (fig. 5). The laminae are considerable in superficial area (*a, g*), exhibiting a surface equalling a tenth of a square inch. The vessels (*d*) are prominent, being readily traced by  $\frac{1}{2}$  an inch power. The walls display a granulated character (fig. 5 *g, g*), in consequence of the contents of the epithelium. This circumstance individualizes each blood-channel most clearly. The flat surface of the leaf is also covered by a flat, scaly, polygonal epithelium (fig. 6), the cells of which are filled with minute granules, and armed with short cilia. Along the base or fixed border of each leaf run two large vessels (fig. 4 *c, c*), one of which is afferent, the other is efferent. Thus, in brief, is written the anatomical history of this remarkable organ. It is at once evident that the key-stone of this structure is the beam of cartilage, which imparts strength and rigidity to the dorsal margin of the slender sheet; and, further, constitutes a point of attachment to a system of muscles, by which, as by a lever, the entire apparatus may be extraordinarily furled and unfurled, and otherwise variously controlled.

Another example of the Muricidan gill may be described, in order to show, that in two closely allied species of the same genus a striking difference of structure may occur in one and the same organ.

The *apices* of the laminae in the gill in *Purpura lapillus* are curved sharply (fig. 9 *a*). In *Buccinum*, as just stated, the dorsal border terminates in a straight point. Although this trait is only a microscopic incident of formation, it is quite enough to constitute the distinctness of the species. In every other respect the laminae discover the same structure as that just explained in *Buccinum*. The gill-leaves of *Murex* and *Nassa* exhibit also slight variations of *shape*, compared with the standard figure of those of *Buccinum*. From such examples the



naturalist may well exclaim, how marvellous and unaccountable, that in establishing the independence of species, Nature should change the very fabric of the minutest parts of the body!

In the Conidæ and Cypræadæ, the author has every reason to believe that the branchiæ conform with exactness to the type of those of *Buccinum*. They may vary in the special outline of the laminæ, but not in essential structure. They lie in the branchial chamber in the same oblique position, and exhibit the same relation to the glands of the cavity.

Although the transition may be strange and abrupt, it is convenient at this point to pass to the consideration of the pulmoniferous Gasteropods; not because there is much in common between their breathing system and that of the branchiferous orders, but because the glands contained in the thoracic cavity of the Pulmonata correspond in structure and dependencies most intimately with those which are contained in the branchial chamber of the Pectinibranchs last described. According to this distribution of subject, the "glands" of the respiratory cavity of both the branchiferous and pulmoniferous orders will come to be considered under one head.

#### *Pulmonifera.*

The leaf-like appendages of *Phyllodoce lamelligera*, which expose to the action of the aërating medium a true chylaqueous fluid, differ very little in intimate structure from the branchial laminæ of the Crab, the purpose of which is to distribute for respiration a current of blood, properly so called. But the tracheæ of Insects have no parallel amongst the respiratory systems of the Invertebrata. Compared with the respiratory organs of the water-breathing Articulata, these tracheæ constitute, in a complete sense, an apparatus invented *de novo*. Insects, with reference to the relations of this system, cannot therefore be said to be to the water-breathing Annulose and Articulated animals what the Pulmoniferous Gasteropods are to the water-breathing Mollusca. In the latter cases nevertheless, the aquatic and atmospheric systems are strikingly diverse.

In the instance of the air-respiring Crustaceans no change of structure whatever occurs in the respiratory system. The branchiæ of the terrestrial Isopoda are precisely the same in every detail of minute structure as those of the aquatic genera. The inference arises at once: these Crustaceans are merely modified water-breathers! But when an animal is to be formed whose medium of life shall *permanently* be the atmosphere, a design in the construction of the breathing system is adopted involving express provisions, which stand at marked variance from every variety of the water-breathing machinery. It is



accordingly observed that the contrast between 'the lung' of Pulmoniferous, and the branchia of the Branchiferous Gasteropods is almost as striking and irreconcilable as that which separates the trachea of the Insect from the breathing plume of the Annelid or the gill of the Crab. In the midst of the aquatic Articulata, the air-breathing Insect arises on the scene ; in the midst of the aquatic Mollusca, the pulmonated Gasteropods are formed. The object being one and the same, namely to produce an air-breathing animal, the artificer being still within the limits of the Invertebrate subkingdom, the question is most natural, Are the means in the two cases also the same by which the one and the same end is sought to be attained ? —No ! they are most wonderfully and extraordinarily dissimilar. The tracheæ of the Insect pervade the entire substance of the body of the animal. The 'lung' of the Snail is a mere bag, inflated as if by some rude and fallible artist, under the skin of the back. The former charms the eye as it discovers the mingling of the infinitely perfect with the infinitely minute. The latter shocks the mind with disappointment as it views the characters of a contrivance at once coarse, clumsy, and inadequate. But is it so in reality, or is it so only because imperfectly understood, and because it is measured by a wrong and unfair standard ? Is not such an apparatus, simple as it is, quite enough to sustain the sluggish vitality of these slow-moving and sleepy animals ? And is not the *end in view* accomplished quite as perfectly as it is in the case of Insects, though by a machinery of incomparably greater apparent intricacy ? These questions will well prepare the mind for the investigation of the actual details.

All the terrestrial and the majority of the freshwater Gasteropod Mollusks breathe air. They are provided with a pulmonary cavity or sac, whose walls are networked with vessels by which the blood is exposed to the aërating element. No form of branchiæ exists. The animals which present this organization are all provided with distinct heads and furnished with tentacula and organs of sight. They walk by the aid of a well-developed creeping disc. One large division of the land snails is supplied with an operculated shell ; the rest are inoperculate and sometimes shell-less. The Pulmonifera are closely related to the plant-eating sea snails (Holostomata) through the Cyclomata, and to the Nudibranchs by *Onchidium*. As a group, the land snails are inferior to the sea snails, on account of the comparative imperfection of their senses, and the union of the functions of both sexes in each individual.

The typical inoperculate Pulmonifera vary in appearance and habits, but agree essentially in structure. The respiratory orifice is small and valve-like, to prevent too rapid desiccation



in the land species, and to guard against the injurious entry of water in the aquatic tribes†. Hence they have been called *Adelo-pneumona* (or concealed-lunged) by Dr. Gray; the *Operculata*, by antithesis, being named the *Phanero-pneumona* or open-lunged.

The Onchidiadæ are sea slugs, breathing by means of a pulmonary cavity, but living immediately in contact with marine conditions. According to the dissections of Mr. Hancock, the "lung is placed in this group at the posterior extremity of the body, and has consequently the heart in front of it."

Respiration in the Limacidæ is accomplished by means of a cavity seated on the back near the neck, and covered by the disc (Pl. XI \*. fig. 1). It opens on the right by a valvular sphincteric orifice, which is endowed with an active power of widely dilating and of closely contracting (*e*). In this family the rectum does not traverse the respiratory chamber; it lies external to, and below its right boundary. The anal orifice therefore is separate from that of the respiratory; it is seen immediately below the latter. This is a fact of structural disparity between the Limacidæ and the Helicidæ. In the latter the intestine is a prominent object in the breathing-chamber, and the vent is confounded with the pulmonary orifice. The position of the generative outlet is variable.

The following description is founded upon numerous dissections of the common Slugs. The breathing-sac presents in all the species the same anatomical characters. It is best studied by fixing the animal with two strong pins, transfixing the body in front near the head and behind near the tail in a cork-bottom dissecting dish. One blade of a strong, blunt-pointed sharp scissors should be inserted into the pulmonary orifice. The point should now be carried round the boundaries of the chamber, the disc being cut as the instrument travels round. Such a section (fig. 1) will enable the lid of the cavity or the respiratory disc (*b*) to be so perfectly raised as to leave the entire space underneath quite uninjured. A part corresponding with the pericardium (*c*) will however be found to be adherent to this roof; it should be snipped with the scissors. The roof, in the substance of which is lodged the rudimentary shell, should now be reflected and pinned down (as shown in figs. 1 & 2). From the central space of the cavity a second membrane (fig. 1 *c*) will require to be raised. This is much more vascular than the former integumentary covering (*b*), and constitutes really a part of the respiratory surface. This structure serves also as peri-

† See the excellent Manual on Recent and Fossil Shells, by S. P. Woodward.



cardium. It overcovers the heart, and embraces the large curved gland, in the centre of the area bounded by which the heart (Pl. XI \*. fig. 1 *d*) is situated. A perfect view of this pulsatile body is thus obtained. It beats slowly, about 30 or 35 times in a minute; less frequently probably in an unmutilated animal. It consists of an auricle which is situated under or below the ventricle. The ventricle is not a linear continuation of the auricle, separated only by a constriction as it is in the Helicidæ, but a separate organ receiving the auricle by a laterally placed auriculo-ventricular orifice. It will be seen that the large blood-channels (fig. 1 *g*) which are distributed over the floor of the cavity, and which in nature are of an opaque white colour, converge upon the auricle, and that the aorta (*h*) rising boldly up from the ventricle as a vigorous vessel of considerable calibre, pierces the base of the chamber and disappears, travelling backwards among the viscera.

Now of the Limacidæ it cannot with truth be said that they are either Proso-branchiate or Opistho-branchiate. The heart here is certainly not placed either before or behind the respiratory organ, but in its true centre. The ovoid space circumscribed by the gland (*c', c'*), and roofed down by the pericardium, has only one opening through which the air can effect its ingress and egress. This opening corresponds to the point at which the line of the gland is interrupted. In some species it is placed at a point on the left side remote from the external orifice (*e*), in others behind; in others again it has an anterior position. That portion of the cavity which is without the gland, and between it and the outer boundary of the disc (*f, f*), forms a circle, so that the air may course around the cavity from right to left or reversely, according to the tendency of the muscular action by which it is impelled. The movements of breathing are far less manifest in the slug than in the snail. In the slug the pulmonary orifice slowly opens, and the bag is emptied by the slow expulsion of the air. The act of inhalation is performed in a similarly slow manner. The orifice now firmly closes, and remains closed until the next act of expiration, which may occur irregularly in ten minutes or a quarter of an hour.

Two points in the history of the respiratory cavity of the Limacidæ demand special attention. First, the structure and distribution of the vessels, and secondly, the character of the membrane or covering by which the cavity is lined. As a rule, it may be stated that the pulmonary vessels are distributed in the Limacidæ over the floor of the chamber, in the Helicidæ over the roof. In the former the mucous gland is considerably larger than in the latter. The heart of *Limax* lies, like the pulmonary network, on the bottom of the cavity; that of *Helix*,



like its pulmonary *rete*, is located in the roof. These are features of striking dissimilarity.

The pulmonary vessels (*a*) of *Limax* are not, as in *Helix*, gathered into one large trunk, debouching in the auricle. They consist of several trunks, the cylinders of which are so superficially situated as to stand in prominent relief above the main plane of the cavity. This peculiar appearance results from the rigid calcareous walls of the vessels. It seems, according to the author's dissections, as if two or three veins in *Limax* opened into the auricle, but it is not easy to determine their exact number. The peculiar tenacious mucus secreted by the gland (*c'*, *c'*) which surrounds the heart (*d*) is poured out into the respiratory cavity. But although this is the case, it does not interfere with the function of the surface over which it is diffused. It does not become *adherent* to the latter. This mucus is capable of enclosing globules of air, and of becoming frothy. In this state it is frequently extruded from the pulmonary orifice. The study of these glands and their structure is for the present postponed, since they share in no way in the process of respiration.

Cuvier and the older anatomists supposed, when they observed the *white colour* of the vessels in the Limacidæ, that the phenomenon was due to the *milky* character of the blood by which they were filled. This is an error. The white colour results from the mixture of fat and chalk which abounds in the substance of the walls of the vessels, imparting to them a peculiar character and extraordinary thickness; such thickness as renders it extremely difficult to understand how they are not thereby disqualified for the office which they are designed to discharge. The larger vessels (fig. 1 *g*) stand upon a more superficial plane than the smaller ones. This disposition gives a *cellulated* appearance to the surface (fig. 2), like that of the inside of the frog's lung. It is an arrangement which, more completely than a smooth surface, detains the air in contact with the blood. But though a *tendency* to the cellular form is displayed by the pulmonary membrane, it must be understood that it is not *organized* after that fashion, as is the case with the lung of the frog.

The pulmonary vessels in the Pulmonated Gasteropods form but one sheet, that is, the blood traverses the area of aërating surface only *once*. The blood-currents converge upon the respiratory chamber from all parts of the body. Large trunks (fig. 2) may be seen at the sides of the cavity before, behind, and at the sides. These trunks are individually walled vessels; they are true pulmonary arteries. They subdivide into smaller vessels, and these break again into a network constituting the real lung of the animal. Near the position of the heart, they begin to



reunite, large trunks becoming visible, which end in the auricle. The larger trunks are visible to the naked eye; the smallest require all the skill of the microscopist for their examination. The coats of the more visible white trunks are rendered colourless under the joint agency of dilute muriatic acid and æther: neither reagent alone will remove the white colour. The acid will dissolve the lime and leave the fat: the æther will remove the fat and leave the lime. The fat and the lime are contained in *cells*, and intimately mixed. The lime exists in the form of amorphous granules; it does not *crystallize* even in the rudimentary shell contained in the roof, but from the conical masses which adhere into groups in some places, it is evident that a tendency to crystallize is manifested.

It seemed to the author a point of extreme interest to determine whether the lime and fat which render the outline of these vessels, especially in the common Black Slug, so conspicuous, were incorporated in the substance of the vascular walls, and in what manner, or whether they were lodged in a tissue occupying the intervals between the vessels. These questions immediately arose. It appeared so utterly without precedent that vessels, destined to aërate the blood, the smallest, the most subdivided, the most thin-walled, the most naked of all the vessels of the body, in every other animal, vertebrate and invertebrate, should in the instance of the Limacidæ be encumbered with such thick, even inorganic, rigid parietes!

The physiologist is embarrassed in attributing to a machinery, by comparison so coarse and clumsy, a function so subtle and refined as that of breathing. But is it not presumptuous to pronounce a verdict of imperfection upon any of the works of Nature? Is it not possible that faultless skill and matchless adaptation of instrument to purpose, may yet reveal itself beneath the apparent characters of an organ which at present may appear rude and ill-contrived? It is more probable that Nature should be perfect than that her critic should be so.

A transverse section of one of the larger vessels will render it at once evident that each trunk is lined *internally* by a smooth non-calcified membrane, and that the lime-particles are deposited *only in the substance of the external coats*. The presence of this inorganic substance destroys the power of the vessels to contract upon their contents. The blood is circulated therefore through the pulmonary membrane by some other force than that usually due to the elasticity of the vessels. Although the fact is of difficult proof by direct demonstration, it is almost certain that the *exterior* of each vessel is also lined by a non-calcified membrane. It must be so, because active vibratile cilia unquestionably exist



in various parts of the pulmonary cavity in every species of *Limax*\*.

If the internal and external coats of the vessels assume thus the characters of two concentric non-calcified cylinders, it follows that the mineralized layer must occupy the intervening space, representing the middle coat. This is probably the truth. But whether the external membrane and the lining of the cavity be separate structures or not, it is indisputable that the vessels are enveloped in a thick calcareous sheath. It is obvious, therefore, that the respiratory gases respectively leaving and entering the blood must traverse this dense septum,—a peculiarity quite without a parallel in the whole history of the organs of respiration. In the higher animals the pulmonary vessels in all classes are brought so near the aërating surface, that anatomists of eminence are not wanting who assert that such vessels are not covered by any kind of epithelium whatever. If then all structures interposed between the blood and the air are thus studiously reduced to the utmost extreme of tenuity in the higher animals, how is it that in these highly organized Gasteropods the respiratory vessels should not only be encumbered by thick coats, but by those of an inorganic nature?

Either in these animals respiration is reduced to a minimum, or these calcareous coats not only do not interfere with, but literally facilitate the interdiffusion of the gases. Although this idea presupposes a mechanism quite unique in the history of the breathing organs of animals, it involves nothing which contradicts the laws of endosmosis. The mineral which is deposited in the coats of the vessels is the carbonate of lime. It is impossible that such a substance could exert any chemical affinity either for oxygen or carbonic acid. The lime-particles are so loosely strewn together that they are separated by spacious interstices. Such a septum would present no obstacle to the diffusion of gases. In fact the endosmotic conditions of the beautiful experiment devised by Prof. Graham, in which he coated a coarse sheet of brown paper with a thin film of collodion, are precisely imitated in the vessels of the Slug. Prof. Graham found that the organic film so placed did not in the least degree diminish the rate of diffusion at which gases pass through a sheet of brown paper.

It is quite certain then that the vessels of the lung-sacs of the *Limacidæ* are *encircled* by the calcareous coats. The lime is not

\* I invite especial attention to this point, because hitherto all anatomists have denied the existence of ciliated epithelium in the interior of the pulmonary chamber of air-breathing Gasteropoda. I have proved the fact of its presence beyond doubt, and by repeated observations.



deposited in *lines*, as the cilia are disposed along the branchial leaves of the Lamellibranchiate Mollusks, leaving a non-ciliated interval to which the active process of respiration is chiefly limited. The gases *must* consequently traverse the entire substance of the calcareous and membranous coats. The interstices between the calcareous particles might on this view be considered as each representing a *cell*, in which a small volume of air is held stationarily in intimate contact with the blood, and beyond the disturbing control of the ever-moving and varying parietes of the general cavity; and in which, as in the air-cells of Mammals, the interchange of the gases is a *continuous*, not an interrupted, process. But these permeable calcareous coats, while they divide the oxygen into myriads of infinitesimal portions, bringing it thus in a state of extreme subdivision into contact with the blood, act also like other porous bodies upon gases, by *condensing* their volumes. The power thus exerted increases the diffusiveness of the gases, and consequently augments the measure in a given time of the function of the part, because it virtually accelerates the interchange of the gases. The *ultimate* vessels of the abdominal organs are furnished with soft non-calcareous coats. The lime in these parts of the body is present only on the larger trunks. This substance is suppressed, therefore, in those organs in which its presence would interfere with the nutritive and secernent office of the minute vessels. Being present on those of the lung, the inference is unavoidable, that in this situation at least it does not obstruct the function of the organ. It seems on the clearest grounds that the mechanical subdivision of the air in a respiratory organ may be made to supersede the necessity for the subdivision of the blood by the formation of a *rete mirabile*. To this end in the *Limacidae* a contrivance of singular simplicity is adopted: the air is made to rush in steady but infinitely divided currents in the direction of the blood. This is enough to secure the intended result. The blood accordingly flows in channels of comparatively large diameters. Coarse trunks separated by wide intervals, they contrast most strikingly with the elaborately formed parallel capillaries of the gills of all the branchiferous orders of Gasteropods, in which the blood-stream is reduced to the utmost minuteness.

On no other interpretation of the anatomical facts by which the pulmonary sac of the air-breathing Gasteropods is distinguished, is the reproach of rudeness and coarseness of construction to be removed. On this interpretation the rudeness is turned into subtlety and the coarseness into refinement, and the physiologist may cite indeed an organ which at first only shocked the short-seeing mind with a sense of disappointment,



as only another illustration of the illimitable fertility of resource by which every part of every living mechanism is distinguished. It is only by such a contrivance that the *necessary surface* for the aërating process can be realized; for compare the area of this lung-sac with the extraordinarily multiplied superficies secured by the laminose arrangement of the gills in the branchiferous orders, and how considerably the latter will be found to exceed the former! In comparing a gill with a lung, even in the same class of animals, and organized on the same type, it is necessary to remember that in the former case the oxygen, dissolved in water, is brought up to the blood under certain opposing circumstances, and that a compensation is offered in the divided state of the blood, while in the latter a similar amount of work may be done with large vessels and coarse streams, in consequence of the unmixed and direct manner in which the active element is applied to the vital fluid.

The pulmonary chamber of the Helicidæ is distinguished by several anatomical particulars from that of the Limacidæ. In the Snail (fig. 3) the rectum (*a*) enters the precincts of the chamber, and the heart (*b*), mucus-gland (*g*), and pulmonary vessels (*d*) are seated on the roof (*h*) of the cavity. In the Slug, as already detailedly explained, the rectum is external to the chamber, and the heart, gland, and pulmonary *rete* are placed at the bottom of the cavity.

*Helix aspersa* (figs. 3, 4 & 5) is the best, because the most familiar, example of the family of the Helicidæ. In it, as compared with *Limax*, a marked deviation is observed in the position of the mucus-gland. That of *Helix* presents the appearance of a soft oval mass (fig. 3 *g*) situated to the right of the heart when *in situ*; it is considerably less developed than it is in *Limax*. This proximity of place to the heart has probably some meaning which is not yet understood. But in structure the gland is the same in the two families. The auricle (*c*) and ventricle (*b*) of the heart in *Helix* are placed on the same axis; they are separated only by a slight constriction. In *Limax* the divisions of the centre of the circulation are placed on different axes, and more individualized. In this latter genus it is planted in the centre of the respiratory plexus, and also in that of the cavity. In *Helix* it is situated at the posterior boundary of the chamber.

The roof in this shelled genus is a flexible membrane (fig. 3 *b*, and figs. 4 & 5 *c*). It is fixed posteriorly to a sort of diaphragm (fig. 3 *i*) which imperfectly divides the thorax from the abdomen (*j*). In the substance of the roof is lodged a stratum of muscles which contract and relax synchronously with the expiratory collapsing and inspiratory expanding of the cavity. These respiratory movements are very markedly defined in the animal of *Helix* removed



carefully from its shell (figs. 4 & 6). The fixed position afforded by the ligament which ties the body to the columella, yields important service in the mechanical acts of respiration.

The soft abdominal segment (fig. 3 *j*) of the body is covered by a continuation of the mantle. In this situation the membrane is thinner, smoother and more delicate. *It is quite adherent everywhere to the subjacent organs.* There are no vacuoles either between it and the invested viscera, or between the viscera themselves. During retraction the foot may be concealed completely in the cavity of the thoracic moiety of the animal. This explains why it is that the viscera (brain, œsophagus, portions of reproductive and chylopoietic viscera, &c.) are so loosely packed in this region, and why it is that large spaces filled with fluid lie intermediately. Such vacuoles are more spacious in the *Helicidæ* than in the *Limacidæ*, because in the former the head and foot are more retractile than in the latter. The anterior surface or front of the operculum is perforated on the right side by a large, valvular, irritable sphincteric orifice (figs. 4 & 5 *a, a*). In the edge of the mantle directly above this orifice is observed a deep notch (fig. 4 *e*), which, when the animal is tightly coiled up into itself, fits over the orifice. By this simple contrivance, under all circumstances, the patency of the communication between the breathing-chamber and the external air is secured. So important is this point, that, both during hybernation and when the animal remains long attached to a dry calcareous stone in arid seasons, the membranous epiphragm which is then formed from the mucus supplied by the mucus-gland, is valvularly perforated at a point corresponding to the respiratory orifice. Respiration therefore, though sometimes greatly reduced in amount, at no time during the life of the animal completely ceases.

The pulmonary plexus, which in *Helix* is restricted to the roof of the cavity (fig. 3 *h*), presents a much more regular and symmetrical arrangement of the vessels than that of *Limax*. In *Helix* a main vessel (*d, d*) runs obliquely from left to right along the vault of the cavity; it terminates by dilating into the auricle (*c*); it commences at the anterior border (*d'*) in branches which converge upon it with great regularity of course. The lateral trunks are similarly regular. In some places the ultimate vessels can be traced with the naked eye: they are best viewed as opaque objects, by cutting off the entire roof and placing it, vessels uppermost, between two slips of glass, and then examining with a two-inch or an inch object-glass. It will be observed that the primary or large trunks (fig. 6 *a, a, a*) run, on the whole, in parallel directions, enclosing interspaces of pretty uniform diameters; and that the secondary branches (*b, b*) proceed from the



primary also in a determinate manner, separated by tolerably uniform distances, and running in tolerably orderly directions, so that they leave between them spaces which manifest a tendency to symmetry of outline and regularity of area.

The ultimate vessels (fig. 6 c, c) undoubtedly obey a similar method of distribution. If a spot be taken for inspection in which they are densely present, the vessels will be found to lie in parallel columns (as represented in Pl. XI\*. fig. 6, which has been drawn with great care from the actual object). In other places, especially towards the circumferences of the roof, they exhibit a more sparse and less regular distribution. If such portions of this vascular membrane were folded in the "ridge and gutter" fashion, taking care that the secondary vessels coincided with the borders of the folds, a *branchia* would be formed whose structure would conform with the *laminose* principle. It may conversely be said, that the lung of the air-breathing Gasteropod is nothing but the branchia of the water-breathing Gasteropod, having the laminae of the gill so unfolded as to form a straight sheet. This comparison is really not too far-sought. In both instances the ultimate vessels present a uniform cylindrical character, seldom intercommunicating: such a comparison, however, is quite untenable in the case of *Limax* (fig. 2). Here the plexus is arboriform and irregular, circumscribing areas of various sizes and figures. Like that of *Limax*, the lining of this cavity in *Helix* is undoubtedly ciliated at various parts. It is only possible to detect the presence of cilia along the lines of the larger vessels, and here and there in creases in their vicinities.

From the author's observations, it is probable that the spaces between the larger vessels, and coinciding with the capillary areas, are devoid of *ciliated* epithelium. Nor is it easy to separate the layer of epithelium by which these parts are covered, from the elements of which the coats of the vessels themselves are composed.

In *Helix* the coats of the pulmonary vessels (fig. 3 h) are considerably less calcified, less white in appearance, and more flexible than those of *Limax*. They afford, therefore, a more favourable opportunity for determining their minute structure.

The same surprise may be expressed with respect to this lung-sac as with respect to that of *Limax*, viz. that so limited a vascular area presenting vessels so coarsely subdivided, should suffice, in so bulky an animal, to supply the demands of the respiratory function. While all other animals, even those inferior to these Mollusks in serial standard, are furnished with organs which involve prodigious superficies for action, how is it, it may again be asked, that in these superiorly endowed Gasteropods so rudely constructed an apparatus, so carelessly formed an organ



should be enabled adequately to discharge a function so imperious?

Can there be any peculiarity in the structure of the vessels? As the calcareous layer is less developed here than in *Limax*, it is obvious that the presence of this layer is not an indispensable constituent of the organ. The pulmonary vessels in the Snail exhibit a structure which cannot well be proved to exist in the Slug. Their coats bulge out in a cellular-like manner. This occurs all round the circumference of each vessel, most distinctly in the smallest. It is impossible to determine whether the convexities on the exterior correspond with concavities on the interior of the vessels. But, by inference from the character of the outside, it seems almost certain that such an arrangement does really exist. If it does, it is not difficult to understand how considerably it is calculated to augment the surface of contact between the blood and the air. Though such cellulated parietes might mechanically slacken the speed of the current, the function of the part cannot fail to be considerably raised in amount.

*Lymneadæ*.—"These freshwater pulmoniferous snails constitute a very natural family, the animals of all bearing a great similarity to each other, and being similarly organized. All have short, broad snouts, and two tentacula of considerable size, either triangular or subulate in shape, with eyes placed at their inner bases." (Forbes and Hanley.) Little has been done by anatomists to elucidate the structure of this interesting family. In several features they approximate closely to the *Helicidæ*. The most striking character is the siphon-like tube into which the respiratory orifice is prolonged. This siphon (fig. 7 *a*) is capable of being considerably extended beyond the edge of the mantle (*b*). When the animal is floating reversely near the surface of the water, it may be seen from time to time to be slowly pushed above the surface into the air. At this moment, and through it, the effete contents of the respiratory cavity are emitted, and a supply of oxygen is drawn in. So wonderfully sensitive and discriminative is this little organ, that it opens only when it peeps into the atmosphere. Water never enters into the pulmonary chamber of *Lymneus*. The same observation applies to *Planorbis*.

But in these water-snails the breathing-chamber (fig. 7 *c*) is more actively ciliated than in the terrestrial families. Not because they breathe at any time on the aquatic principle, but probably because the whole tissues in these water-inhabiting genera are less calcified, and therefore more favourable to the development of cilia. It must, however, be supposed from these statements that the breathing-chamber is lined with a continuous



layer of ciliated epithelium. It is detectible only on certain parts which chiefly correspond with the lines of the large trunks. The Limneids differ from the Helicidæ in being furnished with a richly ciliated epithelium on the *exterior* of the respiratory cavity. In young specimens vibratile cilia may be detected over the entire abdominal portion of the body. In the old, however, it disappears from this region, and is replaced by a non-ciliated variety.

In *Planorbis* the distribution of cilia is more limited. It is detectible on the siphon and margins of the thoracic cavity. With care it is possible to lay open or to remove the roof of this cavity in a large specimen of *Lymneus*, fixed by pins whilst floating in water. The roof delicately cut away is placed between two slips of glass and examined as an opaque object. The larger vessels present a general arrangement analogous to that formerly described in *Helix*. A large central trunk runs obliquely from the left anterior to the right posterior angle of the cavity (fig. 7 *d*). It is the main venous channel which terminates in the auricle (*e*). The lateral or secondary trunks converge upon the line of this vessel from all sides. It is scarcely possible, in consequence of the absence of lime from the coats of the vessels, to trace the distribution of the ultimate channels. From glimpses obtained here and there, it is however most probable that they observe a parallel mode of division such as that already represented in the Helicidæ. The heart differs from that of *Helix*. The ventricle stands at an angle on the auricle. The axes of these two divisions meeting at the auriculo-ventricular orifice would form nearly a right angle. The gland (*f*) occupies a position to the left of the heart; it resembles that of *Helix*; it is an oval flocculent mass. To the right of the heart, the rectal intestine (*g*) enters within the precincts of the respiratory cavity; it traverses the chamber along its floor, and terminates in the siphon (*a*).

The breathing-chamber in the Lymneadæ exceeds that of all other air-breathing Gasteropods in size relatively to that of the body. The surface for the outlaying of the pulmonary plexus exhibits a greater relative area. The pulmonary sac of *Planorbis* is probably organized after the model of that of *Lymneus*. It is formed however on too small a scale to admit of a direct and satisfactory examination. The siphon is extensile like that of *Lymneus*, and like that of the latter genus, the cavity communicates externally by means of the siphon alone.



*The Glands contained in the Respiratory Cavity of Branchiferous and Pulmoniferous Gasteropods.*

The respiratory cavity of all Cephaloporous Mollusks, in addition to the organs of breathing, lodges one, two or more glandular bodies, the structure and office of which are the subject even at the present time of dispute among comparative anatomists. In different genera these glands affect different relative positions in the cavity.

In some instances they are near and parallel to the rectum, in others they encircle the heart, in others they constitute a mass lying only on one side of this organ. Many of the Pectinibranchs are provided with two glands, in the space between which on the roof the branchia is situated.

By Cuvier they were called the muciparous glands. Dr. Sharpey has supposed the one to be a supplementary branchia, the other he has designated after Cuvier the mucous gland. By Swammerdam, Poli, Blumenbach and the elder anatomists, they were supposed to be concerned in the secretion of calcareous salts. Bojanus conceived that the glands contained in the breathing-chamber of the higher Gasteropods were homologous with certain glandular bodies described by him in the Lamellibranchs, in both holding a similar relation to the branchiæ. As he had proved the latter to be kidneys, he inferred that the former must be so also. The alleged muciparous glands of the Gasteropods were believed by Meckel\* to constitute the true renal system of these animals. A new demonstration of their renal character was subsequently rendered by Jacobson† by the discovery of uric acid in the substance of these glands. His researches comprised analyses of the glands of *Helix pomatia*, *Limax niger*, *Lymneus stagnalis* and *Planorbis cornea*. Jacobson's views, however, had been anticipated by Döllinger and Holmlich‡, who had long previously indicated these glands as the real kidneys of these animals. It is stated by Siebold and Stannius§ that in the dried kidneys of *Helix pomatia* and *Paludina vivipara*, when treated with nitric acid and ammonia, considerable quantities of murexid may be discovered. Treviranus has descended to the minuteness of asserting that in these Gasteropods a portion of the pulmonary or branchial, recently arterialized blood passes through the kidneys in its path to the auricle. In another

\* Müller, Arch. 1846, p. 13. taf. 1.

† Müller's Arch. vi. 1846.

‡ Dissertatio de Helice pomatia. Hirceb. 1813, p. 23.

§ Comparative Anatomy of the Invertebrata, transl. by Burnett, p. 253, note 3.



place in their excellent work, Siebold and Stannius observe that in the Pectinibranchs the *kidney is replaced* by a gland which is situated behind the branchia between the heart and the liver, and which in the marine species *secretes the purple liquid*. This is the gland which Dr. Sharpey has described as a bipectinate and supplementary gill.

Kidneys have also been described by Quoy and Gaimard, under the several names of muciparous glands, organ of the purple, depurating organs, &c., in *Phasianella*, *Turbo*, *Buccinum*, *Mitra*, *Oliva*, *Capraea*, *Harpa*, *Dolium*, *Cassis*, *Purpura*, *Fusus*, *Auricula*\*. Leydig has also given an account of the renal siphon of *Paludina Vivipara*. More recently Mr. Huxley † has expressed his belief in the correctness of the prevailing views as to the true renal nature of the glands contained in the breathing-chamber of the branchiferous and pulmoniferous Gasteropods, and has adopted as conclusive of all doubts, the results obtained by the lithic acid tests in the hands of Jacobson, Meckel and Kölliker ‡.

The preceding outline of the literature of the question which relates to the renal system of the Invertebrata will suffice to reveal a chaos out of which it does not seem easy to evoke aught that is orderly and consistent. It is evident that the same names have been applied by different observers to very different organs. No clear views as to what should and what should not be characterized as distinctive of a renal organ in the Invertebrate animals, have ever been defined by anatomists. If a marked uniformity of structural type and plan runs through the entire series of other organs in the Invertebrata, such as the biliary, respiratory, circulatory, digestive, &c. systems, the inference is highly probable that a similar serial consistency of plan presides over the renal system. If such be the case in the Vertebrate, why should it not be so in the Invertebrate series? In another place § the author has shown, that the fluids, viewed as chemical and vital solutions, grow more and more simple as the zoological scale is traced downwards (or more and more complex as it is followed upwards); he thence argues that the same tendency to simplification is also manifested by the systems of the solid organs. This is the true science of the comparative anatomy of organs. Their history in this sense has never been written. If the true relation between

\* Voyage de l'Astrolabe, Zoologie, ii.; or Isis, 1834, p. 285; 1836, p. 31.

† "On the Morphology of the Cephalous Mollusca," Phil. Trans. 1853.

‡ Entwicklungsgeschichte der Cephalopoden.

§ "On the Chemistry, Physiology and Pathology of the Blood," in the British and Foreign Medico-Chirurgical Review for 1853-4.



the solid machinery of the glands and the fluids could be established, it would be most certainly discovered that at the point in the descending series at which a given constituent of the fluids, which a given gland was specially designed to withdraw, ceased to exist, the gland would also cease to exist. The proposition when thus enounced assumes almost a necessary certainty. The mind feels at once assured that no other law can explain the facts, which are indubitable. Anatomists have always worked on the presumption that the fluids of the lowest animal *must* have the same composition as that of the highest, and that consequently the necessities of the organism in the two instances must be the same. If the highest animal be provided with a kidney, therefore the lowest must be endowed with the same organ. Up to this æra in physiology, such in truth has been the fallacious reasoning by which the most distinguished cultivators of this science have conducted their researches. The same observation applies to the secreted products of the physiological actions of organs. It is supposed that because certain ingredients are found to exist under all circumstances in the secretions of the higher animals, consequently the same principles *must* exist in those of the lowest. This false logic has led astray the minds of men for an entire century. There may be nothing in common between the bile of the Mammal and that of the Cephalopod, yet each may be the product of the action of a *liver*. The same reasoning applies to the urinary secretion and to the renal system. Urea and lithic acid, the supposed basis and essence of this secretion in the urine of the Vertebrated animal, are not *necessarily* to be regarded as the basis and essence of the analogous secretion of the lowest Invertebrata. If such reasoning were grounded on truth, it would involve a ridiculous paradox to deny that the minute anatomy of this system of glands was not precisely the same in every grade of the series. But it may be proved immediately, and most readily, that the Malpighian coils of capillaries, so constantly and essentially distinctive of the kidney even of the lowest Vertebrated animal, disappear *in toto* from that of the Gasteropods and the Cephalopod. Here, at the very first step, the fundamental structural element of the higher phase of the organ vanishes. If it be so, is it not reasonable to infer that a correspondingly marked and essential change has occurred in the secreted product of each organ?

The preceding observations, general though they may be, are abundantly sufficient to justify the assertion, that in the present state of knowledge with reference to the comparative histology of the renal system, and the comparative chemistry of the renal secretion, the physiologist is not in a position to state with



certainty and confidence whether the alleged kidneys even of the higher cephalous Mollusca are really so or not†.

As the complete history of the glandular bodies which are lodged in the respiratory cavity of the cephalous Mollusca will rightly fall within the compass of another series of researches, the author on this occasion will give only a slight sketch of their structure, and that more because they are constant attendants on the respiratory organs in this class of animals, and occupants of the chamber dedicated to respiration, than because they are asserted by some anatomists to be muciparous glands, and by others no less distinguished as true kidneys.

That gland (Pl. XI\*. fig. 1 *c'*, *c'*, and fig. 3 *g*) which Cuvier first designated "l'organe de la mucosité," is unquestionably traceable as one and the same body throughout various changes of form and place and size, in all the pectinibranchiate and pulmonated Gasteropods. Under all diversities, it is identifiable by its anatomical structure. Cuvier thus defines its office and locality: "Le rectum, et oviductus de la femelle rampent aussi le long du côté droit de cette cavité, et entre eux et les branchies est un organe particulier composé de cellules recélant une humeur très-visqueuse, servant à former une enveloppe commune, qui renferme les œufs et que l'animal dépose avec eux‡." That gland which in *Buccinum* is situated between the rectum on the right and the branchia on the left (when the roof is *in situ*), and attached to the roof of the branchial chamber, is the same gland with that which in *Limax niger* (fig. 1 *c*, *c*) lies on the floor of the pulmonary cavity, is extended in figure, and circumscribes a space in the centre of which the heart is situated. These two examples will serve to indicate the extremes of figure and locality which one and the same gland may assume even in kindred genera.

In the Littorinidæ (fig. 7 *f*) it affects the same position on the roof between the branchia and the rectum.

† During my recent studies among the Invertebrata, I have accumulated a large mass of materials elucidatory of the serial anatomy of the renal system. It would be quite irrelevant to enter further into details in this place and upon this occasion. I trust that for such a task another opportunity will occur. I am deeply impressed with the belief that real service will be rendered to the comparative anatomy of the Invertebrata even by the publication of such results as have already been attained. It is certain that the urea and uric acid tests, in determining the renal or non-renal character of supposed kidneys in the case of the lower and lowest Invertebrata, lead to conclusions utterly unworthy of confidence. This point I have abundantly proved. The presence of uric acid in the renal secretion supposes a highly nitrogenous or proteinized composition of the blood,—in fact, such complex conditions as do not exist in the fluids of the lower invertebrated animal.

‡ Règne Animal, vol. sur les Mollusques.



In the Helicidæ (fig. 3 g) it appears under the form of an oval mass, situated still on the roof of the pulmonary cavity; and, when the parts are *in situ*, to the right of the heart. Thus in the particular of locality, this gland in *Helix* differs remarkably from that of *Limax*, in which it is placed on the floor (fig. 1 c, c) of the cavity. In the Lymneadæ it is observed to occupy the same situation as it does in the Helicidæ. The Planorbidæ are too small to render it practicable to examine this gland separately; but, as in the former family, its position is on the roof and on the right of the heart.

That gland which by Dr. Sharpey has been called the supplementary and doubly laminose gill, is a totally different organ from the former. It does not exist under any form in the pulmoniferous orders. It is largest and most developed in *Buccinum*; in the Periwinkle it is also very distinctly observable. It is situated always to the left of, and parallel to, the branchia. It is invariably tinged with a dark green colour. It terminates anteriorly in a long excretory duct which travels under the membrane of the vault and ends near the rectum.

By Cuvier, and all systematic naturalists, it is believed to be the organ which secretes the "purple and other dyes" which these animals are capable of pouring out, and has been accordingly designated the "colour-gland." In relative position and in general and minute structure, it is readily distinguishable from the "organe de la mucosité" of Cuvier.

The author's purpose at present is simply to present a sketch of the structure of these glands. No opinion with reference to their function can assume a stable and reliable form which is not supported by the results of other researches into the structure of the corresponding organs of other classes of invertebrate animals. This more extended task is reserved for another occasion.

Although in *Limax* the so-called "muciparous gland" differs both in figure and situation from that of *Buccinum*, in minute structure they are not only similar but identical. The folds of which these bodies are composed were called the "*feuilletts muqueux*" by Cuvier. They are attached to the internal face of a sort of a *tunica propria*, by which the entire gland is closely bound down. This tunic, regarded in its length, forms a cylinder. The axis of this cylinder is an open space. The sides bear the glandular folds. A transverse as well as a longitudinal section of the gland is required in order to display the true disposition of the glandular laminæ.

These bodies are richly ciliated both within and without. Each fold ends in an excretory duct. The ducts emanating from each fold are tributary to a common duct which runs along the



axes of the gland and joins the rectum at different points in different genera. This fact, which can be readily verified, is worthy of remembrance. From this fact alone the conclusion is beyond dispute, that if these glands be the real bodies by which the "mucosity" with which, almost at will, the respiratory cavity in these animals may be filled, it can only attain this cavity by oozing through or transuding the *tunica propria* of the gland,—a conclusion repugnant to reason, and at variance with all physiological analogy.

In *Buccinum* the gland is flatter and less cylindrical than in *Limax*. This occasions a slight difference in the mode in which the laminae (fig. 8 *a*) are attached to the *tunica propria*. It is by no means difficult to detach a single fold (*a*) in a perfect state and place it under the microscope. By this simple expedient the entire machinery of this gland is rendered at once evident.

A highly ciliated membrane, more delicate than, although the prolongation inwards of, the *tunica propria*, gives its form to, and contains the gland-substance of, this fold. The external surface of this membrane, although within the boundary of the *tunica propria*, is not the true interior of the gland. The true interior spaces of the gland communicating with the duct are not ciliated; nor is the *internal* surface of the rectum in which it terminates. It will be seen that the entire mass of the glandular fold or lamina under examination consists of two elements: first, the Florence-flask-shaped vesicles (fig. 8 *b*, *b*, and B, *b*), which may not incorrectly be said to represent the lobuli or acini of the glands of the vertebrated animal; and, secondly, the intermediate stromatous and cellular structure which fills up the spaces *external* to and between the vesicles. In the recent gland these two parts are so evidently distinct, and indeed so easily distinguishable, that they cannot be confounded. The cells (B, *b*) *within* the vesicles are densely crowded with semi-fluid albumen-looking contents, of low refractive power. The substance contained in these intravesicular cells is unquestionably *the* secretion of this gland. There it is, directly under the eye, in its very place of production. If by micro-chemical analysis its composition while thus isolated in cells could be determined, the problem as to the real nature and office of this gland might indeed very readily be solved; but the minuteness of the quantity thus presented to the eye renders such a determination impossible.

The nucleated cells (*c*) which occupy the interspaces between the caecal vesicles are much larger than those contained within these parts; they are densely filled with oleous granules (*d*) of a greenish-yellow colour and of high refractive index. The nucleus in these cells is filled only with an albuminous formless semifluid



substance. In this respect they will be found to contrast strikingly with the similarly placed cells of the "colour-gland" afterwards to be described. These extra-follicular cells, so densely charged with a secreted product, perform obviously an important part in the office of these glands. They are separated from those within the vesicles only by the walls of the follicles (B, e) themselves. These walls consist literally of only a *hyaline membrane*, structureless, answering simply and exclusively the mechanical purpose of a limitary or circumscriptive sac. No cell-elements are contained in its substance. It is evident therefore that the cells are the real factors in the act of secretion. The large pregnant cells (B, e), which stand on the outside of the cæcal follicles of the gland, are *soaked* in the circulating fluid. It surrounds them on all sides. But the blood does not penetrate in mass into the interior of the vesicles. The cells therefore by which these vesicles are filled cannot derive their contents directly from the blood. From the relative position of these parts—the blood, the extra-follicular or stromatous cells, and the intra-follicular cells,—it seems highly probable that the blood is first subjected to the agency of the externally situated cells which cluster around the grape-shaped ends of the glands, and that the prepared contents of these cells pass thence by endosmose into the interior of the follicles, where they for the second time conduce to form, and where they undergo the elaborative reaction of, a second system of cells. These last cells (B, f) are very unlike the former. In the gland of *Helix aspersa* they are best seen. Those which are disposed around the circumference of the space enclosed by the cæcum of the gland are the largest, and each of these cells contains a very apparent nucleus which is charged with greenish-yellow granules. As the eye approaches the centre of the cæcum, the cells lose their nuclei and become filled only with a mucus-like, pellucid, semifluid substance, which eventually escapes into the excretory channels of the gland. In the gland of *Buccinum* the dark nuclei of the circumferential cells (B, f) are much less distinct. But the mass of cells by which the cæcum is filled presents the same characters as in *Helix*. It is impossible here to avoid the reflection that the *cells* are considerably larger in size and more numerous in the glands of an Invertebrated than in those of a Vertebrated animal. In that of the latter, a network of blood-vessels accurately fits over and embraces externally the cæcal extremities of the gland. In the Invertebrate animal all glands are constructed in this respect on one general type. The blood courses in large streams through the stromatous substance; it never penetrates the hyaline membrane of the follicle. Those parts of the blood which are appointed to nourish



the cells upon the agency of which the act of secretion depends, and which cells in their turn furnish the final secreted product, are destined therefore to pass through an external stratum of cells and through the basement or hyaline membrane of the follicle before they eventually reach the true secreting cells. This exemplifies the important part taken by cells in the act of secretion.

Let the physiologist now review the apparatus whose anatomical constitution has in part been defined. A large excretory duct (fig. 8, B, *g*), discharging its contents into the rectum, is traceable as other ducts into a constantly diminishing series of ducts, until at length the Florence-flask-shaped terminal vesicles (B, *e*) are reached. At this point the microscope discloses a complex system of cells and channels for the transmission of fluid,—a machinery in fact which is little inferior in intricacy to that of the glands of the highest animal. It may be reasonably inferred, that such an organized arrangement in a group of animals comparatively inferior must be designed to furnish a product far more important than the “mucosity” as supposed by Cuvier. It is next to impossible that this secretion can be any other than the *urine*. But this conclusion should receive all the certainty of an unquestionable demonstration, since, in this case, these bodies in the Gasteropods may be recognized as a starting-point of great value in the determination of analogies and homologies in the lower members of the series. This demonstration is reserved for another opportunity.

A second and much smaller gland exists in the respiratory cavity of the Pectinibranchiata, which hitherto has been variously called the “colour-gland” and the bipectinate supplementary gill. This body is not present in the breathing-chamber of the Pulmonata. In *Helix* a fringe-like fold (fig. 3 *e*) of the membrane of the cavity assumes almost the appearance of a gland; it is however nothing but a portion of the vascular respiratory membrane.

The so-called colour-gland is best studied in *Buccinum* and the Littorinidæ. In both it is situated on the extreme of the roof of the cavity, being separated from the other gland by the interposition of the branchiæ. It is considerably smaller in the Periwinkle than in the Whelk. It has a dark green colour. It commences posteriorly in a cæcal extremity. It is prolonged anteriorly into a tube or duct which travels underneath the mucous membrane of the vault until it approaches the termination of the rectum, where it has its outlet by a separate orifice. Viewed as an axis (fig. 9 *a, a*), this duct may be described as supporting the lobes or leaves (*b, b*) of the gland,—as symmetrical, bilateral, ramose diverticula. This gland presents a



general exterior resemblance to the so-called "muciparous gland" of this chamber. It admits of division into two parts—the *lobes* first, which correspond with the *laminæ*; and, secondly, the *lobuli* (*c*) into which the lobes (*b*, *b*) are further subdivided. One of the *lobuli* in minute structure represents the arrangement of the whole gland. These *lobuli* do not exist in the "muciparous gland." This is one distinctive fact. The next is that the latter gland has a yellow colour, the former is of a dark green. But distinctions more essential than the preceding remain to be indicated. A lobule is represented by a bunch of grapes *flattened* (fig. 10). The grapes or terminal follicles (*a*, *a*) do not exhibit the same *figure* or shape as they do in the "muciparous gland;" they are more elongated and conical. From the latter they differ also in their contents. They circumscribe cells which cannot be confounded with those of the muciparous gland of the respiratory cavity. The stromatous tissue (fig. 10 *b*) which envelopes the *cæca* is obviously dissimilar from that of the latter gland. The dark green colour (*c*) of both the extracæcal and intracæcal cells is one striking fact of distinction. This colour is seated in the *nuclei* of the cells. Like those of the "muciparous gland," these cell-elements are divisible into two groups; those, first, which are external to the cæcum; and, secondly, those which are within (*d*). Those which are without are of a deep dark green colour (*c*); this colour is concentrated in the nucleus. Those which are within the limitary membrane of the cæcum are less darkly tinged (*d*). But it is evident that the latter cells circumscribe contents which are the derivative products of the former. The cells situated in the circumference of the vesicles are more dark than those placed in the centre. This gradation of colouring is expressive of the stages through which the secreted product passes. By this coloured substance this gland is strikingly distinguished from that of the "muciparous gland." The follicles differ in figure from those of the latter, but the cells do not; they are distinguished only by the *colour* of the material by which they are filled.

Arbitrating as mere physiologists, it would be quite impossible to say why one of these glands should be a kidney and why the other should not. It cannot be proved by the secreted product of this gland that it is one really designed to furnish a "coloured fluid." This inference is founded simply upon the colour of the cell-machinery by which this product is elaborated—not upon the colour of the finished excretion.

The author proposes for the present to leave this question in an unsettled attitude; but he will venture to state that neither of these glands is the source of the "mucus" or "mucosity" for which the Gasteropod Mollusks are remarkable. This "mu-



cosity" is really supplied by a totally different machinery. It is poured forth by follicles which in all Gasteropod and Nudibranchiate Mollusks are more or less thickly strewn over the mucous and cutaneous surfaces.

### *Cephalopoda.*

The Cephalopod Mollusks stand at the head of the Invertebrated series, not only in virtue of a superiority of bodily form, but also of the higher type of structure which pervades their entire organization. They depart from the Gasteropods in the position and shape of their principal prehensile and locomotive organs, and in the significant fact that in them the 'general cavity' of the body is almost obliterated. They approach the Vertebrated animal in the following respects:—They possess a rudimentary endoskeleton, greatly developed cephalic ganglions, large and active organs of sense, a vigorous and well-formed muscular system, a blood-vascular apparatus more perfect than that of any other class of Invertebrata, a nutritive fluid thickly fibrinized and of high specific gravity, and blood-corpuscles which in figure and structure more nearly resemble those of the Mammal than do those of any other Invertebrated animal. The circulatory apparatus of the Cephalopods does not, however, constitute a perfectly closed system. This point was established by the early classic researches of Professor Owen. The cephalic venous sinus, and its continuation, the great anterior vena cava, appear to form closed-off portions merely of the peritoneal cavity. The vena cava in *Nautilus* is a flattened spacious channel, the parietes of which are perforated by numerous orifices which communicate directly with the peritoneal cavity. This remarkable peculiarity is thus described by Professor Owen: "There are several small intervals left between the muscular fibres and the corresponding round apertures in the membrane of the vein (vena cava) and contiguous peritoneum, by which the latter membrane becomes continuous with the lining membrane of the vein; from this structure it would seem that the *blood might flow into the peritoneal cavity*, or the fluid contents of that cavity be absorbed into the vein\*."

Though, from the small size of the specimens upon which the author's observations have been conducted, he has not been successful in his attempts to verify the statements of Prof. Owen, he thinks it very probable, on the ground of analogy, that they are true. In the Echinoderms and Annelids the vascular system undoubtedly communicates with the peritoneal cavity. Of the Gasteropod Mollusks Milne-Edwards observes, "L'artère aorte,

\* Cyclop. Anat. and Phys., Art. Cephalopoda.



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 les lames de tissu connectif étendues transversalement au devant de la cavité abdominale\*." The cephalic sinus in the Gasteropods forms a part of the arterial system; in the Cephalopods it is a segment of the venous system. That portion of the circulatory system of the Cephalopod which is intermediate, *in the solids of the body*, between the arteries and veins, partakes much more strikingly of the capillary character, or less of the lacunose, than it does in any other Mollusk. It seems, from the researches of Prof. Owen, that in *Nautilus* and *Octopus*, and other genera, the pericardium (or that membrane which embraces the large central vessels) opens immediately into the branchial chamber. Dr. Lacaze Duthiers† has lately shown that the pericardial chamber in the Lamellibranchiata also opens externally. From these analogies the writer of this paper believes that the lung-sac of the pulmonary Gasteropods should be looked upon as the pericardial bag slightly diverted from the character which is normal to it in other Mollusks.

Considered from this homological point of view, the lung of the Pulmonata should be described as the pericardium, receiving air instead of water into its interior. The vascular system of Insects is filled with air, that of the Annelids with fluid. Insects differ from the Annelids, therefore, precisely in the same manner as the Pulmonata differ from other Mollusks. But, notwithstanding the express provisions which are thus made to introduce the external element into the recesses of the body of Cephalopods, these Mollusks are furnished with branchial organs more beautifully and elaborately constructed than those of any other Invertebrated animal.

The general anatomy of this class is well known. The author therefore will at once proceed to state the results of his special researches on the minute structure of the respiratory organs.

#### *Mechanism of the Branchial Chambers.*

The branchial chamber of the Cephalopod is a perfect hydraulic mechanism. It is placed in advance of the viscera. It is enclosed laterally by the mantle, the muscles of which have received an express disposition with reference to the rhythmic respiratory movements which it is designed to perform. Anteriorly the

\* Ann. d. Sc. Nat. 3 sér. 1847.

† Ann. d. Sc. Nat. No. 5, 1855.



chamber is provided with two valvular openings, the valves being so arranged as to afford a ready entrance to the inspiratory water-current, and to prevent its reflux. The water thus drawn or sucked into the breathing-chamber is drawn or sucked also into the hollow axes of the gills (especially in *Octopus*) by a diastolic movement of these organs which seems to be synchronous with that of the mantle. Having freely permeated the branchiæ, the water is expelled through the funnel by an expiratory act in which the gills and the mantle contract simultaneously. The rectum and the ducts of the generative system terminate in this chamber at the base of the funnel. The expiratory current thus conveys externally the excreta. In this character, as is well known, the Cephalopods coincide with the Gasteropods.

The *precise mode* in which the water, during the respiratory movements, traverses the branchiæ, has only recently become known to the author\*. It does not enter, as he formerly supposed, as *one* current at the posterior extremity, but from above downwards, from the dorsal to the ventral side, in as many streams as there are spaces (Pl. XV. fig. 1 *e*) between the secondary lobuli of the organs. By this arrangement the inspiratory pure current is first and at once brought into contact with that half of the gill on which the vascular laminae are suspended. It effects its escape, during the systole of the organ, at the ventral side, through the fissures between the *non*-vascular supports of the lobuli (*d, d*). Although in the genus *Loligo* the gill (fig. 3, 3<sup>2</sup>) does not fold so much upon itself as to enclose a cylindrical axis, as in *Octopus* (fig. 1), the water-currents observe precisely the same direction in both. The admission of the aërating element apparently into the interior of the gill in the Cephalopods may be said, on the one hand, to be parallel to what occurs in the Lamellibranchiata, or, on the other, may be likened to the entrance of the air, in the Mammal, into the lungs. As a respiratory mechanism, it resembles the latter more than the former. The lungs possess the property of dilating and contracting, in order to inhale and exhale the gases concerned in respiration. The branchiæ of the Cephalopod are

\* In a previous part of these papers (p. 141) I have introduced a figure (Pl. IX\*. fig. 7) illustrative of the manner in which I then believed the water to pass through the branchiæ in the act of respiration. Although it was intended only to convey a *general* idea of the mechanism of the chamber and its currents, yet as that figure stands, it may lead to error. The hollow axes of the gills are not *open*, as there represented, at their posterior or attached extremity, but *conically closed*, as they are at the anterior extremity. It will be evident, in the text, that the water cannot therefore enter the interior of the organ in *one* large stream, as there shown.



endowed with the same property. They bear a nearer similarity to the gills of the Pectinibranchiata than to those of any other Mollusks. They are highly muscular and irritable: the disposition of the muscles will be afterwards described. On the floor of the branchial chamber, situated immediately underneath each gill, and running parallel with these organs, may be observed a dense prominent *ridge* (Pl. XV. fig. 1 *h, h*), to which the branchiæ are attached, and upon which they rest. This ridge consists of a dense bundle of muscles, which during contraction are capable of approximating closely together the two extremities of the branchiæ—in other words, of shortening these organs in length. These muscles are richly supplied with nerves from the neighbouring pallial ganglion. They aid in a very material manner the branchial movements of dilatation and contraction. They not only afford a fixed point of attachment to the gills, but they are accessory to the mantle in the respiratory movements.

#### *Structure of the Branchiæ.*

The Tetrabranchiate and Dibranchiate orders are founded simply upon the number of the gills\*. No classification has been attempted on the basis of the remarkable varieties which occur in the anatomical structure of the gills. As far as the author's examinations have extended, he has succeeded in establishing only two main varieties,—that of *Octopus* and *Sepia* (Pl. XV. fig. 1), in which the secondary lobuli circumscribe a hollow axis, by curving from the dorsal to the ventral aspect; and that, 2ndly, of *Loligo* and *Loligopsis* (Pl. XV. fig. 3, 3<sup>2</sup>), in which the secondary parts of the organ pass only half-way round, and float freely in the branchial chamber, instead of being, as in *Octopus*, tied down to the longitudinal pallial muscle upon which the gills rest. He has no doubt, however, that other modifications of structure in the branchial organs of this class exist; but, in consequence of the want of specimens, he is not at present in a position to speak of them. The Dibranchiate order is thus obviously resolvable into two well-marked suborders,—the one in which the gill forms a *cylinder*; the second, in which it forms a *hemicylinder*. This distinction has never before been noticed.

No example of the Tetrabranchiata has ever fallen under my notice. Prof. Owen states that they stand in closer connexion with the Gasteropod Mollusks than the Dibranchiata. In *Nau-*

\* The second pair of branchiæ in the Tetrabranchiate Cephalopods are most probably parallel to, and representative of, the *supplementary gills* of the Lamellibranchiata described in a former paper.



*tilus Pompilius* this distinguished observer figures the branchiæ as having a completely formed cylindrical arrangement.

It must therefore be concluded that the Tetrabranchiata are lower than the Dibranchiata in the Molluscan scale, and that *Octopus* should stand beneath the *Calamary* in zoological rank. This interesting fact, as the ground of classification, is commended to the attention of those who may enjoy opportunities of studying the organization of this most interesting class of animals. In accordance with this view, which regards the gill of *Octopus* as ranking below that of *Loligo*, let us proceed first to the detailed description of the lower variety.

The gills in the genus *Octopus* are strikingly distinguished in apparent structure from those of the other families of the Dibranchiate tribe. Although only two in number, in all the species of this order they exhibit, as stated before, very extraordinary diversities of shape. In the size and disposition of the branchial chamber there is no corresponding variation: it is nearly the same in all species. In *Octopus* the branchia on either side is attached in a peculiar manner to the ventral wall of the breathing-chamber. The dorsal surface is free and unattached: it is so situated as to float on a thin supporting ridge. The water thus rushes into and out of its interior with equal facility. The branchial artery, or afferent venous trunk (fig. 1 *b*), lies on and courses up along the ventral side of the organ: it emanates from the branchial hearts\*. The branchial vein or efferent trunk (fig. 1 *a*) runs along the dorsal border of the gill, and terminates in the aorta (these two trunks are seen in section, fig. 2 *a, b*). These two longitudinal trunks constitute the framework by which the entire apparatus of the gill is supported. To them are attached respectively the two ends of the secondary lobuli in *Octopus*: in *Loligo*, as will be again explained, a slight variation from this type occurs. The plan of this structure is readily understood on a transverse section of the gill (fig. 2). In the gill of *Octopus vulgaris* there are twelve pinnæ or secondary lobuli on either side (fig. 1 *d, d*). Along the external and internal margins respectively (fig. 2 *i, i*, & *e, e*), efferent and afferent vessels are observed to travel. These secondary branches, like the primary trunks from which they proceed, serve to support, in their turn, the tripinnæ (*g*), or the ultimate leaflets in which are distributed the final capillaries of the

\* It will afterwards be shown that these cordiform dilatations of the blood-channels in the vicinity of the branchiæ may be viewed as mere safety receptacles for the retrogressing column of blood (which is either stopped or thrown back in its course during the *extreme* changes of size which the gills are constantly undergoing), with quite as much propriety as they are now considered to be propulsive hearts.



branchiæ. As observed by Professor Owen, the gills of this Cephalopod are tripinnate. This general term, however, serves but very rudely to express the extreme refinement of structure and arrangement which these organs exhibit. The secondary and tertiary divisions are so much longer than the straight space between the points to which they are fixed, that in the ordinary state of the animal, after death, they present remarkably complex foldings and convolutions; but when the organ is in the condition of full and complete distension (with blood in the vessels and water in the hollow axis), the secondary lobuli and their appended system of leaflets are straight or smooth laminæ of exquisite slenderness, delicacy, and translucency. Although the secondary divisions (fig. 1 *d, d*) amount to no more than twelve in number on either side, the tertiary laminæ (*c, c*) which each of them supports are as many as from twenty-five to thirty on either side. The multiplication thus insured is extraordinary. The secondary lobuli are separated from each other by free, open water-passages (fig. 2 *h*). It is through these spaces that the fresh inspiratory streams enter the axial interior of the gill (fig. 2). No exact parallel to these spaces is found in any other Mollusk. The water, indeed, rushes between the secondary divisions of the gills in all the Pectinibranchiata. In these latter, however, the organ does not circumscribe a hollow interior. The tertiary branchial foliage is disposed at right angles on the secondary, just as the latter rest at right angles on the main primary trunks. According to this arrangement, no obstacle is offered to the rapid and free passage of the water-current through the gill, above from the outside to the inside, below from the inside to the outside. In a mechanical point of view, there is much to admire in this contrivance. The more forcibly the water is caused to pass through the branchia, the more completely its delicate leaflets are straightened and rendered smooth. All danger from mechanical injury is thus obviated.

The water is drawn into the hollow interior of the gill much more slowly than it is driven out. No violence to the slender structures of the organ can accrue from its forcible ejection, since the spaces through which the water effects its exit are bounded only by tendon and fibrous tissue. Now, it may be asked with great reason, how is it that during the expiratory shortening of the gill, the water does not again escape through the passages by which it entered? It is not difficult to answer this question. When the large longitudinal muscle (fig. 1 *h, h*; fig. 2 *c*) which is situated underneath the gill contracts, and thus approximates the two ends of the gill, it brings the dorsal half of the organ closer together, forming the concavity of a curve,



while it separates the ventral half, which for the instant forms the convexity of the curve. At this instant the expiratory current escapes. Reversing this movement, it is not difficult to perceive how the act of inspiration occurs.

The gills of all Cephalopods are remarkably elastic; at one moment exhibiting an extraordinary capability of dilatation, at another of extreme contraction. This property is due to the presence of muscular fibres. They are distributed throughout the entire structure of the gill; they embrace the vessels; they course along the edges of the laminæ; they are internally intermingled with elastic tissue, whose normal mode of action is rhythmic; they contribute in a most important manner to the mechanism of breathing.

The branchial system of the Cephalopods is distinguished by one further peculiarity:—in no instance yet examined has the presence of vibratile cilia been proved. In this particular they are allied to the gills of the Crustacea and the Fish\*. In the Cephalopod, no part whatever of the gill is furnished with cilia. At first it might be thought that its extreme flexibility superseded the necessity for such organules. The instance of the Crustacean gill, however, which is perfectly passive, disproves this imagination. *Why* cilia are denied to the branchiæ of the Cephalopod, cannot at present be explained. The fact is attested by all observers.

The *ultimate laminæ* (fig. 4 *g, g*) are arranged in a dense parallel series on either side of the secondary processes. They present the same disposition as those of the gill of the Crab. Those of the latter, however, are comparatively stiff leaves; those of the former are contractile and flexible in the highest degree. The tissue of the Cephalopod gill is extremely extensile, that of the Crab is fixed and passive.

It is very difficult to obtain a satisfactory view of the fully-unfolded flat surface of one of these ultimate laminæ; but with care, it may be obtained. Each lamina is constructed very much on the plan of that of a Pectinibranchiate gill. It is a leaflike structure, bearing two strata of vessels (fig. 6 *a, b*), an afferent and an efferent, which double the one into the other at the free margin (*c, c*). The aërating current laves thus the advancing and the returning capillary streams of blood. The ultimate blood-channels (figs. 5, 6) bear an exact resemblance to those already described in the gills of the Pectinibranchiata. They are parallel, non-dividing channels, of *unvarying diameter*. At the point of curving (*c, c*), or the free margin, they do not dilate, as in the case of

\* I am sorry that, in consequence of the want of specimens, I cannot, from personal knowledge, state at this moment whether the gills of the Pectinibranchiata are ciliated or not.



the Lamellibranchiata. From all others they are distinguished by the circumstance of their extreme distensile and contractile capabilities. If these ultimate vessels united and divided in a retiform manner, they would approach to the plan observed in the branchiæ of the Fish. They form, however, a straight parallel series, laminarily blended together by delicate cellular tissue (fig. 6). In this character they conform to the Molluscan distinctive type of structure. No instance of departure from this type is known, from the Tunicate to the Cephalopod. From the Pectinibranchiate standard they differ in the absence of cilia. The absence of cilia is compensated in the Cephalopod by the extreme muscularity of the organ.

It is *scarcely possible* in the branchial organs of this class to arrive at a certain knowledge as to the point whether the ultimate laminae are covered or not by an epithelium. The parts are so irritable and transparent, that the question cannot with confidence be determined. That they are not lined by a *ciliated* epithelium is quite certain; that they are not invested by any epithelium at all, is improbable; but the existence of this covering cannot be demonstrated convincingly. The conclusion must therefore rest on general analogy: all analogy is unquestionably in favour of its presence.

The branchiæ of *Loligo* (fig. 3, 3<sup>2</sup>) differ from those of *Octopus* (fig. 1) in a remarkable manner. In the latter genus the secondary divisions (*c, c*) are attached to the ventral aspect of the organ (fig. 2 *i, i*). In the former they are loose, and float freely in the branchial cavity (fig. 3 *b, b*, & 3<sup>2</sup> *c, c*). They thus form a curved figure, or half-cylinder. The mode of action of the gill during the respiratory act is precisely the same as in the case of the *Octopus*. The water enters and penetrates in the same direction; it escapes expiratorily in the same manner. In all other respects the branchiæ in these two examples are constructed in precise accordance with the same principle. There is no deviation; in minute structure they are the same.







## EXPLANATION OF PLATES.

### PLATE XII.

- Fig. 1.* Plan in outline of an Asteroid Zoophyte: *a* & *d*, visceral cavity or space between stomach and exterior of the body in which the chylaqueous fluid is contained; *b*, shows the mode in which the tentacles are supposed by some observers to terminate in and open into the stomach itself; *c*, orifice at the bottom of stomach.
- Fig. 2.* Plan of Hydraform Polype: *a*, base of tentacle opening into the perigastric areolæ *c*; *b*, stomach.
- Fig. 3.* Actiniform Polype: *b*, visceral cavity; *a*, orifice at bottom communicating with this cavity; *c*, tubular base of tentacle; *d*, *cilia* lining the interior of tentacle.
- Fig. 4.* Plan of a Bryozoon: *a*, base of tentacle communicating with the visceral cavity *b*.
- Fig. 5.* Plan of *Rhizostoma* (*Medusa*): *b*, digestive sac; *d*, *c*, gastro-vascular canal.
- Fig. 6.* Horizontal plan of the same: *a*, centre of digestive sac *b*; *c*, *d*, gastro-vascular canals.
- Fig. 7.* Vertical plan of a Ciliograde Medusan, *Pleurobranchus*: *c*, *d*, gastro-vascular canals.
- Fig. 8.* Section of an arm of *Asterias*: *a*, mouth; *e*, opening from mouth into the digestive cæcum *b*; *c*, its further cæcal end; *h*, cavity or body filled with the chylaqueous fluid; *f*, *f*, membranous tubular and cæcal processes (the true *branchiæ* of the Starfish).
- Fig. 9.* Vertical imaginary section of *Echinus*: *a*, mouth; *b*, anus; *d*, visceral cavity; *e*, intestine; *f*, *f*, *f*, hollow membranous processes—the true *branchiæ* of the *Echinus*; *g*, suctorial processes.
- Fig. 10.* Head and neck of Sipuncle: *B*, transverse section of one of the *branchiæ*, ciliated within and without; *C*, the same, viewed transparently; *i*, coiled intestine; *h*, corpuscles of chylaqueous fluid; *m*, *j*, blood-vessel; *n*, visceral cavity.
- Fig. 11.* A piece of the skin of Sipuncle showing the *branchial fenestræ* *d*, *d*, *d*: *a*, a pigmented *epidermal* cell in the centre of the unpigmented area *b*; *c*, pigmented cells of the intervals between the fenestræ.

### PLATE XIII.

This plate is designed to express, in outline plans, the natural manner in which the *alimentary* system of the Cestoid and Trematoid Entozoa passes into that of the Nemertine and Planarian Annelida—that they are really constructed upon one and the same principle. Though not represented in this series of figures, the system of the nutritional fluids in these Entozoan



# EXPLANATION OF PLATES.

and Annelidan groups conforms to one type. The channels for the fluids differ little in distribution from those of the alimentary system.

- Fig. 1.* Alimentary system of *Nemertes Camillæ*, the cæca (*b*) of which are charged with a corpusculated chyme; *e*, space external to the latter system filled with the chylaqueous fluid; *d*, shows that the true alimentary organ of this worm, in common with that of all Nemertine Annelids, is closed at all sides; *a*, œsophagus entering the proboscis.
- Fig. 2.* The caudal end of the alimentary organ of another Nemertine Annelid, *Borlasia* —?, proving it to be cæcal also at this extremity: *a*, cavity; *c*, cæca of this organ filled with a corpusculated fluid; *b*, space external to the alimentary cæcum filled with chylaqueous fluid.
- Fig. 3.* Alimentary system of a *Planaria*: *b*, mouth; *c*, cæca; *a*, areolæ external to the digestive diverticula.
- Fig. 4.* Digestive system of a freshwater leech, *Clepsina* —?: *a*, cæca filled with corpusculated chyme.
- Fig. 5.* Ideal, transverse, section of *Aphrodita aculeata*, showing the distribution of the alimentary system, and its relations to that of the nutritional fluids: *a*, stomach; *b*, visceral cavity; *c*, scales, by the rising and falling of which a strong current of sea-water is maintained through the dorsal channel (*e*), by which current the fluid contents of the digestive cæcum (*d*) are aerated.
- Fig. 6.* Alimentary cæcum of one segment of *Tænia Solium*: *a*, mouth of this segment leading into a short œsophagus (*b*), and thence into the ramifications (*c*) of the digestive system.
- Fig. 7.* Alimentary system of a Trematoid Entozoon: *a*, œsophagus; *b*, digestive cæca.
- Fig. 8.* Ditto of *Amphistoma*: *a*, *b*, cæca of digestive system.
- Fig. 9.* Ditto of *Bothriocephalus latus* (a sterelminthous worm): *a*, mouth of a single segment; *b* & *c*, cæca of digestive system.
- Fig. 10.* Plan of a Nematoid worm, showing the great difference between the diameter of the intestine (*a*) and that of the space (*c*) enclosed by the integuments; *b*, reproductive organ.
- Fig. 11.* Another type of a Nematoid Entozoon (*Ascaris lumbricoides*), in which the intestine (*a*) is larger in diameter, and tied by frequent bridles (*b*) to the dense integuments (*c*).
- Fig. 12.* Transverse section of the same.

## PLATE XIV.

- Fig. 1.* (A.) Cephalic end of the body of *Terebella nebulosa*, laid open to show the afferent vessel (*d*) and efferent vessel (*e*) of the true-blood branchiæ (*a*); *c*, denotes a corpuscle of the chylaqueous fluid filling the peritoneal cavity of the body, and communicating directly with the hollow axes of the tentacular filaments (*b*).
- Fig. 2.* exhibits the extreme end of one of the tentacular filaments (*b*, A) viewed by transmitted light; *f*, vibratile cilia; *g*, ditto, covering the under surface; *i*, a true-blood-vessel floating in the chylaqueous fluid, of which the corpuscles are seen rolling out at (*j*).
- Fig. 3.* Extreme division of one of the true-blood branchiæ (*a*, A); *i*, afferent vessel dividing dichotomously, returning upon itself at *m*, and ending in the efferent vessel (*k*); *a*<sup>2</sup> & *n*, mark the thin, contractile envelope by which the vessels are embraced.
- Fig. 4.* Foot and branchial appendage of *Eunice margaritacea*: *m*, afferent



# EXPLANATION OF PLATES.

vessel entering the base (*a*) of the branchial process, of which *b, c, d, e, f*, are five vertical branches. Each branch as seen at fig. 5 consists of a single vessel (*i*) returning in a looped manner upon itself (*j*); *g*, cirrus of superior foot; *h*, inferior foot; *g*, inferior cirrus.

- Fig. 6. Foot of *Syllis* — (Williams\*): *e*, cavity enclosed by the foot and filled with the chylaqueous fluid (*d*); *c*, vibratile cilia clothing the exterior; *a*, branchial process; *f*, its lacunose tissue; *e*, exterior cilia.
- Fig. 7. (A.) Foot of *Nephtys Hombergii*: *a*, branchial process, depending in form of cirrus from the base of the superior foot: (B.) an enlarged view of the branchial process examined as a transparent object. It consists of a hollow process filled with the chylaqueous fluid, in the midst of which is seen floating a long, undividing, complexly coiled true-blood-vessel (*c*). The process is lined externally by a ciliated epithelium.
- Fig. 8. Vertical view of the foot of *Nerine vulgaris*: *k*, cavity enclosed by the base; *m*, corpuscles of the chylaqueous fluid by which it is filled; *h, f, g*, channels penetrated by the chylaqueous fluid in the fleshy lobules; *i*, true-blood-vessel occupying the hollow of the process; *c, d*, flat cirri of the upper and lower feet; *o*, cilia; *a, b*, integuments.
- Fig. 9. *Clymene Ebiensis*: *a*, mouth; *b*, first row of hooked setæ; *c*, branchiæ projecting from the tail; *B*, one frill of the branchial process detached and viewed transparently; *e, f*, corpuscles of chylaqueous fluid by which the lobules are filled; *d*, true-blood-vessel floating in the fluid.
- Fig. 10. A part of the mid-body of *Nais filiformis* viewed by transmitted light—showing the same precise relation between the chylaqueous fluid (*e*) and the true-blood-vessels (*f, f*) as exists in the branchiæ—proving that although the parts are *internal*, the conditions of respiration are complete: *a*, intestine; *b, c*, dorsal and ventral primary vessels; *d*, cavity of the body.

## PLATE IX.

- Fig. 1. Plan of the central parts of the circulatory system of the Myriapod, constructed in part from Mr. Newport's figures and in part from the author's dissections: *a, d*, the dorsal vessel; the arrows mark the direction of the blood; *b*, the œsophageal collar; *c & e*, supraspinal artery; *f*, the systemic arteries (sic) of Mr. Newport.
- Fig. 2. Plan of the central parts of the circulatory system of the Insect: *a*, dorsal vessel. The anterior or thoracic half is a smooth tube, the abdominal chambered by valves; *b*, the supraspinal artery, having on either side venous currents (*c*), as shown by the arrows; *d*, branches, distributive, from the supraspinal artery; *e*, large, loose-walled venous channels entering the capacious abdominal sinuses *g, g*; *f*, the membranous channels which pour their blood into the dorsal vessel at the auricular orifices. The blood in the dorsal vessel moves forwards, that in the supraspinal artery moves backwards.
- Fig. 3. *a, p*, Dorsal artery; *p*, its caudal continuation; *d*, its cephalic; *b*, visceral artery, sending distributive branches (*i*) into the viscera,

\* This species will be described in a subsequent part of these memoirs.



# EXPLANATION OF PLATES.

the blood of which is returned into the dorsal artery by *n, n*, the systemic arteries of Mr. Newport; *c*, the supraspinal artery, conveying blood to the nervous and integumentary structures; *e*, subspinal vein; *f*, branches going to the pneumo-branchiæ (*g*); *h*, origin of the pneumo-cardiac channels (*k, k, k*); *l*, continuation of the subspinal vein into the tail; *m*, branches communicating with the dorsal artery (*p*).

- Fig. 4. Glassy, jelly-like aquatic larva of an Insect, common in the pools about Swansea: *a* (*c*), kidney-shaped tracheal vesicles, without any ramifying tubes; *b*, dorsal vessel; *d*, arrows denoting the returning into the dorsal vessel at the posterior auricles (*b*).
- Fig. 5. Aquatic larva of *Sialis Lutarius*: *a*, branchial appendages; *B*, one of the branchiæ enlarged; *b*, tracheæ; *c*, cell-tissue.
- Fig. 6. Aquatic larva of one of the *Libellulidæ*: *a*, branchial appendages; *B*, the same further enlarged; *b*, trachea; *c*, secondary arborescent branches; *C*, extreme end of one of the tracheal branches traced under a high power to its membranous capillary termination *f, g*.

## PLATE X.

- Fig. 7. Rectal branchiæ of *Æshna grandis*, after M. Léon Dufour: *C, a*, orifices in the rectum of the branchial folds (*A*); *a*, dilated extremities of the tracheæ.
- Fig. 8. Head, tail, digestive system (*d*), tracheal (*h*) and branchial (*g*) systems, hepatic vessel (*e*), of *Agrion Puella*, after M. Dufour.
- Fig. 9. A small piece from the parietes of the intestine of the Cockroach, showing the extreme distribution of the trachea (*a*). The blood-current accompanies the tube only as far as *i*. The trachea then describes a true network (*e, c, d*) of membranous tubes. In the meshes the glandular cells (*f, g*) are placed. A clear space intervenes between the trachea and glandular cells in which the nutritive fluids, without the corpuscles, may probably move.
- Fig. 10. A small piece of the wing of the Cricket drawn under a high power: *a*, a large trachea in the centre of the nervure or channel, surrounded by two opposed currents of blood (*b, c*); *i*, larger branches; *d, e, f*, small terminal tracheæ, entering alone, without coincident blood-currents, into the *scaly* interval; *j*, long, slender, wavy tracheæ floating in the fluid; *g*, blood-corpuscles, travelling in the channel *b*.
- Fig. 11. One of the tracheæ from the *scaly* intervals between the nervures of the wing of the Cricket, showing the mode in which it terminates (*b*) between the scales *d*.
- Fig. 12. A minute portion of walls of the stomach of the Cockroach, showing the wavy manner (*c, f*) in which the membranous capillary tracheæ are distributed around and between the ultimate glandular elements; at *e*, the current of the blood, as traced through the blood-corpuscles, turns back: *a*, large spiral tracheæ.
- Fig. 13. A small portion of a spiral trachea, exhibiting the coats under the action of acetic acid: *a*, outer coat raised, indented like the spiral (*b*); *c*, the internal or mucous coat.
- Fig. 14. A piece of voluntary muscle, representing the manner in which the tracheæ enter the substance of the muscle.
- Fig. 15. One of the above tracheæ traced into the substance of the muscle; *a, b, c*, network of ultimate membranous tracheæ as they are distributed between the ultimate muscle-fibres—the latter being omitted.



## PLATE XVII.

- Fig. 1. Appendages of the ninth pair composing the external foot-jaws of Decapod Crustaceans, and which are homologous with the sub-cylindriform process of the first pair in *Squilla*, with the thoracic feet of the twelfth in Isopodan Crustacea, and with the thoracic feet of the third pair in the Branchiopoda: *a*, internal element; *b*, palp; *d*, branchia; *c*, flabellum.
- Fig. 2. Appendages of the eighth pair constituting the foot-jaws in the Decapoda,—which are homologous with the prehensile jaws in *Squilla*, with the thoracic feet of the first pair in the Isopods, and with the branchial processes of the second pair in the Branchiopods.
- Fig. 3. Abdominal appendage of *Squilla*: *a*, internal member; *d*, external; *b*, branchia.
- Fig. 4. Abdominal appendage of the *Isopoda*: *a*, external or cutaneous process; *b*, internal and branchial.
- Fig. 5. Abdominal appendage of a Branchiopod. The dotted process is the respiratory.
- Fig. 6, A. *Caprella linearis* (male): *a*, respiratory appendages; *b*, the same still further magnified; *b'* shows the *single* blood-current moving round the circumference of the process; *C*, corpuscles of the blood.
- Fig. 7, B. A single pair (magnified and viewed by transmitted light) of the branchial leaflets of the Hermit Crab: *c*, *d*, two longitudinal blood-channels, seen in section; *f*, *g*, embrace a deep groove between the leaflets for the branchial current of water; *i*, *h*, denote the parenchymatous islets situated between and dividing the blood-streams (*o*); *M*, a single seta, *mop-like*, from the roof of thoracic cavity; *k*, sharp teeth on its shaft; *h*, another variety of seta.
- Fig. 8, A. A single gill of the Lobster, represented as a transparent object in transverse section: *a*, section of afferent vessel. The arrows exhibit the division and direction of the afferent blood in its course towards the ultimate branchial tubules (*a'''*). The ultimate afferent current occupies the *axis* of each tubule; *a''*, marks (in section) the great afferent trunk of the gill, receiving its blood as shown by the arrows from the *circumferences* of the tubules. B, a single tubule enlarged; *b*, afferent vessel, having cribriform walls; *c*, *c*, the efferent stream; at (*c*) the capillary system of the tubule is seen. C, the same tubule seen in section. D, one of the interbranchial flabella. E, a single mop-like seta from its edge; *f*, one from its flat surface.
- Fig. 9, A. A single pair of the branchial laminæ of the Crab: *a* & *b*, afferent and efferent trunk, connected together by means of the intermediate branchial laminæ. These latter are composed of parallel epithelial plates tied together by means of minute intermediate nodules of fleshy substance. Between these the blood streams in *imparietal* passages. B, horizontal flabellum of the Crab; C, D, E, setæ with which it is armed.

## PLATE XVIII.

- Fig. 1. Leg, and the projecting free border of the epidermal plates of *Talitrus*. Intended to express typically the *ultimate* respiratory structures of all Crustaceans: *a*, a nodule of fixed parenchyma,



## EXPLANATION OF PLATES.

composed of *slightly refracting* oil-cells, nucleated granular cells, and molecules;—generally such a group is destitute altogether of embracing membrane; *b*, the irregular imparietal, angular passages lying between the parenchymatous nodules; *c*, the cells of the epidermis, *attenuated*.

- Figs. 2, 3 & 4.* Varieties of epithelial cells met with in different parts of the Crustacean: *a*, a cell shown in full, under a high power, to bring out its granular character; *b*, the same in outline.
- Fig. 5.* The parenchymatous patch *a*, fig. 1. enlarged, to show its minute structure: *a*, *b*, epithelial laminae; *c*. represents exactly the peculiar, low refractive character under which oily-element exists in the fixed solids of the Crustacea. The whole *interior* of this patch is permeated by lateral slow-moving currents of blood, diverted from the main stream.
- Fig. 6.* A small piece of the wall of the large branchial vessels, showing the hooks (*a*) on which act the setae of the flabella.
- Fig. 7.* A portion of the proximal end of a *hair*, to exhibit the absence of vessels and to show the lacunose to-and-fro character of the blood-movement.
- Fig. 8.* The active, vibratory, abdominal palp of the Shrimp.
- Fig. 9.* The same viewed transparently: *b*, *c*, epithelial laminae; *e*, radiating muscular fascicles; *d*, radiating imparietal blood-channels; *d*, setae.
- Fig. 10.* Liver-follicle of the Lobster, viewed by transmitted light: *a*, *b*, caecal end, having glandulose walls by the swelling of the parietal epithelial cells; *c*, the secreted product in its first stage, oil-cells colourless and minute; *d*, *d*, the same increasing in size and becoming yellow in colour; *g*, oil-cell; *h*, yellow cell.
- Fig. 11* is *fig. 12* enlarged. It shows the ultimate structure of the tentacle of a Prawn. The muscular masses occupy the axis, and the blood-corpuscles course along the sides.
- Fig. 13.* Illustrates the mode in which the ultimate nerve-tubules are distributed in the gill-laminae of several Crustacea: *b*, *c*, nerve-tubules; *c*, patches of parenchyma.

## PLATE I.

- Fig. 1.* *Clavellina lepadiformis* (after Milne-Edwards): *a*, mouth and inhalent funnel; *b*, large horizontal blood-channels, running regularly between the vertical ones *q*; *p*, the intervascular stigmata through which the water passes from the branchial chamber into the cloacal cavity (*o*), whose outlet is at (*h*) the exhalent or anal siphon; *f*, rectum terminating in the cloaca; *n*, mantle; *m*, test, the intermediate space being filled with blood.
- Fig. 2.* *Pyrosoma giganteum* (after Milne-Edwards): *a*, mouth; *b*, branchial sac; *c*, oesophagus; *d*, stomach; *e*, intestine; *f*, liver; *g*, anus; *k*, ovary; *l*, ganglion.
- Fig. 3.* *Perophora Listeri*: *a*, branchial siphon; *b*, tentacles at its base; *c*, large blood-channels in which the blood-corpuscles are seen; *d*, branchial, *e*, cloacal chamber; *d*, exhalent siphon; *e*, space, tunnelled with spacious blood-channels, between the test and mantle.
- Fig. 4.* Plan of vessels in the branchial band of *Salpa maxima*: *a*, large vessels constituting a separate layer; *b*, smaller; *c*, caecal processes from the vessels and filled with blood, and communicating



## EXPLANATION OF PLATES.

with their internal channel; *d, d*, water meshes: fig. 4 *a*, a separate bar, showing cilia, and bore.

Fig. 5. One of the branchial folds of *Cynthia microcosmus*: *a, c*, water meshes between the blood-channel; *b, d*, the attached borders; *e*, free border; *d*, transverse blood-channels.

Fig. 6. Branchial system of *Pholas dactylus*: *a*, intra-branchial or exhalent siphon; *b, b*, extra-branchial or inhalent siphon; *b, b*, pallial or extra-branchial cavity; *c*, external or inferior branchial lamella; *d*, internal or superior lamella; *e*, membrane tying the attached border of the superior branchial lamella to the side of the foot and visceral mass, roofing the intra-branchial or anal chamber (*f*); the arrows (*g*) show the currents descending from the branchiæ into the anal chamber, and thence out through the excurrent siphon, under the membranous roof (*f*) connecting the branchiæ of the two sides; *h*, mouth; *i, i*, palpi. The arrows indicate the direction of the currents.

Fig. 7. is a transverse ideal section of the preceding figure. It exhibits the relation of the water-currents and cavities: *a*, incurrent siphon, leading (at *a'*) into the extra-branchial or pallial chamber *d, d*; *b*, excurrent siphon leading out of (at *b'*) the intra-branchial or anal chamber *c*; *e, e, e, e*, branchial lamellæ.

Fig. 7<sup>2</sup>. One-half of *Mytilus* (fig. 10) in transverse section, showing the mode in which the branchial lamellæ are attached to the mantle *h, h*; *a, b*, branchial lamellæ of one side; *c, c'*, free proximal border of respectively the upper lamella of the internal gill-plate, and the lower of the external. The attached lamellæ (*d, d'*) of each gill-plate are joined by a membrane at *e*; *g*, shows the continuous membrane which at the proximal borders connects the branchial bars, so that at this point no water can permeate the lamella; *f, f'*, denote the spacious grooves which receive the water from the interlamellar tubes and convey it to the cloaca. The arrows mark the direction of the currents.

## PLATE II.

Fig. 8. Vertical view of the common Cockle, showing the relation of the branchial system to the siphons and cavities: *a*, excurrent siphon leading out of the anal cavity (*a'*) surrounding the visceral mass (*i*); *b*, incurrent siphon conducting (at *b'*) into the extra-branchial cavity (*c*); *e*, arrows marking the excurrent currents coming from the branchiæ; *g*, palpi; *f*, mouth.

Fig. 9. Ideal transverse section of the former figure: *a*, excurrent siphon leading out of the anal cavity (*e*) at *a'*; *b*, incurrent ditto opening at *b'* into the general cavity of the mantle (*c, c*) at *b'*; *d, d'*, branchiæ; *f*, the line of the mantle uniting the branchial lamellæ together. The arrows show the order and tendencies of the water-currents.

Fig. 10. Vertical view of *Mytilus*, exhibiting the systems of respiratory and alimentary water-currents: *a*, mouth; *i, i*, palps; *b*, extra-branchial or pallial cavity; *c*, two longitudinal halves of the rectum, terminating in the excurrent channel in the mantle; *e, e & f*, surrounded by the grooves (*c*) indicated by the arrows which convey the expiratory water from the branchiæ in the direction of the cloaca; *d, d'*, branchial lamellæ; *j, j*, arrows showing the direction of the currents along the distal or free border of the gills which convey food to the mouth.



# EXPLANATION OF PLATES.

- Fig. 11.* Ideal transverse section of the former—compare with *fig. 7<sup>2</sup>*. Pl. I. It is designed only in outline plan to display the relative anatomy of the extra-branchial (*b*), the branchiae and pallial membrane (*d*), and the intra-branchial or anal chamber (*c*); *a*, openings of the mantle.
- Fig. 12.* Oyster: *a*, mouth between the palpi; *b*, anus, emerging out of the visceral mass; *c*, upper half of the mantle arching over the branchiae; *d*, lower mantle; *e, e', e''*, arrows showing currents entering the cavity of the mantle (*l*); the arrow (*l*) also marks the food-bearing currents tending towards the mouth; *h*, intra-branchial or anal cavity; *g* is that portion of the pallial membrane which stretches from the proximal border of the upper branchial lamella to the side of the visceral mass, thus shutting in completely the intra-branchial cavity; *j*, the excurrent.
- Fig. 13.* Ideal transverse section of the preceding figure: *a*, mouth; *b*, general cavity of the mantle; *c*, openings between the valves (*f, f'*) of the mantle; *g*, membrane uniting the branchiae with the mantle, and dividing the pallial chamber (*c*) from the intra-branchial cavity (*e*); *d*, the anus.

## PLATE VI.

- Fig. 1.* Complete view of the *double gill* of *Pholas candida*. The attached border is held upwards as it were. *a, b*, are the large afferent and efferent trunks (of which there is a *set* in the border of each lamella) communicating with the parallel vessels, as shown at (*n*) and (*h*); *c, c, c*, mark the longitudinal pieces of the intra-tubular framework of solid structures; *k, k, k*, show the mode in which these longitudinal pieces form and bound the interlamellar water-tubes (*j, j, j*); *d, d, d*, are the transverse pieces of the framework on which the lamellae (*m, c*) of parallel vessels rest, and by which the latter are held apart, and which cross at right angles the axes of the interlamellar water-tubes; *e, f*, denote the *two* series of loops of which the free border of this *double gill* is composed; they lie on two distinct planes one above the other; they are shown *as if they were few in number and far between*; they exist in nature in innumerable multitudes and packed with dense closeness. *m, n*, represent the course of the bars in the upper lamella; *e, i*, that of the lower. The arrows at the base of the gill emerge out of the interlamellar water-passages. *g*, intervascular *fibrous connecting* pieces.
- Fig. 2.* Is a view of a small portion of the entire *single* or *supplementary* (sic) gill in *Pholas candida*. *a, b*, afferent and efferent trunks giving and receiving the blood of *two separate lamellae*, not that of the *same* lamella as in the case of the double gill; *h, h*, bars of the upper lamella; *f*, those of the lower; *e*, connecting fibrous threads tying together the bars; *d*, the bars of the lower lamella, *i, j*; *c, c*, the interlamellar framework as explained in the double gill. *g & f*, show the *single* row of loops of which the free margin of this single gill is composed: but here the *plane of each loop* is placed *vertically*, not *horizontally* as in the double gill.
- Fig. 3.* A diagram representing the arrangement of the loops, *a, a, c, d*, at the free margin of the gill in some species; *b*, is the water-channel conveying a current towards the mouth. The loops are placed on vertical planes. Each lamella in this case is composed of afferent or efferent vessels *exclusively*.



## EXPLANATION OF PLATES.

- Fig. 4.* Two loops from the free margin of the double gill of *Pholas*, showing the mode in which the *continuous* membrane, *a, a*, which in some bivalves, if not in *Pholas*, really forms the blood-channel. In such cases the bars, *b, b, c, c*, would be *solid*. The water-stigmata (intervectoral orifices), *d*, are in such instances present only between alternate pairs of bars.
- Fig. 5.* Plan representing the manner in which the bars, *a* & *b*, of two separate lamellæ placed on the *same* vertical planes, but different horizontal planes, are tied together by vertical partitional perforated membranes (*e*); *d*, shows the water-orifices in that connecting structure (*e*) which unites the bars of the same lamella *horizontally*.
- Fig. 6—6<sup>2</sup>.* Minute anatomy of the branchial bars in those cases in which the hyaline cartilages, *a, a*, are so closely approached as to form the boundary of the channel (*c*); *b, b*, pieces of the cilia-bearing epithelium stripped off.
- Fig. 7.* View of a piece of the entire gill of *Thracia convexa*. The free, distal margin is turned upwards. *a, b*, the double rows of *vertically disposed* loops of which this margin is made up; *g*, the contraction which occurs between the interlamellar water-tubes (*e*); *f*, one of the transverse pieces of the interlamellar framework in view, crossing the water-tube, indicated by the arrow.
- Fig. 8.* The same cut horizontally along the length of the bars. The free edge (*b, c*) of the upper lamella is left. *d, d*, show the mode in which the transverse pieces of the intra-tubular framework lie between the lamellæ, *a, b*, which constitute the walls of those tubes; *e, e*, arrows denoting the direction of the water-currents in the tubes.

## PLATE VII.

- Fig. 9.* A small piece of the free edge of the double gill of *Venus striatula*. *a, b*, loops of the bars of the two component lamellæ lying horizontally; the loops lobed (fig. 10) as they are in *Mytilus*. *c*, the afferent and efferent bars of a single loop. The arrow descends from the interlamellar water-tubes.
- Fig. 10.* One of the loops from fig. 9, enlarged, representing the lines and disposition of the vibratile cilia, *a, b*; *c*, is a fleshy nodule tying the loop to its neighbour.
- Fig. 11.* The free margin of the gill of a minute freshwater bivalve. It is produced with a view to illustrate the *continuous* membrane which in some cases ties the branchial bars together at the *free* border of the gill. *a, b*, the loops of the two lamellæ are shown as if they were separated by the intervening tube (*c*), but in *nature* the lamellæ are fused together at the free border, and the intermediate tubes are cæcal.
- Fig. 12.* A few looped bars from the preceding, magnified, showing the delicate transverse threads, *c, c, c*, which cross the branchial bars at distant intervals. They lie on the *inside* or *tubular* aspect of the lamellæ, and sometimes supersede the intra-tubular framework. The open spaces (*d*) between these cross threads are the "intervectoral" water-orifices. *a, b*, are either vascular bars, or two rigid sides bounding an intermediate membranous channel, which then is the blood-channel.
- Fig. 13.* A small portion from the distal edge of the double or upper gill of *Cardium*. *a, b*, the upper and lower loops of which this border is composed. The planes of the loops have a vertical position in



# EXPLANATION OF PLATES.

relation, that is, to the plane of the whole gill. *c*, the fleshy or membranous structure which unites the loops. It belongs probably to the intra-tubular apparatus, *d, d*. Although in *this* double gill, as in *all* double acephalan gills, the free edge is double, the interlamellar water-tubes *f*, and arrows *g*, are *single*. The double row of loops runs into one at a little distance from the margin, in order to form *one* system of tubes. This union of the bars is shown at *i* and *e*. *h*, indicates the fleshy structures,—a part of the intra-tubular cross bars by which the lobes or “pectinations” of the gill are held together.

*Fig. 14.* A portion of the free margin of the inferior or *single* gill of *Cardium*. This figure exhibits perfectly the manner in which the limbs (*b*)—(which, arranged in a linear series, form the upper wall of the tube (*d*), or the upper lamella of the gill)—of the *same* system of loops pass, by looping *vertically*, as shown at *a*, into those of the lower wall of the tubes, or, which is the same thing, into the lower lamella of the gill.

*Fig. 15.* Shows the *alternate mode* by which the membranous blood-channels (*b, b, b*) are formed by the *solid* bars (*a, a, a, a*) of contiguous, but distinct loops. In such a case, which is the normal type in the branchiæ of all Tunicata, the cilia are disposed in lines *only* on that side of each bar which is nearest to the water-fissures (*c*). These fissures, in such examples, are not crossed by transverse connecting threads.

*Fig. 16.* Represents one of the lobes, or tubular pectinations, from the single gill of *Cardium*, cut longitudinally, illustrating the mode in which the water-tubes are formed.

## PLATE VIII.

*Fig. 17.* The “bars” from the gill of *Mytilus*, followed throughout the whole of their minute anatomy. *a, b*, are the afferent and efferent blood-trunks, running along the attached margin of the upper lamella *A*. This border of the gill in *Mytilus* is represented as including *two* trunks, on the theory, as yet not quite proved, that the *two* edges, *c* and *c*, would then be the beginning of the blood-channel along the *blunt* edge, and *a, a, a*, would mark the termination of that, travelling along the acute margin of the *same* penknife-shaped process. *j, j*, are the corresponding trunks at the proximal border of the inferior lamella; *e, e*, mark the *continuous* membrane by which, in this gill, the bars are tied together at the proximal border, so that no water can pass between the bars; *f, f, f, f*, are open orifices between the fleshy nodules, *o, o, o, o*, by which the aerating water enters from without into the interlamellar water-tubes; *q, q, q*, are the superior lobes of the *single* loop, of which the free margin of the gill in *Mytilus* is composed; *p*, is the lower lobe. The deep groove between these lobes is the great alimentary water-channel, bearing a current moving in the direction of the mouth. *l*, is a fleshy nodule, by which the loops are united into a series; *k, k, k*, are *horizontal* water-passages; *m, m*, fleshy nodules, which connect the contiguous bars. The system of arrows, *g, g, g*, indicate the direction of the great respiratory current, along the upper surface of the lamella; *i, i, i*, the lower: *both* having the same direction—towards the free margin of the gill.

*Fig. 18.* Is a transverse section of one tube from the gill of *Mytilus*,



# EXPLANATION OF PLATES.

- exhibiting the mode in which the laminae *separate*, in order to form a tube (*a, b*).
- Fig. 19. Four bars from the same gill, illustrating further the *vertical* parallel planes on which the penknife-shaped bars are placed, and the mode more exactly in which they are tied together.
- Fig. 20. A magnified view of a minute portion of a *single* blade-like bar from the gill of *Mytilus*. It illustrates the distribution of the cilia; and the water-currents, denoted by the arrows, set in motion by them. *a, b*, are intended to show the position of the blood-channels in the axes of the thickened lines of either edge of the blade. If the upper lamella in the exceptional gills of *Mytilus* should be hereafter proved to carry only a *single* system (afferent or efferent) of blood-currents, the channel carrying such a single current must prove to be a *flat* passage, whose transverse section would extend from *a* to *b*; *e, e, & c*, fleshy nodules.
- Fig. 21. Two longitudinal lobes, or pectinations, from the gill of the common Oyster. *a, c*, the *double* loops of which the free margin is composed. They are drawn as if separated from each other, in a tubular form; but, naturally, the two planes of loops lie in close apposition. At this border in *Ostrea*, the branchial bars are soldered together by a *continuous* membrane over the interval included in the dotted lines *g, f*, are the transverse pieces of the intra-tubular framework. By these transverse pieces, the lamellae forming the water-tubes are sometimes drawn into quadrilateral figures, *d, e*.
- Fig. 22. A few of the "bars" from the same gill, showing that each bar is an independent vessel. The component hyaline cartilages, *d, c*, are brought *close* together, so as to form a cylindrical channel, *e*. *a, b*, exhibit the transverse structures, as running along *one* (the internal) of the tubes. This arrangement proves that the latter cannot be transverse *vessels*.
- Fig. 23. A portion of the *single* gill of *Venus*, drawn as an outline plan. *e, d, f*, mark the course of the blood, and the character of the blood-channel, from the attached margin (*a*) of the superior lamella, to the end of its course at the proximal border (*b*) of the inferior lamella.
- Fig. 24. A second plan of the gill of *Mytilus*, constructed on the supposition that each *lamella* carries only a single blood-current, of which the beginning is shown at *d*, margin *a*, and the end at *d*, margin *b*. The border, *h*, depicts the order of the vibratile cilia.

## 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



# EXPLANATION OF PLATES.

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 defecatory orifice. The arrows define the position and the boundaries of the breathing-chamber.
- Fig. 6.* *Planorbis corneus*, Lamk., taken out of its shell. *a*, respiratory siphon; *b*, space embracing the mantle; *c*, outline of pulmonary chamber; *d, d*, abdominal segment of the body.
- Fig. 7.* Plan of branchial chamber of *Sepia officinalis*. *a*, expiratory siphon; *b*. and arrows, inspiratory fissure; *c*, bottom of the branchial cavity; *d*, plan of the hollow cones of the branchiæ; *e*, the open hollow bases of the branchiæ by which the water enters the interior of the organ.

## PLATE XI.

- Fig. 1.* Respiratory chamber of *Vermetus elegans* laid open, after Quoy. *a*, branchiæ; *b*, excretory ducts.
- Fig. 2.* A single branchial conule of *Chiton* much magnified and viewed on its broad side. *a, a, a*, leaves; *b*, base.
- Fig. 3.* The former viewed edgewise, showing the axis (*b*) and the lateral leaves (*a, a, a*).
- Fig. 4.* A transverse section of the gill near the base, so as to exhibit the main trunk's artery (*a*, arrow) and vein (*b*, arrow) in section. *e, e'*, secondary afferent and efferent trunks running along the fixed border of the ultimate laminae (*d, d'*), in which the ultimate vessels (*c, c'*) are laid out, in parallel series.
- Fig. 5.* A portion of the mantle of *Patella vulgata* detached and magnified, showing the gill-laminae, *a, a, e*, resting on a thickened ridge of the mantle (*b*); *d*, tactile papillæ; *c, c*, line of the mantle.
- Fig. 6.* A portion of the free edge of one of the branchial leaves, viewed partly sideways in order to display the space (*e, g*) by which the sheets of vessels *a, i* and *b* are separated; *h*. are the delicate threads or *trabeculae* by which the component vascular layers are held together; *f*, the fleshy nodules to which the latter are affixed.
- Fig. 7.* expresses the course of a single ultimate branchial blood-channel from the fixed border (*a*) of the lamina, round the free border (*c*), back to the fixed border (*b*), proving the independence and continued individuality of the vessel; *e*, the space circumscribed by the loop (*c*); *d, f, g*. are the connecting thread and nodules.
- Fig. 8.* exhibits one branchial leaf of *Patella in situ*; it has a vaulted figure. *a*, convex part; *b*, concave; *c*, the thickened border; *d*, the row of fleshy nodules next to the free border.
- Fig. 9.* Outline sketch of the branchial system of *Emarginula huzandi* (Cuv.). *a, a*, branchiæ foliated on one side only; *b*, notch in the shell; *d*, base to which the branchiæ are attached; *c*, rectal intestine.
- Fig. 10.* Outline sketch of the branchial system of *Fissurella græca*.



# EXPLANATION OF PLATES.

- a, a*, branchiæ foliated on both sides of the supporting axis;  
*b*, perforation in the apex of the shell; *c*, rectum.
- Fig. 11. Branchial and cardiac systems of *Haliotis tubercula*. *a, a'*, *a, a'*, branchiæ doubly foliated; *b, b*, the afferent trunks; *c, c*, the efferent; *d, d*, the double auricles; *e*, the single ventricle; *f*, the aorta; *g*, the rectal intestine.
- Fig. 12. Transverse section of the former.

## PLATE V.

- Fig. 1. Animal of *Littorina littorea*, removed from its shell, having the branchial chamber laid open,—the roof being everted in order to show its under or internal surface. *e, e*, roof; *d*, colour-gland of the author, "double"-gill of Dr. Sharpey and other naturalists; *a, a*, branchia, consisting of many hundreds of parallel leaves; *b*, a gland of the mucosity, supposed to have a renal function; *c*, extremity of the *intestinum rectum*; *g*, a second gland whose function is not determined; *j*, duct of the generative organ; *i*, floor of the branchial chamber; *h*, mantle; *k*, abdominal portion of the body.
- Fig. 2. Animal of *Buccinum undatum*, removed from its shell, and showing the roof of the respiratory chamber everted: *f*, siphon; *b*, the so-called double-gill, the colour-gland of the author; *a, a'*, branchia, consisting of many hundreds of parallel leaves; *d*, duct leading from the colour-gland and terminating near the rectum, *e*; *c*, gland of the mucosity, supposed to have a renal function.
- Fig. 3. Enlarged view of a single branchial leaflet of the Periwinkle: *a, a*, cartilaginous thick or dorsal edge; *b, b*, folds or secondary plications of the surface of the leaflet; (B), the same in sectional view, showing that the *plicæ* exist on both faces of the leaf; *c, c*, a second set of *plicæ*; *h, h*, the blood-channels as they course in a parallel order towards the free margin (*g*), at which place they loop round as shown in fig. 5; *d, d*, (fig. 3) indicate the fixed border of the lamina where the afferent and efferent trunks are situated; *j*, the extreme tapering end of the lamina.
- Fig. 4. Four branchial leaflets from the gill of *Buccinum undatum*, with a portion of the roof from which they depend: *a, a*, the dorsal or cartilaginous border of the lamina; *a, f*, rows of cilia on the same; *e, c*, section of roof to which they are attached; *d, d*, the flat surface or face of the leaflet, traversed by wavy parallel blood-channels; *a, b, g*, the free border at which these channels loop, so as to reach the opposite face; *c, c*, the attached base at which the afferent and efferent trunks are placed.
- Fig. 5. is a small portion of the free border, *b*, of the last figure, highly magnified, showing the mode in which the blood-channels, *g*, curve round the free border in passing from one face of the lamina to the other.
- Fig. 6. A small portion of the epithelium from the face of the lamina.
- Fig. 7. The hyaline cartilage which gives rigidity to and is enclosed in the substance of the dorsal border of the lamina.
- Fig. 8. Two epithelial ciliated scales from the free margin, *b*, of fig. 4.
- Fig. 9. *a, a, a, a, a, a*, six leaflets from the gill of *Purpura Lapillus*: *a'*, shows the hook-like manner in which the dorsal border curves at the point—a contrivance which increases the elasticity of the cartilage in unfurling and tightening the lamina; *c*, marks the course of the blood-channels across the area of the leaf; *b*, is the



# EXPLANATION OF PLATES.

- free or floating border; *d*, the base; *b*, the base of the cartilaginous border.
- Fig. 10.* is a diagram of the entire gill in *Purpura Lapillus*, showing the general form of the organ, the largest and longest laminae being in the middle, the smallest at either end.
- Fig. 12.* The hyaline cartilage from the dorsal border of the gill-leaf of *Purpura Lapillus*.
- Fig. 12 b.* One of the blood-channels from the same, traced at the free border, showing the mode in which it loops.
- Fig. 13.* Seven branchial laminae from the gill of *Trochus magus*: *a*, cartilaginous border; *d*, base of the same; *e*, face of the lamina indicating the course of the blood-channels; *b*, free border; *c*, base.
- Fig. 14.* Seven leaflets from the gill of *Trochus cinerarius*: *a*, *d*, cartilaginous border; *b*, free border; *c*, denotes the directions of the muscular fibres which are attached to the base of the hyaline cartilage; *e*, *e*, base.

## PLATE XI\*.

- Fig. 1.* *Limax niger*, showing the roof (*a*) of the respiratory chamber reflected. On its under surface (*b*) is seen a plexus of vessels, which are more distinct on the pericardium (*c*); *c'*, *c'*, represent the mucous gland; *d*, heart; *g*, vessels distributed over the floor of the respiratory chamber; *e*, orifice of the breathing-chamber; *h*, aorta.
- Fig. 2.* A small portion of the vascular plexus from the breathing-cavity of the preceding specimen, magnified, exhibiting the tendency to a cellular or locular arrangement (*a*) in the plan of the vessels; *b*, a large circular trunk circumscribing a "cell."
- Fig. 2 (b).* A small portion of the same plexus from another situation.
- Fig. 3.* *Helix aspersa*, removed from its shell: *a*, *intestinum rectum*; *b*, ventricle of the heart; *c*, auricle; *d*, *d'*, main pulmonary artery; *k*, secondary vessels of the pulmonary plexus (*h*); *i*, diaphragm which divides the thorax from the abdomen (*j*); *f*, floor of thorax, or respiratory chamber.
- Figs. 4 & 5.* *Helix aspersa*, out of its shell. *Fig. 4* shows the animal in the act of creeping on the foot (*d*), and with the respiratory cavity (*c*) in a state of inspiratory distension: *a*, orifice into the breathing-chamber; *e'*, notch in edge of disk (*e*). *Fig. 5* illustrates the same animal, the foot being retracted, the respiratory chamber (*c*) collapsed during expiration, and the orifice (*a*) being open to take in a fresh supply of air; *e*, the disk.
- Fig. 6.* A portion of the vascular plexus from the roof of the pulmonary chamber of *Helix aspersa*, showing the parallel disposition of the secondary and ultimate vessels.
- Fig. 7.* Animal of *Lymneus stagnalis* removed from its shell: *a*, siphon in the projected state; *b*, *c*, respiratory chamber; *e*, heart; *g*, denotes the position of the *intestinum rectum*; *f*, gland of the mucosity; *h*, flattened ciliated tentacles.
- Fig. 8.* A. Muciparous gland of *Buccinum undatum*: *a*, *b*, *b*, vesicles; *c*, intervesicular stroma; *d*, cells from the interior of vesicles.  
B. A group of vesicles, seated on a peduncle, magnified: *e*, a vesicle; *b*, the cells, containing the true secretion with which the vesicles are filled; *f*, ultimate cells.
- Fig. 9.* Transverse section of the "colour-gland" of *Buccinum undatum*: *c*, lobules into which each lobe (*b*) is subdivided; *a*, section of a large vessel; *d*, axis.



# EXPLANATION OF PLATES.

Fig. 10. A lobule of the former section magnified: *a, a*, vesicles; *b*, intervesicular stroma composed of coloured cells; *d*, a small portion further magnified; *c*, ultimate cells.

## PLATE XV.

Fig. 1. The left gill of *Octopus vulgaris*, *in situ*: *a*, efferent vessel or branchial vein; *b*, afferent vessel or branchial artery; *c*, branchial heart; *d, d*, secondary lobuli of the branchia; *e, e*, tertiary leaflets; *f*, the hindmost lobule, showing that the axis of the gill is closed both behind and anteriorly at *g*; *h, h*, the sub-branchial longitudinal muscle.

Fig. 2. Transverse section of the gill (effected through the interlobular space): *a*, branchial vein (in section); *b*, branchial artery; *c*, longitudinal sub-branchial muscle (in section); *d*, attachment to mantle; *e, e, g, g*, secondary lobular artery (or afferent vessel); *f*, the frænum or membrane which forms a framework and supports the branchial foliage, *i, i, i, i*; *h*, represents the water-spaces between the lobuli.

Fig. 3-3<sup>2</sup>. Gill of the common *Calamary*, viewed from the dorsal side; 3<sup>2</sup>, the same, viewed from the ventral side: *a, a*, secondary lobuli; *b, b*, afferent primary and secondary vessels; *c*, the tertiary lobuli.

Fig. 4. Transverse section of the gill of the *Calamary*: *a*, efferent vessel, in section; *b*, afferent ditto; *c, c*, secondary efferent trunks; *d, d*, secondary afferent ditto; *e, e, e*, tertiary foliage; *f, f*, water-spaces; *g, g*, vessel; *h*, frænum by which the gill is attached to the mantle.

Fig. 5. Plan of ultimate vessels.

Fig. 6. Plan of the same at free border.







