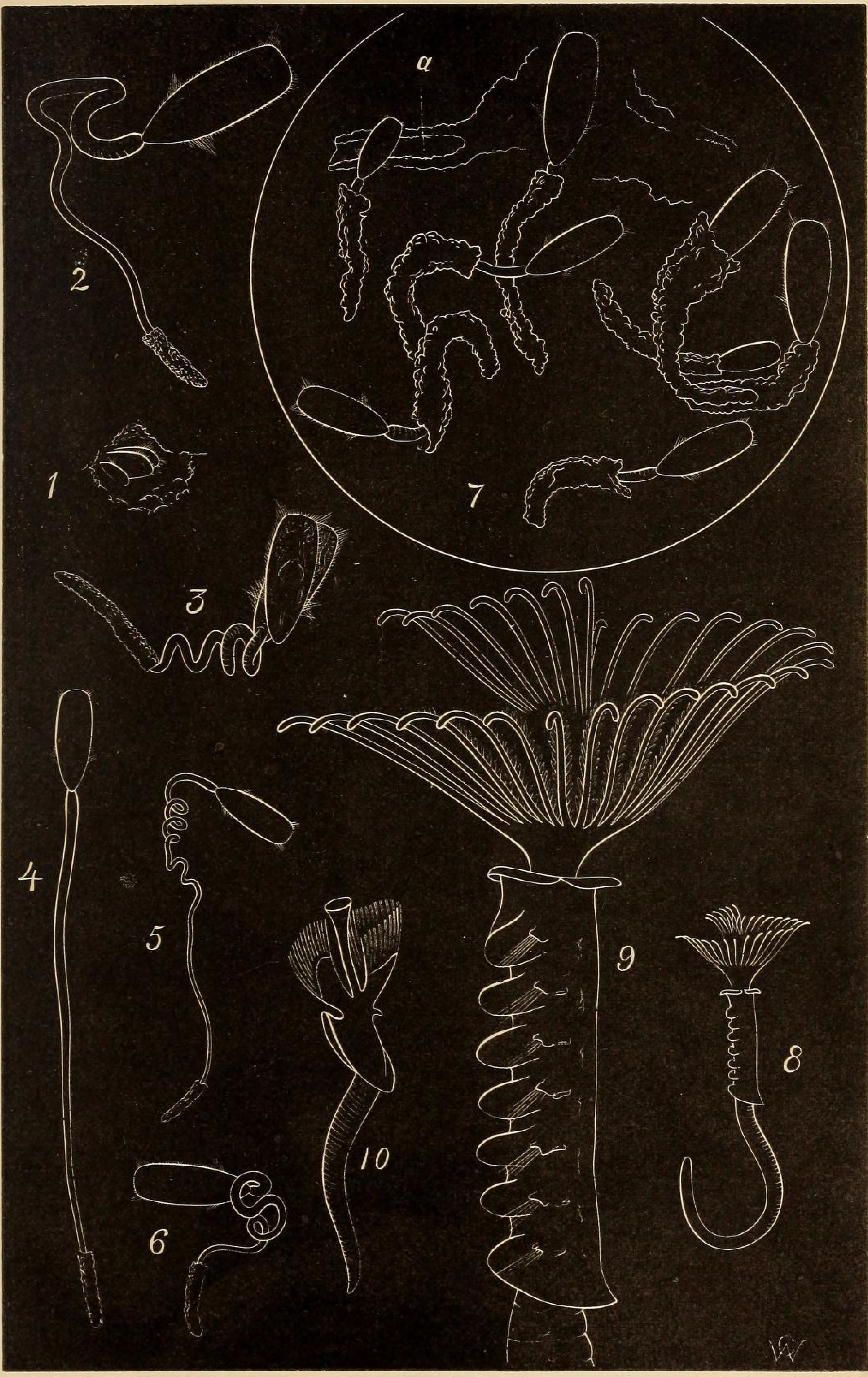


MORSE, SYSTEMATIC POSITION OF BRACHIOPODA.

was it until a few weeks before his end, that illness obliged him to relinquish his daily attendance at the assay-office. He died as he had lived, quietly, surrounded by an affectionate family, and cheered by the hopes of a Christian. His name is written imperishably in the history of American botanical science, and his monument is Torrey's Peak, that lofty summit of the Rocky Mountains which bears his name, and rises side by side with Gray's Peak, named for our other great botanist, his life-long friend and fellow-worker, who can alone do justice to the story of the long, busy and useful life of Dr. John Torrey. T. S. H.

The following paper was presented: —

The Systematic Position of the Brachiopoda.

By Edward S. Morse.

To Japetus Steenstrup,

Who first recognized the Annelidan Affinities of the Brachiopoda, this Contribution is respectfully dedicated.

Preface.

To the systematic zoölogist it is instructive to mark the changes that have taken place in the classification of animals within the last thirty years, changes not only resulting from further knowledge of the internal structure of animals, and of their embryology and early stages, but changes resulting from a new interpretation of data previously well known.

Up to comparatively recent times, such distinguished authorities as Agassiz, and Vogt, have suggested the association of the Vorticellidæ[1] and Foraminifera[2] and the Ctenophora[3] with the Mollusca.

Not only were these additions rejected, but already have been removed the Cirripedia, and the shell-bearing Serpula, Spirorbis, and other forms originally grouped with the Mollusca. Are we now to believe that this work of elimination has ended? If further dismemberment of this perplexing branch is to take place, one would naturally look for it in that association of classes called the Molluscoi-

[1] Louis Agassiz, Essay on Classification. 8vo. ed., p. 108.
[2] Ibid., p 113.
[3] Carl Vogt, Zoologische Briefe.

dea, first separated by Milne Edwards, and afterwards adopted by Dana, with pregnant suggestions as to its value as a group by itself.

Recently Kowalewsky, Kupffer, Schultze and others, have assailed the Tunicata, and demonstrated their kinship with the lower Vertebrata through Amphioxus. Leuckart has long maintained that the Polyzoa have no sort of relation to the Mollusca, but belong to the Vermes, and recently the distinguished Gegenbaur, in the second edition of his Outlines of Comparative Anatomy, not only assigns the Polyzoa to the Vermes, but places there also the Tunicata. And now in this paper I wish to show that in every point of their structure, the Brachiopoda are true worms, with possibly some affinities to the Crustacea, and that they have no relations to the Mollusca, save what many other worms may possess in common with them.

In nearly every case the unnatural association of certain groups with the Mollusca has been due entirely to superficial resemblances, to "formal analogy," as Forbes would say.

The same reason that first led conchologists and zoölogists to include Spirorbis and Serpula and the Cirripedia, as well as the Foraminifera, with the Mollusca, namely, the presence of a calcareous shell, also brought the Brachiopoda into the same category. But while there was some resemblance between the cases of certain tubicolous Annelids and the shell of Vermetus, or the flattened form and lateral shells of Anatifa, and the lamellibranchiate shell, or the chambered shell of certain Foraminifera and the Nautili, there was but little to suggest an affinity with the lateral lamellibranchiate shells, in the dorsal and ventral plates of the Brachiopoda.

The mere possession, however, of a calcareous shield of some sort, whether in one piece, or several pieces, whether a tubular or a chambered shell, furnished sufficient reasons for most zoölogists to include creatures bearing such shelly coverings with the Mollusca. Hence we find Lamarck, at one time placing Anomia and Discina together. And Cuvier, allowing the accepted views of the time to lead him astray, forsook his principles based upon internal structure, and regarded the relations of the Cirripedia as molluscan.

It is amusing now to look back and see with what quiet resignation the conchologists (for such they were rightly called) permitted the removal of those forms which possessed no shelly covering, with what stolid indifference they allowed other unprotected forms being forced upon them, and with what obstinate pertinacity they withstood the removal of such groups as possessed a limy shell.

Says Mr. G. B. Sowerby, the great English conchologist, after Thompson had so clearly shown that the Cirripedia were crustaceans and not molluscans; " Without describing the facts, or entering upon the arguments, with which he (Thompson) supports this opinion, we must be permitted to say that we do not think he has fully demonstrated it ; at the same time, considering that, as far as we hitherto knew, the Cirripeds were all attached, the circumstance of their being free when very young accounts well to our mind for the fact of each species being found attached to peculiar situations, which would only be compatible with the notion of their being at one time free agents, and possessed of an intuitive volition, determining their choice of situation." ![1]

Every worker knows how blindly one will work, when his mind is imbued with the accepted views of the subject, when he does not dream of questioning what he has always been taught to believe, particularly when those teachings come from the highest authorities. Even so distinguished a naturalist as Prof. Huxley, after he had re-repeatedly observed the external openings of the oviducts in Rhynchonella, confesses that "pre-occupied with the received views on the subject (namely, that oviducts were hearts), I at once interpreted them as artificial."[2] In the same way Prof. Owen thought he saw a minute perforation at the extremity of the intestine of Terebratula, where no such opening exists. As Lingula, and Discina had an anal opening, it was quite natural to believe that the other Brachiopoda formed no exception to the rule.

Many elaborate investigations of the Brachiopoda had been made by such eminent naturalists as Cuvier, Vogt, Owen, Hancock, Huxley, Davidson, Lacaze-Duthiers, Gratiolet and Carpenter, and in all their memoirs no doubts had been expressed as to their molluscan nature; therefore, on commencing the study of the Brachiopoda, thirteen years ago, I had no more doubt of their molluscan character, than of the vertebrate character of birds, and attempted only to show more closely the homologies which I believed existed between the Brachiopoda and Mollusca. When at last they had been forced into the place where I believed they rightly belonged, the result of that work was published in the Proceedings of the Essex Institute,[3]

[1] Sowerby, Genera of Shells.

[2] Huxley, Proc. Royal Soc., London, Vol. VII., p. 113.

[3] Classification of the Mollusca based upon the Principle of Cephalization. Proc. Essex Inst. Vol. IV. 1865. And Silliman's Journal, Vol. XLII, July, 1866.

and afterwards republished in Silliman's Journal. The fact that in that paper the Brachiopoda were turned up side down, and end for end, shows the violent methods resulting from faith in accepted views. It is a simple matter of justice to myself that I make this confession, and I may also say that my studies of the Brachiopoda have been made, not for the purpose of describing new species or genera, to show their geographical distribution, or to tabulate the number of species known, but simply and solely, to determine their affinities; and that some weight may attach to the radical views here advanced, I may, with satisfaction, state that my investigations on the subject embrace a series of observations on the anatomy and early stages, of Discina, from an immense mass of material in alcohol furnished me by Prof. Verrill. I have also carefully studied living Lingula, Rynchonella, and Terebratulina, and the early stages and embryology, of the latter.

Some of these investigations have already been published, and I had hoped to present them all before publishing this paper, but as some time will be required to prepare the results, and the necessary plates on Lingula and Discina, I am reluctantly compelled to present this first.

Introductory Considerations.

The changes here proposed in the removal of the Brachiopoda from the Mollusca, and their association with the Vermes, make necessary a comparison between the Mollusca, as now restricted, and the Vermes.

Many naturalists now hold the opinion that the Mollusca are descended from the Vermes. Indeed, it would seem from the rapidly accumulating data that the Vermes underlie the whole animal kingdom, with the exception of Protozoa. Only on this hypothesis, that the Mollusca are derived from the Vermes, can we understand the otherwise strange assemblage of characters displayed by such Mollusks as Chiton, Dentalium, Pneudermodon.

In our comparisons we are justified in selecting as typical Mollusca[1] those groups which have remained unchanged the longest.

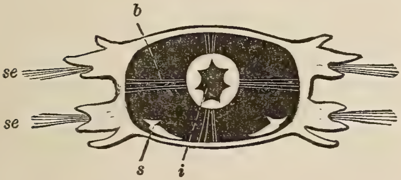
[1] We leave out of consideration the Polyzoa, since they are not only related to the Brachiopoda, but because they are regarded as worms by Leuckart, Gegenbaur, and many others, and also the Tunicates, regarded by many naturalists as forming the base of the vertebrate series; others placing them with the Vermes, and by all separated from the Mollusca proper.

A typical Lamellibranch, and a typical Gasteropod, will be admitted by all, as best representing this branch, for while other groups have widely changed since their first appearance in past ages, we find the Lamellibranch and Gasteropod of the lower Silurian as typical as present existing forms, *e. g.*, Modiolopsis, Avicula, Murchisonia, Pleurotomaria, and from the tracks and tubes, and still later setæ, we are safe to assume that the Annelids were as characteristic of their classes in past geological times, as at present.

We cannot compare the Trematodes and Turbellarians, with the Nudibranchiate Mollusks, for however much resemblance some may see in their adult condition, as among the Planarians,[1] certain characters of external symmetry in common, their respective embryos are identical with their respective divisions, the one being annulated, the other developing a foot, and a nautiloid shell.

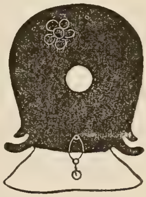
Leaving these out of consideration, then, and taking the dominant characters displayed by the Vermes on the one hand, and the Mollusca as cited on the other, we have in the Vermes, a form, whose length is much greater in proportion to its breadth than in the Mollusks; the

Fig. 1.



Transverse section of Annelid after Carus.

Fig. 2.



Transverse section of molluscan archetype after Carus.

b. bands suspending intestine in perivisceral cavity. *i.* intestine. *s.* segmental organ. *se, se.* setæ.

worms being drawn out as it were, the Mollusk being concentrated. The worm is perfectly bilaterally symmetrical, depressed, flattened or circular, the dorsal and ventral regions so near alike in many cases, as to be distinguished with difficulty, and the body never flattened laterally. The Mollusk is also bilateral, but often asymmetrical, the dorsal and ventral regions are very unlike, and the body almost always flattened laterally. This latter character is so marked, more especially among the Lamellibranchiata, as to have led Prof. Agassiz

[1] Girard placed the Planarians with the Mollusks.

to apply the term *laterality* as distinguishing the Mollusks, while the term *tergality* was applied to the whole Cuvierian branch of Articulates. Agassiz has also called attention to the fact that while the display of structure is upon the sides in Mollusca, it is upon the back in the Articulata, though numerous and important exceptions occur in both groups.

In the worm, the locomotor muscles are intimately connected through the entire length of the body with the integumentary system, especially on its dorsal and lateral walls (Rolleston). In the Mollusk, on the contrary, the locomotor muscles are connected ventrally with a specialized creeping disk, the foot.

In the Mollusk, with few exceptions, the viscera are carried above the foot in a protruding chamber.

Fig. 3.

Molluscan archetype from Carus.

In the worm, the symmetry of the body is never disturbed by the viscera. The tegumentary envelope, when separate from the body proper, forms at most a projecting, or an everted collar about the head, and, in a few instances, a continuous free membrane along the sides of the body. In the worm this envelope, and adjoining parts possess chitinous outgrowths in the shape of scales, rarely a shell, but commonly setæ, the latter being a marked character of the Vermes.

In the Mollusk the tegumentary envelope is prolonged, and oftentimes continuous, forming a sack or mantle, inclosing a conspicuous cavity, and protecting the gills. Hence the name Saccata, proposed by Prof. Hyatt. Setæ, or scales, are not present; while the possession of a calcareous shell, composed of one or more pieces, furnishes the only material to nine-tenths of those who study them. In the worm the plates, when present, and the thickened integument, are perforated with minute tubules, a character not possessed by the Mollusk.

In the worm, the digestive canal is straight, rarely convoluted, and suspended freely in the perivisceral cavity. (See Fig. 1, *b.*)

In the Mollusk, the intestine is always convoluted, not suspended freely in the perivisceral cavity, but intimately blended, or united with other organs.

In Vermes there is a peculiar depuratory apparatus characteristic of all. In the Annulata this apparatus takes the shape of bilaterally symmetrical tubes, in pairs, opening externally and communicating with the perivisceral cavity by distinct independent infundibilform orifices. (See Fig. 1, *s*.)

In the Mollusca, with exception of certain Cephalopoda, nothing of the kind is found, and where such communication does exist between the organs and the surrounding medium, it is by means of simple orifices in the walls of the cavity.

In the Vermes, especially in the Annulata, a nerve collar is found, from which start two parallel chains of ganglia, oftentimes widely separated.

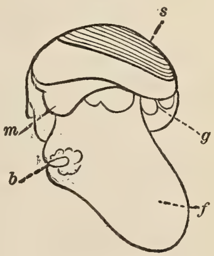
In Mollusks there is also a nerve collar surrounding the œsophagus, and no double chain, but nerves are thrown out to the sensory, motor, and parieto-splanchnic regions. Hence the names Homogangliata, and Heterogangliata. In the Annulata, with the exception of the Discophora, the generative products are set free in the perivisceral cavity, receiving from the fluid therein contained, certain nourishment. In Mollusks this never occurs, though in certain Cephalopods the products of the generative organs are set free into a compartment of the perivisceral cavity, and from there find egress through the oviduct.

With the exception of the Octopoda, the oviduct is single. In the latter group there are two oviducts bilaterally symmetrical, all of these features being vermian.

In Vermes the embryo never possesses a single or double shell, and with few exceptions is distinctly annulated,[1] while among the Mollusks, even when devoid of a shell in the adult, the embryo early develops a shell composed of one or two pieces.

Other differences of minor importance might be mentioned as separating distinctly the typical worm, from the typical Mollusk, but the leading characters here pre-

Fig. 4.



Embryo of Lamellibranchiate.

s, shell; *m*, mouth; *f*, foot; *b*, byssal gland; *g*, gills.

[1] See "NOTE," p. 10.

sented sufficiently indicate the wide divergence of the two great Divisions.

NOTE. The annulated embryo of the worms is characteristic of most of them, from the Rotifer to the highest Chætopod. In all, the body is generally divided into a few transverse segments. In the Lamellibranchiate and Gasteropod the embryo early develop the velum, or foot, projecting from a bivalve, or a nautiloid shell. In Chiton the larva is annulated, according to Loven. Pneumodermon, among the Pteropods, has the body banded by transverse circles of cilia. In Dentalium the larva resembles that of a true worm.

The affinities of Dentalium are not clearly understood. It was placed among the Annelids by Cuvier and Lamarck, and then among the Mollusks by Deshayes and De Blainville, as Gasteropods. Since then they have been bandied about from one end of the series to the other. Lacaze-Duthiers,[1] who has made the most thorough investigation of them, makes a separate class, Solenoconchia, with their affinities mostly among the Lamellibranchiates. Huxley places them with the Pteropods, on account of the rudimentary head, neural flexure of intestine, presence of epipodial lobes, and the character of the larva. With all these diverse relations, I would suggest that they certainly bear some relations to the Tetrabranchiate Cephalopods, in the numerous and retractile tentacles, the dorsal turn of the shell, and the strict identity between a peculiar bilateral cartilaginous body which occurs in the head of Dentalium, as well as in the head of *Nautilus pompilius.*

Having thus connoted the leading features characteristic of each Division, our next object is to inquire whether all the characters of major and minor importance possessed by the Brachiopods are not held in common by the worms, and are in no wise possessed by the Mollusks.

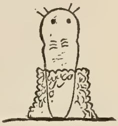
General Proportions of the Body.

In Mollusks, while we may have the body divided into a creeping disk, and a visceral portion, the visceral portion usually carried above in a protruding chamber (See Fig. 3), or the mantle prolonged behind, to form the tubes, we do not have the body constricted transversely, forming a thoracic, and an abdominal portion. We do not find such a feature as a caudal appendage, nor are the Mollusks ever attached, save by the adhesion of the calcareous shell, or by the byssus. Among the lower worms, as, for example, some Rotifera, certain forms are fixed by their posterior portion. In the Rotifera, as well as in the tubicolous Chætopods,

[1] Annales des Sciences Naturelles, 1856–57.

the body is in most cases distinctly divided into a thoracic portion, and an abdominal, or caudal portion. In Pectinaria the caudal portion is separated from the body by a deep constriction, and is apodous. In Serpula, Protula, and Lysilla, the separation of the body into two regions is strongly marked. In *Sabellaria alveolata*, the caudal portion is very long, cylindrical, and apodous.

Fig. 5.

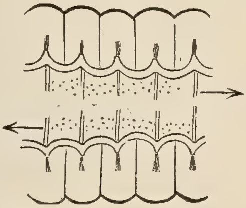


Young Rotifer.

In the Brachiopods, the body is also distinctly divided into a thoracic and caudal portion. The caudal portion varying greatly in function and character, in different groups. In some, this portion is very short, and firmly fixed to some point of support. In Rhynchonella and Terebratulina it is capable of sustaining the body, and of twirling it round in various directions, or more correctly the peduncle appears to be firm and elastic, and the body is capable, by certain muscles, of twirling round upon it. In other Brachiopods, as in Discina, the peduncle, or caudal portion, has its special set of muscles, attached to the outside of the ventral plate, and its cavity is in direct communication with the perivisceral cavity by an azygos opening.

In *Lingula pyramidata* (and I presume the other forms of Lingula will present no essential difference) the peduncle is nine times as long as the thorax, free, active in its vermian contortions, and possessing the power of fabricating a sand tube. The thorax also possesses this power. (See figures 1 to 7 in Plate I.) Not only is the body often enveloped in a sand case, but this species of Lingula has the power of covering the bottom of any vessel in which it may be confined with a sinuous sand tube, precisely similar to the tubes made by Terebella, and allied forms under like circumstances. (See Fig. 7, Plate I.) Though the peduncle of Lingula is capable of varied and rapid movements, is partially annulated, shows a constant circulation of the perivisceral fluid within, is possessed of mucous pores, yet no trace of setæ are seen upon its walls, and this is in

Fig. 6.



Portion of peduncle of *Lingula pyramidata* showing annulations and circulation of fluid within.

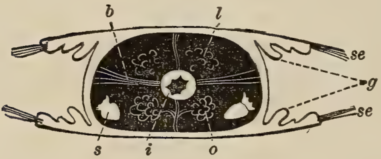
accordance with what we see in worms, that those segments without appendages or setæ are the caudal ones.

A prominent character of the higher worms is the annulations, or rings marking the body. In the Gephyrea, however, this feature is not so obvious as in the peduncle of Lingula, while in many of the lower worms, *e. g.*, Chætognatha, Nematoidea, Acanthocephala, there are no segments, and in the Rotifera the segmentation is external. Therefore the absence of this character in the Brachiopoda is unimportant.

The presence of more than one segment in the Brachiopoda is possibly marked in Rhynchonella, where two pair of segmental organs, or oviducts, occur. In Lingula, also, a deep constriction occurs just back of the posterior occlusor muscles, a membraneous partition at this point tends to separate the perivisceral cavity, and the stomach has a corresponding ridge upon its walls. All these features certainly suggest segmentation. The arrangement of the muscles in Lingula into distinct sets, first the anterior occlusors, then the posterior occlusors, next the external, central and posterior adjustors, and finally the divaricator muscles, suggests segmentation of the body, as seen in the Arthropods. This feature is less marked in Discina, though still apparent, and with their external peduncular muscles one might, with propriety, theoretically form a number of rings.

The dorsal and ventral symmetry is a distinctive character in worms. This symmetry is often so complete as to render the determination of above and below a matter of great difficulty, and, as in Sternaspis, a source of confusion. (See transverse section of Annelid, Figure 1.) The same feature is likewise characteristic of many Brachiopoda, particularly with Lingula, where these regions externally are almost precisely alike, and where single valves of Lingula are found fossil, or their impressions are seen upon the

Fig. 7.



Transverse section of Lingula.

b. bands suspending intestine in perivisceral cavity. *i.* intestine. *s.* segmental organ. *o.* ovaries. *l.* liver. *g.* gills. *se, se.* setæ.

rocks, it is almost impossible to determine whether they are dorsal or ventral.

No one, however, would mistake these regions in the Lamellibranchiate, or Gasteropod.

In the Brachiopoda, with the exception of Lingula, there is a a great concentration of the body, quite unlike anything seen in the Vermes. Lancaster, however, describes, in the Annals and Magazine of Natural History, a worm, *Chœtogaster vermicularis*, one of its chief points of interest being the exceedingly small number of segments, four or five only.

Many Rotifera are also highly concentrated, or cephalized, with dorsal and ventral flattening, and with a chitinized integument.

As to this concentration of parts in the Brachiopoda, it would be strange indeed if the worms alone should not show this concentration of structure in some of their forms. This same diversity occurs in all the other groups, as in the Crustaceans, the highly cephalized Brachyurans, and the elongated Macrourans, and among the Cirripeds, the concentrated and flattened Coronula, and the long pedunculated Anatifa. Or among the Echinoderms, the flattened Mellita or Scutella, and the worm-like Holothurian. Or, again, in the Lamellibranchiates, the concentrated Isocardia and the attenuated worm-like Teredo. Other examples might be given in the Polyps, Ctenophoræ, Gasteropods, Insects, Fishes and Reptiles.

Concentration, or cephalization of a structure, while modifying the character and functions of parts, and even obscuring their ready interpretation, can in no wise affect the relation of the animal sustaining such features, though it may account for certain peculiarities attending such conditions, in the same way that parasitism may account for the absence of certain organs, characteristic of related forms.

Integumentary Organs.

In Mollusks the tegumentary envelope is almost always extended to form a sac, or mantle, which is open below, sometimes resting like a cap upon the back, or better, extending itself in a wide membrane about the viscera, or it may hang upon the two sides of the body, split below in a median line, but not on the sides.

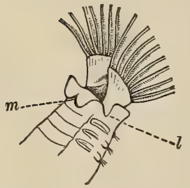
This envelope, or mantle, usually secretes a shell composed of carbonate of lime, and is attached to it by special muscles in limited areas, so that when these are separated, the envelope is found to have no sort of connection with the inner walls of the shell secreted by it, from which the shell readily drops. This feature renders possible the formation of pearls, by irritating substances or parasites, finding their way between the mantle and shell.

The molluscan shell is never perforated with tubules passing perpendicularly through, from one surface to the other, nor are there any minute ramifications of the mantle, or, other portions of the soft parts, entering the substance of the shell, and consequently no adhesions of the body, save by the special muscles above alluded to.[1]

In the Annulata the integument is rarely ever extended beyond the limits of the body. When this is the case, it forms a broad membrane bordering the thorax, as in Protula, *Serpula crater* (See Plate I., fig. 10), and others, or it surrounds the head in a collar, often everted, *split upon the sides* and *notched in the median dorsal region*, and separated in a *median line below*. In *Protula Dysteri*, a broad membrane borders the lateral aspect of the thorax, from which the setæ spring. In *Serpula crater*, the membrane borders the thorax *diagonally, being free at the posterior dorsal region of the thorax.*

In Brachiopods we have an extension of the tegumentary envelope from above and below, enclosing the arms. This membrane is also *split upon the sides*, and is directly to be compared with the cephalic collar in certain tubiculous annelids, as Sabella, for instance, where it differs only in degree. In Sabella the cephalic collar does not cover the bilobed arms, but it is a split upon the sides, and notched in the median dorsal line. In many Brachiopods there is also a notch in the median line, and the genus Pygope of Link, the notch divides the collar into two lobes, which afterwards unite, leaving a hole, or space in the shell. In other words, this membranous collar covers simply the base of the arms in those worms possessing it. While in the Brachio-

Fig. 8.



Showing cephalic collar of Sabella.
m. median dorsal notch.
l. lateral notch-

[1] In his work on the Microscope, Dr. Carpenter has described, as peculiar to Anomia, an irregular net work of minute tubules, running parallel to the surface of the shell, scantily distributed in the inner layers, but very abundant in the outer layers. In his last edition of this valuable work, Dr. Carpenter explains the character of these minute tubules, and refers them to the action of a parasitic fungus. Mr. Mark Stirrup, at a meeting of the Manchester Philosophical Society, England, exhibited sections of various shells, and showed that in Anomia, the ramifying tubules were produced by a fungoid growth.

pods the collar covers and protects the arms, which, however, may partially project, as in Terebratulina and Lingula, and wholly so in *Rynchonella psittacea*, as I observed last year.[1]

Furthermore this pallial membrane, or cephalic collar of the Brachiopods, is not to be compared to the mantle in the Mollusca, as pointed out by Dr. Carpenter in 1854. In a paper on the peculiar arrangements of the sanguiferous system in Terebratula, and other Brachiopods,[2] he says : "The membrane which is commonly spoken of as the *mantle*, and which may be stripped from the shell by the use of sufficient force to overcome its adhesions, must, I maintain, be considered as really its *inner layer* only ; for I find that an outer layer exists, so intimately incorporated with the shell as not to be separable from it without the removal of its calcareous component by maceration in dilute acid. When thus detached, this outer layer is found to be continuous with the membrane lining the perforations in the shell." I have observed that when the test[3] is removed in *Lingula pyramidata*, the perivisceral cavity is often exposed, of such extreme tenuity is the inner lining membrane.

From a figure and description given by W. Baird,[4] of a peculiar worm case *Terebella flabellum*, the cephalic collar might have had the proportion of many Brachiopods, in being broader than long. He describes the orifice of the tube as being circular, and says, "the most characteristic feature, however, in the structure of this tube, is the fan-shaped expansion of filaments at its upper orifice. This orifice is circular, and has on its dorsal surface a projecting lip, or kind of hood, which extends beyond the mouth for a short distance, whilst from the ventral side springs another lip or hood."

Dr. Dawson[5] represents the worm case of *Vermilia serrula* from the Gulf of St. Lawrence, in which there is a marked thoracic enlargement.

In a few worms only, do we find dorsal scales, as in Polynoe, or posterior and ventral scales, as in Sternaspis, and when these occur, they are chitinous, as in Discina. In Brachiopods the dorsal, and ventral shells, or plates, are unlike anything we know of in worms. Their composition and structure, however, their dorsal and ventral

[1] American Journal Science and Art, Vol. IV., Oct., 1872.

[2] Proc. Royal Soc., London, Vol. VII., p. 32.

[3] The test of this species, when dried, wrinkles and folds together like the scutæ of Lepidonotus.

[4] Journal Linnæan Soc., Vol. VIII., p. 157, pl. 5, figs. 1, 2.

[5] Canadian Naturalist, Vol. V., p. 24.

arrangement, the fact that in Lingula and Discina and allied forms the shells have their borders free all round, while in those that interlock at their posterior margins, there is no ligament to act upon them, as in the lateral shells of the bivalve Mollusk, all these features together preclude the possibility of any comparison between them and the molluscan shell. It is, therefore, more natural to regard the Brachiopod shell as a dense and thickened integument, to be compared to similar regions in the Arthropods and in the worms, simply as dorsal and ventral plates, and from certain considerations to follow, we believe this relationship will be admitted. The presence of nearly fifty per cent. of phosphate of lime in the test of Lingula, both recent and fossil, is a feature peculiar to the hardened integuments of the higher Arthropods, and entirely unlike anything found in the molluscan shell. In the hardened integument of Crustacea, tubular pores exist, which according to Dr. C. De Morgan[1] are organs of general, or special sensibility, as he finds in many cases the tubules surmounted by hairs.

He says, " The shell canals are comparatively fine, more resembling coarse dentinal tubes, but they are lined by a sheath, and have contents prolonged from the vascular layer. The relations of the contents of the tubes to the internal integuments, may be shown by tearing away the latter from the shell, when the contents will often be drawn out of the canals; and it may be seen that they are prolongations of the outer layer of the integument, enclosing the elements of the vascular layer within their cavities."

In the Annelida, also, there appears a system of minute pores, and Kölliker (we copy from Claparède) asks whether they are not homologous to the tubular pores (*porenkanäle* of the Germans) of the Arthropods, or whether they may not be compared to the apertures of the cutaneous glands, such as those discovered by Mr. Leydig in the Piscicolæ. To this, M. Claparède says, positively, that the two categories of pores exists in the Annelida. Those which serve for the discharge of certain secretions seem to exist in all species. He says, furthermore, that the canalicular pores are much smaller, and much closer together, *and do not correspond with glands*, and that they *occur only* in the species with a *thick cuticle*, and not even in all these.

In the test of most Brachiopods, similar minute tubular canals

[1] On the structure and functions of the hairs of the Crustacea. Phil. Trans., London, Vol. 148, p. 897.

exist. They do not open outwardly, at least, not so far as known at present. In the test of *Lingula pyramidata*, they are exceedingly minute, and closely crowded together. Dr. Gratiolet has also observed them in the test of *L. hians*. In Discina I have failed to find them. Dr. Carpenter,[1] who is one of the highest authorities on the subject, states that these tubules are intimately connected with the vascular layer, which sends cœcal prolongations into each one of them. Hancock questions this view, and states that from his observations, the cœcal processes spring from the reticulated layer of the pallial membrane, though he admits the constant presence of corpuscles in the cœca, which strongly resemble the blood corpuscles.

Hancock, in speaking of the tubules, says: "The best mode of investigating these organs is to dissolve the shell, and then they are exposed in various stages of growth, adhering to the margins of the mantle. They are arranged in rows, and are cylindrical, with the distal extremity obtusely rounded, and are pedunculated from the first; the peduncle is long and narrow; the cœca at the extreme edge are small, but rapidly increasing in size backward; the terminal, or enlarged portion, is almost constantly stuffed full with the so-called blood corpuscles. When observed in this way, these organs have very much the character of secerning follicles, but what function they really subserve is difficult to determine; it may be that they have something to do with the growth and reparation of the shell, though it is not easy to understand how. They are probably, as suggested by Prof. Huxley, the homological representations of the vascular processes that penetrate the test of the Ascidian; and if so, it would seem likely that they have lost much of their functional importance; and, in fact, their entire absence in forms closely allied to those in which they are highly developed, augurs that they are not of high functional importance." Albany Hancock, on the organization of the Brachiopoda. Trans. Phil. Soc., London, Vol. 148, p. 837.

See also Prof. W. King, on the Histology of the test of class Palliobranchiata. Trans. Royal Irish Acad., Vol. XXIV, part XI, 1869. In some observations on the early stages of Terebratulina, I found the tubules in the very youngest stages of the shell.[2]

Claparède states that only worms with a thickened integument have those peculiar canals, and not even all these, and accordingly we find in Brachiopods, as worms with a thickened and indurated integument, that while many possess these canalicular tubes, in others they are quite absent.

[1] Proc. Royal Soc. London, Vol. VII., p. 32.

[2] Memoirs, Boston Soc. Nat. Hist., Vol. II.

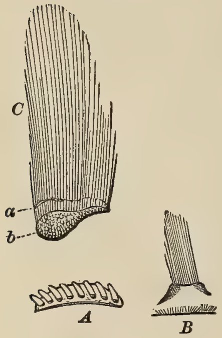
It seems then reasonable to believe that some sort of relation exists between this marked feature of the Brachiopod test, and similar features in the worms and Crustacea. In the Brachiopods these tubules may have undergone some functional change, but until otherwise proved, they must be regarded as a distinct vermian character.

In a large sipunculoid worm from Panama, kindly loaned me by Prof. Verrill, the inner lining membrane sends minute cœcal processes into the integument, which is much thickened. There is possibly here some relationship.

We also find in the Annelida mucous pores. This character must be common to all those animals secreting mucus from the surface, whether Mollusk, or Annelid; and as the peduncle of Lingula is glairy with mucus, we should naturally expect to find them present. This I easily succeeded in doing in living Lingulæ, using a $\frac{1}{8}$ inch objective of Powell and Leland. They were very minute, and closely crowded together. Their presence has never before been observed. The test of Lingula was also very glairy, but whether the mucus, which appeared to cover it, was exuded from the test, I could not determine.

Setæ.

Fig. 9.



Chiton spiculosus Gray.

A. side view of Chiton, magnified. *B.* side view of one tuft of bristles in the girdle. *C.* a tuft of bristles largely magnified. *a.* line of girdle. *b.* base of tuft.

In Mollusks, locomotion is effected mainly by a special organ, the creeping disk or "foot." There is never secreted hairs, spines or setæ.

In the embryo of some Lamellibranchiates, there is said to occur two or three little spines, which are arranged along the ventral median line.

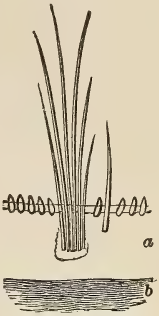
In some species of Chitons, tufts of stiff spines issuing from the girdle have long been known.

Whether these spines are homologically related to the setæ of worms, remains to be seen. From a cursory examination of them, they appear to be modifications of the minute pavement-like granules that occur in the girdle of many Chitons.

In *Chiton spiculosus* Gray, (alcoholic) from Gaudaloupe, kindly loaned me for examination by Mr. Bland, the tufts of spines readily separated from the girdle; the whole tuft is closely united together, and seems to be almost entirely superficial. The following figures represent an outline of the species, with a tuft separated and enlarged as well as a single tuft, as it appears upon the girdle, showing as well the minute spines which project from the exterior border of the girdle. The bases of the spines in the tuft are abruptly truncated.

A section of the girdle of *Amicula Emersoni* shows the shorter granules, which are but slightly embedded, as well as the longer spines, which are more deeply seated, and one spine intermediate between the long and short ones, which is again only partially embedded. These all arise from the homogeneous cartilagineous portion of the girdle, and do not reach to the muscular layer beneath, from which they are entirely separate. They are therefore probably immovable, save what mobility attends the folding of the girdle.

Fig. 10.



Amicula Emersonii

a. cartilaginous layer. *b*. muscular layer.

In worms, there is found, as characteristic of the higher as well as many of the lower groups, the production of setæ, or bristles, which perform important service in locomotion. Claparède says, in regard to the setæ of worms, that "some authors regard them as enclosed in a sac, which is only an invagination of the integument; others think they are formed in an internal follicle, and only secondarily arise to the surface. This second opinion only is correct. In certain cases (in Hesione and others, for example), the whole bundle issues in a compact form through a single pedal aperture, but in others, the seta has its own orifice; this is the case especially with the flabelliform bundles. The pore from which each seta issues is not previously formed, but is perforated by the seta itself."[1] Mr. Lancaster regards the setæ in the earth worm as secretions of the so-called setigerous gland.

The arrangement of these setæ in worms is usually upon the sides, in two series, above and below.[2] They are moved by muscles, and not only have the power of protrusion, but freely swing back and forth.

A marked feature of the Brachiopods is the peculiar setæ fringing

[1] In Pectinaria, a transverse row of long ones project forward from the head. In Sternaspis, nine bunches project from the borders of each scutum behind.

[2] See translation of introduction to Claparède's paper, Ann. Mag. Nat. Hist., 3d Series, Vol. xx., p. 344.

the borders of the extended membranes. (See Plate I.) As in worms, they are arranged upon the sides and front, in two series, above and below. (See Fig. 7, and compare with Fig. 1) and are also secreted by regular follicles, each seta protruding from the follicle singly, or, in some cases, two or three setæ issuing from the same orifice. In the fixed Brachiopoda, they have only a limited power of motion. In these forms they are very short in the adult, but very long in the young, even much larger than the animal, as I have repeatedly observed in young Terebratulina, Rhynchonella, and Discina; in the latter genus, even exceeding the length of the animal three or four times. In the errantian Brachiopoda, as in *Lingula pyramidata*, the setigerous follicles are entangled in a mesh of muscular fibres, and locomotion is effected chiefly by them; the setæ swinging freely back and forth, the dorsal plate oscillating from side to side, as first noticed long ago in another species of Lingula, by Carl Semper.

In Discina, the setæ are very long, and crowded together. According to Fritz Müller, in the early stages of a species of Discina, from the east coast of Brazil, the animal not only has the power of swimming, but uses the larger pair of setæ thrust out behind, to push itself along. He says these bristles have great freedom of motion, sometimes thrust out horizontally, and again crossed to opposite sides.[1]

In the Annelid Arenicola, the first few anterior segments are setigerous only. They bury themselves in the sand, forming a sand tube, loose and not adhering, a tube which leaves room for the ramified branchia to display, and the setæ, by arching over the branchia, protect them, and prevent the sand in which they are buried, from falling in upon the gills.

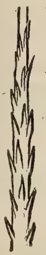
Lingula pyramidata also protects the gills in the same way, as I have repeatedly observed in specimens kept in confinement. When buried in the sand, the dorsal and ventral shells considerably separated, the setæ are brought together in such a position that their extremities meet, and the sand is thus kept back while the water freely enters.

In worms the setæ are often of various kinds in the same individual. A similar diversity is seen in the bristles of Discina. The setæ of the embryo worm are peculiar in being very long, strongly

[1] Reichert and Du Bois-Reymond's Archiv, 1860, p. 72.

barbed, and deciduous. In the young of all Brachiopods thus far observed, the setæ are also very long, as above remarked. And Fritz Müller has shown that in the embryo of Discina there are also remarkably *barbed* setæ of great length, which are *afterward discarded.* Alex. Agassiz has also called attention to the fact, that in Paleozoic worms the setæ were barbed.

Fig. 11.



Nerine cirratulus.

Deciduous seta of larval worm, *Nerine cirratulus*, from Claparède.

Fig. 12.

Discina.

Deciduous seta of larval Discina, from Fritz Müller.

Tube Building.

The fabricating of sand tubes for the protection of the body is not a characteristic feature of Mollusks. Lima builds a peculiar "nest" in attaching pebbles and fragments of shells together by byssal threads, and imprisoning itself in that way. Gastrochœna also forms a flasked-shape cavity, in which it lives, and from which it has no means of withdrawing. These features in Mollusks may be said to bear only a remote resemblance to the tube building of worms.

In worms, the building of tubes is a prominent feature of several groups, from the lowest to the highest.

Certain Rotifers, after attachment by their caudal portion, fabricate a sand tube into which they retract. (See Fig. 5.)

Many sipunculoid worms occupy the dead shells of Dentalium, Littorina and other shells, and partially close the aperture, and even extend it by a mud tube of considerable density.

Of great importance, however, in these comparisons, is the fact that those worms, which are edentulous, which have the body divided into two regions—the thoracic and caudal, and which have a bi-lobed lophophore, the two arms often appearing spirally twisted, surrounding the mouth, and supporting ciliated cirri, are all famous tube builders. Sometimes the case is gelatinous or chitinous, often the tube is calcareous, deposited in successive lines of growth, and resembling the shell of the Gasteropod; but more frequently the tube is made of fine sand, mud, bits of shell, and coarser debris that the builder meets with. When Terebella is kept in confinement in a bowl or dish, it covers the bottom of the vessel with an irregular sand tube. When I first found *Lingula pyramidata* buried in the sand shoals of Beaufort Harbor, North Carolina, I was surprised to find them living free in the sand, and not attached by their peduncle as I had supposed. My astonishment was greater to find that the peduncle was sheathed in a sand tube. When this tube was broken or removed from the peduncle, they promptly formed another one. The shell, nearly to the anterior margin, would often be enclosed in this sand case. When the peduncle was broken off, a bulb of sand would soon be agglutinated to protect the broken end, and not only sand was used, but bits of seaweed; and in one case a little stick was incorporated in this structure.

I brought home with me to Salem, Mass., a number of living specimens, and these were kept alive in large bowls, from June till October, by imitating as far as possible their natural surroundings. They would often protrude above the surface of the sand, and instantly jerk back when alarmed.

On emptying the sand from the bowl one day, great was my surprise to find that all of the Lingulas had covered the bottom of the bowl with large irregular sand tubes, cemented to the sides and bottom of the dish, the tubes running over each other, and presenting precisely the appearance as that produced by Terebella and allied forms when kept in dishes in this way. (See Plate I., Fig. 7.)

In this place it is proper to state that the peduncle of Lingula is highly mobile. When removed from the sand it twists and turns in all sorts of worm-like contortions, and in Plate I., accompanying this paper, some actual sketches are given of different individuals, showing the various contortions of the peduncle, as well as the character of the sand tubes. Fig. 6 shows a portion of the peduncle of *Lingula pyramidata*, drawn from life, showing its annulated character. The direction of the corpusculated fluid circulating through the central cavity is indicated by the arrows.

Muscular System.

In respect to the muscles of the integument, the Brachiopods bear the closest resemblance to the worms.

In worms, the muscles of the integument are arranged in two layers, transverse and longitudinal, producing a reticulated appearance. The same arrangement is distinctly seen in the perivisceral walls of Discina and Lingula, as well as in the peduncle of the latter. In the early stages of Discina, the reticulated appearance produced by the two layers of muscles is particularly noticeable.

The presence of a ponderous dorsal and ventral plate, so peculiar to many Brachiopods, accounts for the extraordinary muscular apparatus to control their movements, as well as to move the body upon the peduncle, in those forms that are attached. This muscular apparatus is unlike anything we find in the worms, though the powerful retractors of many sipunculoid worms, with their broad expanded bases, recall similar features in certain muscles of the Brachiopods. The massive character of the muscles is more like the Lamellibranchiates, save that in the latter the muscles are transverse, and their only function seem to be to close the shell, their relaxation allowing the elastic ligament within or without the shell to force or pull the shells open, as the case may be. In the Brachiopods no such ligaments are seen, the dorsal and ventral plates being opened, as well as closed, by special muscles. In one group of Brachiopods the plates interlock at their posterior margins, and are restricted to opening and closing in a vertical line. In Discina and Lingula the plates do not interlock, and their posterior margins are free, the dorsal one lapping some way over the peduncle; it can therefore swing freely back and forth, or oscillate from side to side, as observed by Carl Semper in *L. anatina*, and by myself in *L. pyramidata*, in its acts of crawling, or burying itself in the sand. (See Plate I., with references.)

Perivisceral Cavity and Circulatory System.

In the higher worms, the perivisceral cavity is lined by a delicate membrane noticed by Rathke, Quatrefages, Claparède, and others. Delle Chiaje designated it the *tunica peritoneale.*

In some worms having a rudimentary vascular system, according to Claparède, this membrane is ciliated, and prompts the circulation of the perivisceral fluid. This fluid in worms appears to be corpusculated and nutritive blood. Most worms appear to possess an extensive vascular system which contains a colored, but not a corpusculated fluid ; this is the pseudo-hæmal system of authors.

In Brachiopods, also, the perivisceral cavity is lined by a delicate membrane, which in Terebratulina and Rhynchonella is strongly ciliated, as I have plainly observed in living individuals.

In Lingula this membrane appears to extend into the pallial sinuses, as is probably the case with other Brachiopods. At all events, the circulation in Lingula is induced by ciliary action, as can be plainly seen through the transparent shell of *Lingula pyramidata*, and this fluid is that of the perivisceral cavity, and is corpusculated.

Carl Semper,[1] in his studies of *Lingula anatina*, says, that in that species there is no heart proper, and that the blood is propelled through the vessels by vibratile cilia. As early as the year 1862, he gave particulars, and has repeatedly insisted upon this anomalous state of things.

To John B. Macdonald, however, belongs the credit of first calling attention to these peculiarities in Lingula.

In the year 1861, Mr. Macdonald[2] announced the discovery "of a determinate circulation of spherical and violet-tinted corpuscles in all the ramifications of the pallial sinuses, not dependent on the contractions of a pallial cavity, but upon the undulations of a ciliary lining."

The vascular system described by Hancock, with a vessel upon the dorsal surface of the intestine, I have never succeeded in studying satisfactorily. In *Lingula pyramidata* I have not been able to find the vescicle upon the back of the intestine, but the vessel I have clearly made out. In Discina I have made out the vescicle. This difficulty of finding a heart has been shared by others. Carl Semper could not find it, and Dr. Lancaster in the February number of the Annals and Magazine of Natural History for 1873, p. 93, says in regard to *Terebratula vitrea*: "I entirely failed to convince myself that the organ regarded by Mr. Hancock as a heart really has the function of one in *T. vitrea*. I repeatedly opened fresh specimens with rapidity, in order to witness its contractions, if any, but never saw such contractions ; nor could I find vessels in connection with it, nor evidence that it had muscular walls. Dr. Krohn, of Bonn, had equally been unable to obtain evidence that this curious little dilatation has the function of a heart."[3] From injected specimens of Lingula, and from observations on living Terebratulina and Rhyncho-

[1] Zeitschr. für Wissensch. Zoöl., XIV., p. 424.

[2] On the Physiology of the Pallial Sinuses of the Brachiopoda. Trans. Linnean Soc. XXIII., p. 373, plate XXXV.

[3] In a late study of living Terebratulina I observed a distinct circulation going on in the sinuses of the pallial membrane, but whether these currents were induced by ciliary action I failed to make out. The fact, however, that the delicate membranes in the perivisceral cavity are clothed with cilia, I clearly established.

nella, the various membranes, called by Huxley and Hancock the gastro-parietal, ileo-parietal, and lateral parietal bands, are found to be vascular, and the circulation taking place within these membranes may be looked upon as representing the pseudo-hæmal system of authors.

These membranes intimately invest the oviducts, and in Rhynchonella the circulation of this system can be seen following the spaces between this membrane and the outer walls of the oviduct.

The red corpuscles in Lingula occur in the perivisceral fluid. Other bodies of a fusiform shape, some elongated and others nearly round, are also met in the perivisceral fluid. These are amœboid in their appearance, and may be seen bending and turning as they course through the more delicate ramifications in the pallial membrane.

All these features I hope to figure in my memoir, now in preparation, on Lingula. The colored corpuscles are similar to those which occur in the perivisceral fluid of the Sipunculoid worms, as well as in Glycera, and other worms, noticed by Claparède.

According to Lacaze-Duthiers, the two systems of circulation are remarkably distinct in Bonellia and Sipunculoid worms, and he queries whether the Brachiopods *do not possess the same two systems.* Claparède says: "L'immense majorité des Annélides ne présente pas de mouvement ciliare dans la cavité périviscérale, sauf à l'entrée des organes segmentaires. Je ne connais, pour ma part, le vêtement ciliare périviscéral que dans les groupes suivants: chez tous les Aproditiens, chez tous les Glycériens, chez tous les Polycirrides, chez les Tomoptéridiens, et enfin chez une petite Térébelle assez anormale (*Terebella vestita*). Chose frappante, toutes ces Annélides, à l' exception de la petite Térébelle et de l'*Aphrodita aculeata*, sont complétement dépourvues de vaisseaux. Or, de ces deux exceptions, l'une, l'Aprodite, est un animal à système vasculaire dans tous les cas rudimentaire, appartenant à une famille d' ailleurs toute anangienne, l'autre, la Térébelle, appartient à une famille en général vasculaire, mais dont une tribu cependant, celle des Polycirrides, est anangienne. Je dois, en présence de ces faits, regarder le mouvement ciliare périviscéral comme une fonction vicariante de la circulation, chèz les Annélides dépourvues de système circulatoire proprement dit."[1]

[1] Mém. de la Soc. de Phy. et Hist. Nat. de Genève. Tome XIX., 2d part, p. 329.

In the Brachiopods, therefore, particularly in Lingula, where the vascular system appears to be quite rudimentary, the presence of a ciliated perivisceral coat is to be expected.

It must be confessed that much work has yet to be done in clearing up the obscurity which still exists in regard to the circulatory system of the Brachiopods. What little is known about it, however, points to vermian affinities.

Digestive System.

In worms, the digestive tract usually takes a direct antero-posterior course without convolutions. There are, however, marked exceptions to this rule.

In the Sipunculoid worms, the intestine is not only convoluted, but in many of them the anus terminates in front. In a curious worm, described and figured by Philippi,[1] under the name of Hæmenteria, an anterior vent is described.

In those remarkable worms, Phoronis and Crepina, whose external outlines in every particular so closely resemble the Hippocrepian Polyzoa,[2] the anus terminates in close proximity to the mouth.

In the Acanthocephali, the digestive tract is said to open into the general cavity of the body in some, while in others it ends in a cœcal sac.

In Temnocephala,[3] a Trematode worm, the cœcal processes from the stomach are much like those in young Brachiopods.

Among the Rotifera, in some groups the female has the œsophagus terminating in a cœcal stomach. The anus, when present, terminates anterior to the caudal portion. The Turbellarians are also devoid of an anus.

The anomalous features here presented by some worms, in the absence of an anus, or the possession of a cœcal stomach, and the anterior termination of the anus, are fully repeated in the Brachiopoda. In one entire division of the Brachiopoda, represented by Terebratula, the stomach terminates in a cœcal sac. In Terebratulina the alimentary tract is closed posteriorly. Nor has the slightest

[1] Acad. delle Sci. di Torino, series II, tom. x.

[2] In Phoronis the oviducts with bilateral openings also terminate in front. Its bilobed lophophore, reddish circulating fluid and embryonic stages all resemble the Brachiopoda. In fact, Phoronis represents an important connecting link between the Polyzoa and the worms.

[3] Zeitschrift für Wiss. Zoöl., Vol. xx, p. 307.

trace of an anus has been detected in Thecidium, Waldheimia, Rhynchonella, and several other genera that have been examined. In the very early stages of Terebratulina, I have seen the rejectamenta escape from the mouth, and in no case has the appearance of an anal perforation been discovered. In Terebratulina, the alimentary tract pursues a direct antero-posterior course without convolutions, while in Lingula and Discina the anus terminates anteriorly on the right side. In Lingula, the intestine makes a few turns, while in Discina it makes a single turn to the right.

In many worms, diverticular channels often spring from the lateral walls of the intestine. In certain worms the liver appears as protrusions of the alimentary canal.

In Brachiopods the liver is composed of masses of cœcal ramifications which in young Terebratulina, Rhynchonella and Discina, commence as simple diverticular channels of the stomach.

In *Lingula pyramidata*, an examination of these cœca to their extremities revealed the presence of diatoms and other food, showing that the contents of the stomach enters these diverticular processes, and that the process of digestion is carried on in these parts, as in the lower worms. The fact that in young Rhynchonella, a distinct *peristaltic action* is seen going on in the hepatic cœca strengthens this supposition. While the brown hepatic lines are arranged parallel to the longer axis in the cœca in Terebratulina, in Rhynchonella they are curiously arranged in a spiral manner.

In the higher worms, the intestine is freely suspended in the perivisceral cavity, and held there by delicate membranes which spring from the parietes of the body. (See Fig. 1.)

In Brachiopods, the intestine is likewise suspended freely in the perivisceral cavity by delicate membranes which. spring from the parietes of the body. These membranes were called by Huxley, the gastro-parietal, ileo-parietal, and lateral parietal bands. (See Fig. 7.)

Cephalic Region.

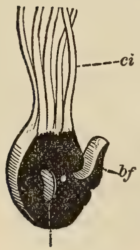
In many of the tubicolous Chœtopods, as well as in Phoronis, the head is furnished with a tuft of ciliated cirri. Sometimes these appear to surround the mouth in a single circle, as in the marine Polyzoa, and in certain fluviatile forms. In others, they spring from arms, spreading like two fans in some, while in others, each arm is developed into a closely wound spiral of several turns. These spring from what has been called a cartilaginous base. In *Protula media* Stimpson, each arm makes a single graceful turn. The cirri springing from these arms, are often highly and beautifully colored, sometimes each cirrus is banded with brown.

In those with a closely wound spiral arm, as in *Amphitrite ventrilabrum*, the outer margin of the arm at the base of the cirri, is bordered by a delicate membranous frill, possibly corresponding with the calyx in Polyzoa, but precisely identical with the brachial fold in the arms of the Brachiopoda, as will be seen by reference to the sections to be presently given.

In the Brachiopods, the two arms springing from the head are to be directly compared to similar parts just described in the worms. They also spring from a cartilaginous base, and sustain ciliated cirri, and in Lingula, Discina and Rhynchonella, they are developed in a closely wound spiral, as in Amphitrite. Furthermore in Rhynchonella, they can be unwound and protruded from the pallial cavity as I had the good fortune to observe in living Rhynchonella from the St. Lawrence.[1] (By instantly dashing the strongest alcohol upon the specimen, I was enabled to preserve it with the arms extended.) In Lingula the arms can be partially unwound, and what is very significant, the cirri in *Lingula pyramidata* are banded with light brown, as in certain species of Sabella.

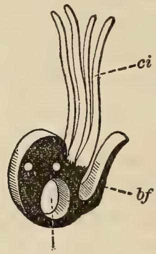
The cirri in Brachiopods show a rapid circulation through their transparent walls. They are employed to secure particles of food, which they convey to the mouth, and in every respect they are strictly identical with similar organs in the Annelids. A transverse section of the right arm of *Amphitrite ventrilabrum*, Fig. 13, and of the right arm of *Lingula pyramidata*, Fig. 14, is here presented. These sections are, in each case, taken midway between the base and extremity of the arm. They much more closely resemble each other, than corresponding sections of two Brachiopods resemble each other.

Fig. 13.



Transverse section of arm of *Amphitrite ventrilabrum.*

Fig. 14.



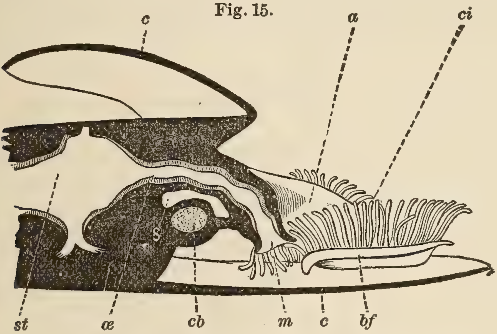
Transverse section of arm of *Lingula pyramidata.*

ci. cirri. *bf.* brachial fold. *s.* sinus.

[1] Am. Journ. Science and Arts, Vol. IV, Oct. 1872. Otto Frederic Müller, according to Von Buch, also saw Rhynchonella gracefully uncoil its arms.

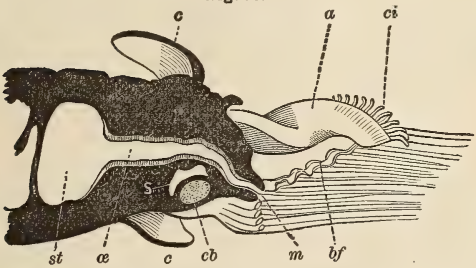
In Lingula the brachial sinus is quite large, while in Amphitrite, it is smaller. The brachial fold in the former is wider. The differences between the two, however, are differences of porportion of parts simply. In certain Polyzoa, just as in that curious worm, Phoronis, the cirri spring from a horse-shoe-shaped lophophore, hence they are called hippocrepian Polyzoa. In the early stages of Terebratulina, I have shown that at first the lophophore is circular, as in the lower Polyzoa, and afterwards the hippocrepian character reveals itself.[1] It was important to learn whether the mouth opened between the

Fig. 15.



Longitudinal section of anterior portion of Lingula.

Fig. 16.



Longitudinal section of anterior portion of *Amphitrite ventrilabrum.*

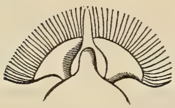
m. mouth. *œ.* œsophagus. *st.* stomach. *a.* arm. *ci.* cirri. *bf.* brachial fold. *cb.* cartilaginous base of arm. *s.* sinus leading to arm. *c. c.* cephalic collar or pallial membrane.

[1] Morse. Early Stages of Terebratulina. Mem. B. S. N. H., Vol. 1. These observations have since been confirmed by Dr. E. Ray Lankester in Annals Mag. Nat. Hist., February, 1873, on the young of *Terebratula vitrea.*

outer and inner folds of the arms, in those worms possessing these appendages, as in the Polyzoa, Phoronis, and the Brachiopods. I sought in vain the works of Claparède, Quatrefages and others, for a figure of a longitudinal section through the mouth of some worm of this character. Mr. Alex. Agassiz kindly gave me a large specimen of the *Amphitrite ventrilabrum*, from the Bay of Naples, and I made a careful longitudinal section through the head (Fig. 16). The right arm was developed in a closely wound spiral of several turns, and greatly exceeded the length of the left one. I have shown the latter, however, as it presents a clearer view of the twist and character of the arm, as well as the crenulated membrane, or brachial fold which borders the base of the cirri. In this section, as well as in the accompanying one of *Lingula pyramidata*, the cirri are partially removed, as they form a confused tangle, and thus obscure the parts that are desired to be shown.

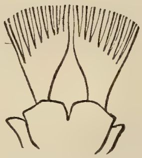
The mouth is bordered by two membranous lips, which in the Brachiopods are highly sensitive and movable in all those thus far examined. The mouth in Amphitrite, as well as in other worms of that nature, is placed in the same relation with the head, and points downward, as in the Brachiopoda. The almost membranous shells have been removed, and the dorsal pallial membrane is turned back, to correspond in position with the dorsal cephalic collar in Amphitrite, which is normally turned back, as in Sabella and Serpula. In other respects the sections are correct drawings of their leading features, and are in no way modified to resemble each other. I have lettered the parts alike, and their almost absolute identity may be readily seen without further comments. The relations insisted upon as existing between the cephalic collar of the Annelids possessing it, and the pallial membranes of the Brachiopods, are well shown in these sections. Even the relative position of the base of the dorsal cephalic collar in the worm, corresponds to the same parts in Lingula and Discina, the dorsal one springing from the head in advance of the ventral one. See also Fig. 8, p. 14.

Fig. 17.



Head of Discina.

Fig. 18.



Head of Sabella.

Figures are here given of a young Discina, Fig. 17, and of a

Sabella, Fig. 18, to show the similarity of the cephalic arms in the two. In one the portions are concentrated, while in the other they are drawn out.

Dr. E. Ray Lankester,[1] in an exceedingly interesting sketch of *Terebratula vitrea*, compares its arms and cirri, to the gills of a Lamellibranchiate. In this comparison he is certainly wrong, for the gills of the Lamellibranch develop upon the sides, and in Sphærium and other genera, towards the posterior end; while the cirri, with the arms sustaining them in the Brachiopods, are strictly cephalic. Had he compared the arms of the Brachiopod with the membranous palpi of the Lamellibranch, he would have come nearer the true affinities, for these form folds above and below the mouth, are united partially on their inner margins as I have observed in Unio and other genera, and in some species are very long.

Renal Organs.

Claparède has noticed that in the segmental organs of many worms a portion of the tube is glandular, and he has reason to suppose that the glandular portion represents the renal organ. Whether Claparède is right in his conjectures or not, it is interesting to recall the fact that years previous to this statement, Huxley suggested that the glandular portion so very conspicuous in the oviducts of Brachiopods was of a renal nature.[2]

The slightest examination of the oviducts of Brachiopoda shows the tubular portion not only glandular, but colored, as in the oviducts of worms. This portion is also intimately connected with the vascular system, and whether renal in its nature or not, the closest similarity exists between these portions and similar parts in the segmental organs of Annelids.

Nervous System.

The general plan of the nerve system in the Vermes appears to be that of a nerve collar surrounding the œsophagus, sending off a ventral cord in a median line of the body. In the lowest worms there seems to be simple cephalic ganglia without the ventral cord. In Sipunculoid worms a single cord running along the ventral portion of the body sends off delicate threads at right angles to it. In the higher worms the ventral cord is longitudinally divided into two symmetrical halves. In some worms there appears only a slight space

[1] Annals and Mag. of Nat. Hist. Vol. xi, Fourth Series, No. 62, p. 93.
[2] Hancock, ibid., p. 822.

separating the two halves; in others the ventral cord is distinctly separated, but united at each segment by transverse threads, as in Sabella, or its two halves may be united by ganglionic enlargements, which sometimes correspond to the number of segments. In the Hirudinæ the ventral ganglia are fewer in number than the segments. In Aphrodite and Polynoë, according to Grube, there are more ventral ganglia than segments.

It was at one time believed to be typical of the Articulata that each segment was characterized by a ganglionic enlargement of the ventral cord, and it was supposed to be particularly so with the higher Annelids. Claparède calls attention to the fact that this is not so in all cases, *and especially in relation to the cephalic and thoracic ganglia.*

In the Nemerteans the ventral cord is widely separated, and runs along each side of the body, and without ganglionic enlargements. There appears to be, therefore, various conditions of the nervous system, in which there is in some a simple œsophageal collar; in others, a ventral nerve cord, which may be single, or divided into two lateral halves, sometimes widely separated, sometimes nearly approximating, with, or without, ganglionic enlargements or threads connecting them. In some worms accessory pedal ganglia are found.

In the Brachiopoda we have two lateral ventral cords, widely separated, and connected at the œsophagus by ganglionic enlargements, which send off threads to the pallial membranes, and to the various muscles.

In Lingula these lateral threads seem to be double, connected by commissures. In Discina, whose nervous system I have more especally studied, the nerve cords are bilaterally symmetrical, and widely divaricating. There are no ganglionic enla.gements during their course to the posterior end of the body, but in their track sending off delicate threads, which in Lingula blend with their muscular fibres, or pass round the muscles blending with their exterior fibres. In Discina these lateral nerve cords terminate by ganglionic enlargements in the last two posterior muscles. These nerve cords were correctly interpreted by Cuvier and Owen though mistaken for arteries by Hancock. This error was corrected by Dr. Gratiolet, in his study of *Lingula hians*;[1] and while studying Discina, before becoming aware of Gratiolet's researches, I found these supposed

[1] Jour. de Conchyliogie. 2 Serie. Vol. IV, p. 162.

arteries to be nerve cords, and traced them to their posterior ganglionic enlargements.

Respiratory Apparatus.

The pallial membrane in the Brachiopoda sustains the principal respiratory apparatus. It is in this membrane that the larger vessels occur, and as I shall show in my memoir on Lingula, the pallial membrane is divided into oblique transverse sinuses, which run parallel to each other. From these arise numerous flattened ampullæ, which are highly contractile.

The circulating fluid courses in regular order up and down these sinuses, entering each of the ampullæ in turn.

Vogt and Owen were quite right in their determinations of these organs. They represent the branchiæ of Lingula; but from the contractile nature of the ampullæ, and their almost certain contraction in alcohol, they have escaped the notice of others who have studied specimens in which the ampullæ were inconspicuous.

Thus Hancock was unable to find them in the two species of Lingula, studied by him, and says, "The bladder-shaped enlargements of the lateral pallial sinuses, alluded to by Dr. Vogt, are nothing more than swellings occasioned by the contraction of the pallial, or marginal fold, which, pressing upon the extremities of the sinuses, throw their walls into wrinkles, and hence their peculiar appearance."[1]

These ampullæ are very conspicuous in living Lingulæ. On one side of the dorsal pallial membrane in an ordinary specimen there are twelve sinuses, having in the aggregate eighty-five ampullæ, numbering from five to eleven in each sinus. In life they form very interesting objects. They project, or hang from the walls of the pallial membrane, like teats. Their walls are perfectly transparent, and the circulating fluid can be seen rapidly coursing into, and out of each one in turn.

Fig. 19.

The following figure (Fig. 19) shows a row of five ampullæ drawn from life, within which the blood corpuscles can be seen circulating.

Claparède says that in the normal branchia of an Annelid there cannot be any mixture of arterial and venous blood. The artery travelling as far as the end of the branchia, where it returns as a

[1] Hancock, Trans. Royal Soc. Vol. CXLVIII, p. 852.

vein. He says, "Veine et artère sont exactement parallèles l'une à l'autre. Dans toute la longueur de la branchie, ces deux vaisseaux sont mis en communicateur par une double série d'anses vasculaires qui passent dans la couche sous-cuticulaire et qui subissent avec la plus grande facilité l'action de l'eau chargée d'oxygène à travers la cuticule tres-amincie.' [1]

He denies, however, the independent contraction of the ampullæ, but says there is a rhythmical contraction of the whole branchia, Quatrefages, to the contrary, notwithstanding.

In the family Serpulæ, Claparède finds features remotely resembling the description of Quatrefages, where in these Annelids "l'artère se continue directement dans la veine à la base des branchies, et de leur point de réunion part un vaisseau unique qui pénètre dans chaque rameau branchie." In Discina I have not been able to discover the slightest trace of these ampullæ, though the pallial sinuses are very prominent; and the central partial partition of ciliated epithelium which induces the flow of the circulating fluid in these parts, are as distinctly marked in Discina as in Lingula. In the other Brachiopods the prominence of the pallial sinuses, with their diaphanous walls, must be regarded as a respiratory organ. In all the Brachiopoda the cirri of the arms must also share with the pallial membranes in this function.

Genital Organs.

Under this head we study the ovaries, oviducts, or segmental organs, and spermaries. In the Annelida, according to Claparède, the sexual elements, in course of growth, form ruffs all around the vascular axes.

In all cases the ova, when arrived at maturity, detach themselves from the ovary to float freely in the perivisceral cavity, where they are afterwards gathered up by the ciliated mouths of the segmental organs, and discharged by them.

This is precisely the case in the Brachiopoda. In Discina the borders of the delicate vascular membranes are thrown into conspicuous ruffs by the development of the ova. In Lingula the ovaries are intimately bound to the same membranes. In Terebratulina and Rhynchonella they not only gather about the large vascular sinuses in the pallial membranes, but hang in clusters from the genital bands

[1] Soc. de Phy. et d'Hist. Nat. de Genève. Tome XIX, 2d part, p. 331.

in the perivisceral cavity. In all these cases the eggs are discharged freely into this cavity, and there float in the perivisceral fluid until they are discharged from the body.

If we now consider the ducts by which these products in the Brachiopoda find egress from the body, we shall find a startling identity of structure with similar parts in the Annelida.

In all worms, with few exceptions, these ducts assume the shape of tubes, bilaterally disposed, suspended in the perivisceral cavity by delicate membranes, and communicating with this cavity by flaring orifices, which are strongly ciliated, as well as the tubes themselves, to their external orifices; the ciliary action always directing the currents out of the body. These are the segmental organs, or oviducts.

According to Claparède, the segmental organs in the Annelida present only very simple modifications of a *very constant type*. In a large number of worms, these segmental organs are repeated many times, a few of them only modified as oviducts. In other worms they are reduced in number; in Branchiobdella, according to Dorner, to two pair; in *Terebella parvula* to three pair, as Dr. Williams states. In Protula,[1] Spirorbis, Sabella, and allied forms, a single pair of segmental organs, modified as tubiparous glands are found in the anterior part of the thorax.

In Phoronis the ovarian openings are reduced to a single pair, and these open at the extreme anterior surface of the body between the arms, from which the eggs escape after having been discharged from the ovary into the perivisceral cavity. In the Brachiopoda the ducts, by which the generative products find egress from the body must be described in precisely the same terms as those used in describing the segmental organs of the Annelids. The ducts assuming the shape of tubes, bilaterally disposed, suspended freely in the perivisceral cavity by delicate membranes, and communicating with this cavity by flar-

[1] The tubiparous glands, according to Claparède, represent modified segmental organs. In *Protula* (*Salmacina*) *ædificatrix*, Claparède represents the tubiparous glands as opening by a common pore, as in Spirorbis. A careful study made by me of a species of Protula (probably *P. Dysteri* Huxley) at Eastport, Me., showed the wide separation of these glands, and the fact that they opened by two distinct pores, thus bringing them nearer the Sabellarians.

The minute structure of these glands, revealed a sinuous line rapidly undulating, following the inner outline of the gland. This appearance appeared due to ciliary action. Other features were presented by these curious organs, which led me to believe that other functions were performed by them beside that of secreting the tube. Their relations to the segmental organs were unquestionable, however.

ing orifices, which are strongly ciliated, as well as the tubes themselves, even to their external orifices, the ciliary action always directing the currents out of the body.

The concentrated character of the Brachiopods, and the limited perivisceral cavity, reduce the segmental organs, or oviducts, to the lowest number, and consequently we find in most of them but a single pair, as in Lingula, Discina, and Terebratulina, while in Rhynchonella two pair of oviducts are present. It is significant to note that in the last named genus both pair of oviducts have their inner mouths turned toward the back.

In a special memoir on the oviducts of Brachiopoda, now in preparation, I shall demonstrate the unquestionable character of these organs.

Having studied them in living Lingula, Rhynchonella and Terebratulina, and in alcoholic Discina, I find them presenting only simple modifications of a constant type.[1]

In Terebratulina the eggs were watched through the transparent anterior walls, after their separation from the pallial sinuses. While floating in the perivisceral cavity, they were seen gathered up by the flaring ciliated mouths of the oviducts, and were followed, as they slowly passed through the tubes, and caught as they escaped from the external orifices.

In Lingula, Discina and Rhynchonella, the external orifices of the oviducts are simple slits, while in Terebratulina they project from the anterior parietal walls, like tubercles, as figured by Claparède in the Annelid *Lepidonotus* (*Hermadion*) *fragile*. The glandular nature of the oviducts, and their striking resemblance in this respect, to similar parts in the worms has been alluded to under *Renal Organs*.

The following figures of the oviducts of Brachiopods, from my own studies, and the oviducts of certain worms, as figured by Claparède and Lancaster, are here given for comparison.

Having considered that portion of the genital system referring to the ovaries and oviducts, and shown their entire vermian character, we come to study the male organs of generation, and in this line of investigation we have to push into an almost untrodden field.

The Brachiopoda have been regarded by some authors as diœcious, the vascular sinuses presenting ovaries or testes, according to the sex

[1] Morse on the Embryology and Oviducts of Terebratulina. Am. Jour. Sci. and Arts. Vol. IV, p. 262.

Fig. 20.

Fig. 21.

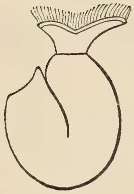


Fig. 22.

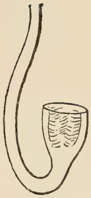


Fig. 23.

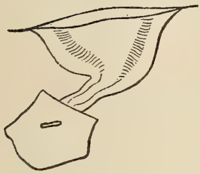
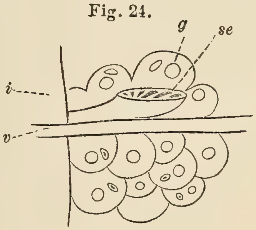


Fig. 24.



Segmental organs of Worms

Fig. 20. Lumbricus. Fig. 21. Pectinaria. Fig. 22. Eunice. Fig. 23. Stylodrilus. Fig. 24. Nereis. *se.* segmental organ. *g.* genitalia. *v.* vascular channel. *i.* intestine. Fig. 20 is from Lankester, the rest from Claparède.

Fig. 25.

Fig. 26.

Fig. 27.

Fig. 28.

Segmental organs of Brachiopods.

Fig. 25. Discina. Fig. 26. Lingula. Fig. 27. Rhynchonella. Fig. 28. Terebratulina. These figures are from my own studies.

of the individual. Hancock [1] however was inclined to believe the sexes united in all the forms coming under his observation. Oscar Schmidt [2] also says that in Terebratula the testicles and egg stocks are united in the same individual.

After patient study of these parts, I believe that in all the Brachiopoda the sexes will be found to be separate. In Lingula the spermaries occur in the perivisceral cavity, in masses like the ovaries. Having studied them alive it was found that while in some individuals the ovarian masses nearly filled the perivisceral cavity, in others spermaries occupied similar positions.

As Discina presents precisely the same characters in the ovaries springing from the vascular membranes, and filling the perivisceral cavity, it is reasonable to suppose that the spermaries correspond in position with those of Lingula.

A careful study of Terebratulina, lately made during its breeding season, shows also that in this form the sexes are distinct. While some specimens revealed the vascular sinuses filled with eggs, and even where the eggs had escaped by dehiscence the scars could be seen, in others the sinuses showed no traces of eggs, but on the contrary were filled with a creamy mass, slightly granulated, the borders of these masses being highly ciliated, and when crushed or separated under the compressor, bunches of spermotozoa and single ones were revealed. This probably represents the ovigerous mass of Hancock.

In several females examined, the eggs were attached in clusters to the genital band, even to the very edge of the mouths of the segmental organs. And in several males the spermaries were likewise attached in clusters to the genital band, and in such masses and so close to the segmental organ that the accessory vescicle of Huxley was obscured by them.

The masses of spermaries adhering to the genital band, and floating free in the perivsceral cavity, presented some curious features. They assumed the shape of long filiform appendages, attached by common centres to the genital band, and surrounded by an almost imperceptible cellular mass. The threads widened gradually to their distal extremities where they ended bluntly, and were capped with a few large brownish cells. The spermatozoa were thickly clustered in blunt fusiform masses at the extremities of the threads, forming a sort of brush. The same brownish granules appeared in the sinuses,

[1] Hancock, ibid., p. 824.

[2] Zeitschrift für ges. Naturwissenschaften, 1854, p. 325.

and likewise tipped the clusters therein contained, only these clusters were not supported on long threads, as in those which sprang from the genital band in the perivisceral cavity. The glandular portion of the segmental organ in the male appeared much darker than in the female. As Rhynchonella presents similar features in the ovaries contained in the pallial sinuses, we believe that the spermaries will be found in like positions.

In this connection we must also consider the accessory vescicles of Huxley (accessory hearts of Hancock). After careful study of these minute organs from a large number of living specimens, I am convinced that they do not bear Hancock's interpretation, and that they properly belong to the genital system and not to the circulatory system as stated by him. Hancock describes the walls of the "accessory hearts" as more delicate than the walls of what he regards as the central dorsal heart. This is certainly not so in regard to Terebratulina. In *T. septentrionalis*, the organ presents all the appearance of a gland. The walls are thick and glandular, in fact, no sure evidence of a cavity within has yet been met with. It is irregularly pyriform in shape, slightly flattened, and in some is attached by a very constricted neck to the genital band just beneath the flaring margin of the mouth of the segmental organ.

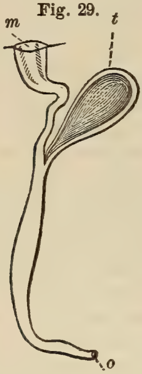
The exterior wall is made up of prominent transparent cells; at the base of the gland, and also on its walls, masses of yellowish granules in patches appear. On the genital band also I have seen irregular masses of cells, presenting all the appearances of the accessory vescicle. Repeated observations failed to detect any vascular communication with the band to which it is attached, not the slightest trace of circulation within its walls has been observed, nor the slightest evidences of dilatation or contraction, nor evidence of muscular fibre. I have repeatedly crushed it beneath the compressor, yet no signs of forcing out contents has been observed. Moreover the organ differed in appearance in different specimens, and even differed in appearance in the same individual upon the right and left sides of the body. With the idea at first that the sexes were united in Terebratulina, I was inclined to regard them as the testes, since they always occur in the immediate vicinity of the segmental organs.

Where a single pair of segmental organs occur, as in Terebratulina, two accessory vescicles occur, one to each segmental organ. Where two pair occur as in Rhynchonella, four accessory vescicles are found likewise; one accompanying each segmental organ. In Lingula, and Discina, though the segmental organs are large and conspicuous, and their study rendered comparatively easy, yet in no case has the accessory vescicle been met with. So far as we know then, the accessory vescicle occurs in Rhynchonellidæ and Terebratulidæ, or in those groups with the dorsal and ventral plates interlocking, which have no anus, and in which the ovaries are contained in the vascular sinuses of the pallial membrane. The accessory vescicles do not occur in Lingulidæ or Discinidæ, or in those groups having the dorsal and ventral plates free, possessing an anal outlet, and which have the ovaries entirely free in the perivisceral cavity. That they have nothing to do with the circulation is evident from the fact that a portion of the pallial membrane separated from the animal, shows the circulation going on as usual. The vascular bands are also strongly ciliated, and in Terebratulina, as in Lingula, the perivisceral circulation is probably induced by ciliary action.

That the accessory vescicles, then, belong to the reproductive system, and not to the circulatory system, there can be no doubt, but just what their function may be, has yet to be discovered.

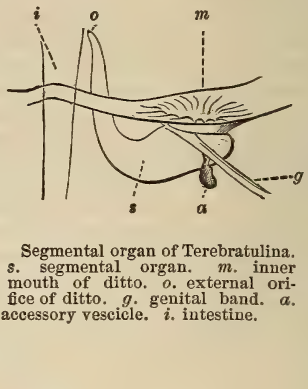
I copy from that inexhaustible work of Claparède, the Annelids of the Gulf of Naples, a figure of the segmental organ of *Alciope Cantrainii*, and accompany it with a figure of the segmental organ of *Terebratulina septentrionalis* with its accessory vescicle attached in the same position. There is at least something suggestive in the relations of the two figures, though by this suggestion I would not throw doubt on Claparède's determinations. With the impression that the sexes were united in Terebratulina, I was inclined to regard

Fig. 29.



Segmental organ of *Alciope Cantrainii*. *m.* inner mouth of segmental organ. *o.* external orifice of ditto. *t.* testes.

Fig. 30.



Segmental organ of Terebratulina. *s.* segmental organ. *m.* inner mouth of ditto. *o.* external orifice of ditto. *g.* genital band. *a.* accessory vescicle. *i.* intestine.

the external parietal glands discovered by me as representing the testes. With the identification of the spermaries as above described, and the consequent separation of the sexes, we must seek for another interpretation of the glands. As they are extremely mucous, and intimately surround the external tubular orifices of the segmental organs, the egg cannot possibly escape without first coming in contact with whatever substance these glands may secrete, and it is highly probable that they are instrumental in investing the egg with some external coat. The glands are very white in color, and are filled with minute granules which I at first mistook for spermatozoa. It is interesting to observe that they are present in both sexes, but what service they do in the male it is impossible to conjecture.

In connection with the external parietal glands, it is interesting to recall the capsulo-genous glands as described by Dr. Lankester[1] in the common earth worm. He says "Besides the regular glands developed on the parietes of the body, the earthworm exhibits numerous glands destined to form the egg capsule, in which both zoösperms from the spermatic reservoirs, and ova are deposited, These glands were first detected by D'Udekem. . . . The white color, and thick fleshy look which is sometimes observed about the exterior of these segments, is due to the developement of the capsulo-genous glands. Whether the capsulo-genous glands have everything or anything to do with the formation of the egg capsule is very difficult to determine; but the supposition of M. D'Udekem is so plausible, and comes from so good an authority, that it cannot but be received until absolutely disproved."

Embryology.

It seems a little remarkable that of the class of Brachiopods, upon which so many admirable memoirs have been written, so little should still be known about the embryology, or early stages of any of its forms. Yet all that has been done, thus far, to shed any light on this portion of their history, points to the unquestionable vermian characters of the class.

The earliest paper on which we find any rêference to the embryonic form of the Brachiopod is by Oscar Schmidt, contained in the "Zeitschrift für ges. Naturwissenschaften," 1854 p. 325. He gives the following figure of the larval form of a species of Terebratula. (Fig. 31.)

Fig. 31.

Embryo of a Brachiopod.

In this figure the body shows a deep constriction in the centre, the lower end is abrupted truncate, as if that were to be the point of attachment. If that is the case it would correspond to certain Rotifers which also attach themselves by the posterior segment of the body.

(See Fig. 5 of Rotifer, on page 11, *Melicerta ringens* by Huxley, showing its first attachment by the posterior end, the animal at the same time surrounding itself with a sand case.)

Lacaze-Duthiers was the first naturalist to make known several stages of the embryology of a Brachiopod. In a memoir on Thecidium[2] this author gives several figures of the embryos of this Brachiopod. The body is composed of four deeply constricted seg-

[1] Journal Microscopical Science. Vol. V, 1865, p. 14.

[2] Annales des Sciences Naturelles, 4th Série, Vol. xv.

ments, the anterior one small and running back on the second segment. On one embryo he found two red eye-spots on the first segment, while on another embryo he found four red eye-spots. In the same number of rings, the peculiar form of the cephalic ring, and if Oscar Schmidt is right, the attachment of the embryo by the caudal segment, we observe the closest similarity between the embryo of this Brachiopod and that of *Melicerta ringens*, figured by Huxley.[1]

It will be seen by the accompanying figures of the embryo of Thecidium, copied from Lacaze-Duthiers, and the embryo of *Melicerta ringens*, that in the Rotifer embryo the body is drawn out, while in Thecidium it is condensed.

For several years I have endeavoured to secure some data regarding the embryology of Terebratulina, and in the early summer of 1872, I had the good fortune to find Terebratulina spawning.[2] The eggs were round and ciliated, and had the peculiar pencil of long cilia so peculiar to the embryos of many worms. The body was gradually cut up into three deeply constricted segments, and these at a later stage had the characteristic vermian contraction, the rings shortening upon themselves and then gradually expanding. Though I made several hundred drawings from fifty different embryos, yet

[1] Jour. Mic. Soc., Vol. I.

[2] Since this paper was in type, I have again visited Eastport, Maine, and have had an opportunity of studying the embryology of Terebratulina under more favorable circumstances. I have only room here to state that after swimming actively for a while the segmented embryo becomes attached by the caudal segment which is to be the peduncle, the middle or thoracic segment increases in diameter, one portion becoming more prominent; the first or cephalic segment continues to move and bend on the thoracic segment. Meanwhile the thoracic segment grows rapidly at opposite points, and finally engulfs the first segment by lobes above and below, these lobes being the dorsal and ventral valves. The mouth becomes apparent, and at the same time two groups of setæ make their appearance on the sides and front of the lobes, these are delicately barbed and *deciduous*.

The relations pointed out on pages 29 and 30 regarding the cephalic collar of the Annelids and the pallial membranes of the Brachiopods receives confirmation in this unlooked for simple developement of Terebratulina, and so far as these forms are concerned, we can for the first time state positively that the mouth and arms represent the first segment, the pallial membranes with the shells, the second or thoracic segment, while the peduncle represents the caudal segment.

The first three tubules in the shell are bordered by long delicate hairs, indicating that these are sense organs as in the tubules of certain crustacea, surrounded also by hairs as described by De Morgan, see p. 16. Regarding barbed setæ, see page 21.

These results were communicated to the Boston Soc. Nat. Hist., June 18th, 1873, and will soon be published in their Memoirs.

Fig. 32.

Fig. 33.

Fig. 34.

Fig. 35.

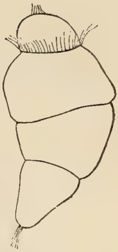
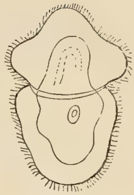


Fig. 36.



Embryos of Worms.

Fig. 32. Serpula. Fig. 33. Spio. Fig. 34. Melicerta (Rotifer). Fig. 35. Pileolaria. Fig. 36. Phoronis. (Fig. 32 original. Figs. 33 and 35 from Claparède. Fig. 34 from Huxley. Fig. 36 from Dyster.)

Fig. 37.

Fig. 38.

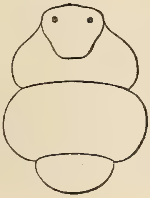


Fig. 39.

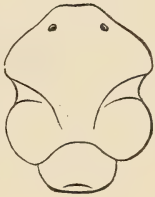


Fig. 40.

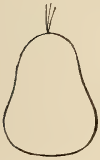


Fig. 41.

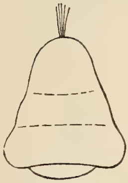
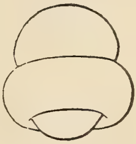


Fig. 42.



Embryos of Brachiopods.

Figs. 37, 38, 39. Thecidium (from Lacaze Duthiers).

Figs. 40, 41, 42. Terebratulina (original).

owing to the difficulty at that time of keeping the water at the frigid temperature they were accustomed to, the embryos all died. I saw enough, however, to lead me to believe that they eventually become attached by their caudal segment.

Thus the three series of observations by Schmidt, Lacaze-Duthiers and myself, on entirely different forms of Brachiopods, show the most perfect vermian development.

In regard to the early stages of Brachiopoda, Fritz Müller[1] has published some interesting observations on the early stages of Discina, which he studied at Santa Catharina, Brazil. The larva is described as having a perfectly orbicular dorsal and ventral plate, the pallial membrane gaping all round, and the dorsal plate freely moving, or sliding back and forth. Five pair of very stiff setæ project from the periphery, two pair forward and three pair backward, one pair much larger and stronger than the rest, and these were coarsely barbed. The posterior half is occupied by the alimentary canal, two auditory vescicles, and two eyes. The anterior half is occupied by four pair of cylindrical tentacles or cirri, strongly ciliated, between which a rounded knob is situated. (Possibly related to the rounded knob in Spirorbis and allied forms.)

The arms or cirri are supported upon a *long retractile neck* or œsophagus, at the forward extremity of which the mouth is situated. The larva not only swims by means of the cilia lining the cirri, but crawls by means of the ventral scale, and pushing itself along by the larger pair of bristles which have a vigorous motion, often crossing behind.

These barbed bristles of Discina, Müller finds, are deciduous, and it is interesting to remember in these comparisons that the larval worm has also coarsely barbed bristles which are likewise deciduous. What could be more annelidan than the description of this larva. It is true there are no larval worms possessing the dorsal and ventral plates, though in that degraded worm Sternaspis there is a pair of ventral plates or scuta, from the edges of which setæ project, and by means of which the worm shoves itself along. (The lines of growth are prominent on these scuta, as in Discina.)

Since then I have received, through the kindness of Dr. Hagen, a letter from Herr Müller, accompanied with a sketch of another larval form of Discina, in which he describes features similar to those

[1] Reichert und Du Bois-Reymond's Archiv., 1860, p. 72. Wiegmann's Archiv. 1861, p. 53.

above mentioned, and states that the species has been defined by Prof. Dunker as *D. radiata.*

The Brachiopods possess other affinities to Rotifera, beside the resemblances between the embryos pointed out above. We give here a definition of the Rotifera condensed from Rolleston's Forms of Animal Life, p. cxxxviii, Class Rotifera, inserting in italics those portions in which some agreement may be claimed.

"Vermes with a *retractile ciliated disk at the anterior extremity of their bodies.* (To be compared to retractile cirri in young Discina.) Usually plainly annulated externally, *never divided internally by transverse septa.* (Except Lingula.) In most Rotifera *entire body divisible into a 'body' proper, and a tail, anterior to which the digestive and reproductive viscera with their ducts are situated.* The body can often be seen when chitinization has not advanced so far as to form a carapace, not only to be distinctly annulated, *but to possess circular and longitudinal muscles in its walls. Cilia are never found on the external surface of the body, except upon the cephalic organ.*

The chitinous surface of the integument may develope setiform outgrowths of various shapes, or the animals may secrete or agglutinate a tube for the lodgement of their bodies. The tail is usually annulated when its integument is soft, (quite marked in *Lingula pyramidata*) or segmented when it is indurated.

(The paired claw-like processes is unlike anything found in Brachiopods. The anus is on the back and not on the side as in Brachiopods. The differences between the sexes is unlike the Brachiopods, though the cœcal stomach as in Ascomorpha, Notommata and Asplanchnia finds a parallel in the cœcal stomach of many Brachiopods. The jaws and gizzard are again different from what has yet been observed in Brachiopods.) *Two or more cœcal appendages are affixed to the commencement of the stomach, which, as also the intestine, is clothed with cilia.* (See Morse, "Early Stages of Terebratulina," and since observed in young Rhynchonella and Discina). The Rotifera have no heart. *The periviseral cavity contains a corpusculated fluid. No specialized breathing organs.* (save the curious ampullæ on the pallial membrane of Lingula.) The water vascular system has five ciliated infundibuliform orifices, (to be compared with the segmental organs in Worms and Brachiopods). The reproduction in Rotifera by means of winter eggs possibly finds a parallel in the statoblasts of Polyzoa."

Features of dissolution.

Believing the Brachiopods to be true worms, every feature of relation, no matter how trivial, becomes important in these comparisons. The mere fact of Lingula pyramidata agglutinating a sand tube is of small moment in itself, since such a feature might of course be a matter of secondary acquisition. The unquestionable fact however, that many groups of worms are notable tube builders, and this peculiarity is almost entirely confined to the worms, the feature of tube building in Lingula becomes a matter of importance in these comparisons. Therefore the points to follow, trivial in themselves, cannot, with justice, be overlooked in these comparisons.

Dr. Williams, in his elaborate work on the British Annelida,[1] in describing the dissolution of Arenicola and Nais, says in regard to the former, that the division occurs somewhere within the middle third of the body, though sometimes the head is detached, and sometimes the tail. This process, both in the Nais and Arenicola, occurs in July or August. The cephalic and caudal portions continue for some time to writhe in the sand. Towards September the fragments disappear by decomposition, the parts turning black. He further says that the sand of the sea-shore, and the water of the fresh water pools are thickly strewn with the mutilated bodies of these worms. "It is a catastrophe which every fall involves the whole community." He believes therefore that these Annelids are annuals. "They are born during the latter months of one summer, and survive the winter, attain the maturity of growth, reproduce the species, and die by the spontaneous subdivision of their body into fragments."

In studying *Lingula pyramidata*, I had come to the conclusion that with this Brachiopod at least, their duration of life did not probably exceed one year. Of over one hundred specimens of Lingula collected by myself in June, and as many more collected by Dr. Elliott Coues in July, I had remarked as a noteworthy fact, that specimens varied but little in size. I did not meet with a single young specimen, or, rather, a single small specimen. Furthermore the shells in all cases presented the same features of newness. There were no erosive or parasitic growths upon them (though late in the fall there is no reason why hydroid growth might not occur on that portion of the shell exposed). This fact, coupled with the absence of even a small specimen, for which I particularly searched, led me long ago to believe that they were all of the same age, and that their life did not exceed one year.

I brought several specimens home with me to Salem, Mass., and kept them alive during the summer months; imitating as far as possible the conditions in which I found them, keeping them in the same sand in which they were collected. They all died within a few days, during the last of September, and in their death they repeated almost precisely the features described by Dr. Williams in Arenicola and Nais. Spontaneous division occurred between the thorax and peduncle. The thorax was thrown out on the surface of

[1] Report of the Brit. Asso. for Ad. of Sci. 1851, p. 248.

the sand, while the peduncle lay embedded in the sand. The thorax lived for a few days in a weak condition, the setæ moving feebly, and the dorsal plate slightly oscillating. This portion finally turned black, and as one after the other perished in this way, I removed them from the vessel, in order that their decomposition might not vitiate the water, and thus imperil the lives of the survivors.

Several days after they had all been removed in this way, curiosity led me to turn up the sand, to find the condition of the peduncles, and judge of my astonishment at finding the perivisceral fluid contained in the peduncular cavity still rapidly circulating in several, though the region at which the separation had occurred was blackened by decomposition. In a few days more this circulation ceased, and decomposition envolved all parts. Here we have the most complete relation between the dissolution of this Brachiopod and that of the Annelid described by Dr. Williams.

Opinions of Authors concerning the Relations of the Brachiopoda.

Naturalists are sufficiently well acquainted with the relations repeatedly pointed out, as existing between the Brachiopoda and Polyzoa,[1] and there is no need of again repeating them here.

It is also a matter of history that the Polyzoa were placed with the Mollusca solely on the relations which were supposed to exist between them and the Tunicates, and afterwards the relations recognized between the Polyzoa and the Brachiopoda.

Again, there can be no question that at the outset the association of the Tunicata with the Mollusca arose from the relations supposed to exist between the external sac or tunic, with the two apertures of the one, and the shells and syphons of the other. Aristotle[2] dwells on this resemblance where he says, in speaking of them as Mollusca, "They are the only kind whose whole body is enclosed in the shell, and that shell of a substance between true shell and leather. They are attached to the rocks by their shell. They have two separate

[1] In the affinities of the Polyzoa with the Vermes, the curious genus Phoronis offers an important link. Claparède thinks the affinities of Phoronis are with the Gephyreans on the one hand, and the Polyzoa on the other. Kowalevesky has discovered that the larva of Phoronis is an Actinotrocha, and possibly the young Sipunculoids that Schneider saw resulting from a transformation of Actinotrocha, are early stages of Phoronis. Certainly no one studying the characters of Phoronis and Crepina can fail to see many very intimate relations between these forms and the hippocrepian Polyzoa.

[2] Fourth book of "History of Animals."

openings, which are very small and difficult to notice; the one to take in, the other to eject the water," etc.

The branchial sac was also believed to be the homologue of the gills of the Lamellibranchiate Mollusk, though Hancock[1] has shown that the branchial sac of the Ascidian is not the anatomical equivalent of the gills of the Lamellibranch, but is a portion of the alimentary canal.

Milne Edwards, in his splendid memoir on the composite Ascidians,[2] in speaking of their molluscan affinities, said that these relations were far less intimate than was usually believed, and that they departed from the Mollusca in their mode of circulation, in the metamorphosis which their fry passed through, and more particularly in the singular feature that most of them possessed in multiplying by gemmation.

Now since the Polyzoa are placed with the Vermes by Gegenbaur and others, and indeed were long ago placed there by Leuckart, while the Tunicates have been assigned to the Vermes by many of the most eminent German investigators, while others still would place them at the foot of the Vertebrate series, it is unnecessary for me to consider the affinities of the Brachiopods through their relations with these groups.

Kowalevsky, Kupffer, Schultze and others, assign the Tunicates a position at the base of the Vertebrate series, through the unquestionable affinities of certain of their forms to Amphioxus, as well as their singular embryological relations with the Vertebrates.[3] In this connection it is instructive to note that Gegenbaur sees a relation between the branchial sac of Balanoglossus, and the branchial sac of an Ascidian.

In the year 1848, the far seeing Leuckart was inclined to believe that the Tunicates formed an *intermediate class between the Echinodermata and the Vermes*, while others traced a resemblance between certain Nemertean larva and the early stages of the Echinoderms, causing Huxley to unite the Echinodermata with the Articulates. And lastly, a Tornaria described by Müller, Krohn and Alex. Agassiz, was taken to be an unquestionable Echinoderm larva. Now thanks to the brilliant investigations of Mr. Agassiz,[4] this Tornaria turns out to be the young of that odd worm Balanoglossus; though Mr. Agassiz finds a wide gap between the Tornaria of Balanoglossus and the Echinoderm young, yet he admits the striking resemblance between the two. He says, "This remarkable type recalls the Tunicates, from the nature of its gills and mode of

[1] Annals Nat. Hist. 4th Series, Vol. v., p. 196.

[2] Memoires de l'Acad. des Sciences. T. xviii, 1842.

[3] Early Stages of an Ascidian. Proc. Bos. Soc. Nat. Hist., Vol. xiv., p. 351.

[4] The History of Balænoglossus and Tornaria. Mem. Amer. Acad., Vol. ix., p. 434.

formation. It has, like Echinoderms, a ring canal; its larva is eminently Echinodermoid, allied to Star-fish larvæ, which in their turn are more closely allied to the larvæ of Holothurians and Crinoids, than to those of Echinoids and Ophiurians."

Aside from the roundabout way in which the Brachiopods have been entangled with the Mollusca (their preposterous comparisons with Anomia will be considered presently), it is interesting to observe how often certain features of the Brachiopods have been compared to the lower Articulata by those who have made special researches upon them. Thus Dr. Gratiolet,[1] who studied *Lingula anatina*, says the organization of the arms resembles the branchia of certain Crustacea. He also expresses the opinion that the Brachiopoda are allied to the Crustacea in respect to their vascular system, and not to the Mollusca; least of all to the Tunicata. Again, after recounting the peculiar character of Lingula in the annulated hairs, developed from veritable glands, the structure and arrangement of their muscles, their arms and other features, Gratiolet says, the Brachiopods are very far removed from the Lamellibranchs, and have no kind of relation to the Tunicates.

Lacaze-Duthiers,[2] in speaking of the oviducts of the Brachiopods, recalls the fact that in Bonellia (of which he made an elaborate study) there are similar openings, which are the genital openings, through which the visceral fluid can escape. He also queries whether there are not two kinds of circulation in the Brachiopods, as in Bonellia. On the development of the young, studied by himself in Thecidium, he observes points entirely unlike anything existing in the Lamellibranchiates.

Burmeister compared the gills of Lingula to the gills of Lepadæ.

Gegenbaur, in his "Outlines of Comparative Anatomy," points to certain worm-like features in the Brachiopoda, and repeatedly calls attention to their worm-like genitals.

Dr. Williams,[3] in his elaborate work on the British Annelids, calls attention to the outlying affinities of the Vermes, recalling Dentalium, Chiton, Amphioxus, but no where alluding to any approach of the Annelids to the Brachiopods. None of the above authors, however, had ever suggested the removal of the Brachiopoda from the Mollusca, nor had they, or Owen, Vogt, Huxley or Hancock, ever made the slight-

[1] Jour. de Conch. 2d Series. Tome II, pp. 237, 252, 257.

[2] Annales des Science Naturelles. 4th Series. Tome XV.

[3] Report of the Brit. Asso. for A. of S. 1851. p. 164.

est allusion to Prof. Steenstrup's views on the subject, and until quite recently I had thought that to myself belonged the entire credit of the views advanced in this paper, until I was made acquainted with the fact that twenty-five years ago Steenstrup had not only considered the Brachiopods as worms, but had placed them near the tubicolous Annelids. Before presenting the views of this distinguished naturalist, it is proper to go back to the relations that many naturalists, as Agassiz, Deshayes, Owen and others, believed to exist between Terebratula and Anomia.

In the light of our present knowledge of the subject, it seems as incomprehensible that such views were held, as that the Cirrepeds were ever included with the Mollusca, and it is still more a matter of astonishment that to this day there are a few naturalists who have a vague idea that Anomia forms a sort of connecting link between the Brachiopods and the Lamellibranchiates.[1]

In the year 1853, Forbes[2] wrote as follows: "Linnæus included in his genus Anomia the species of Terebratula. Mislead by a false analogy, he considered these very different Mollusks to be organized on the same plan, and the perforation of one of the valves in each, to be of similar origin.

"Lamarck, in like manner, fancied that in Anomia he saw a passage into Terebratula and the Brachiopods; and some anatomists even believed that they had discovered transitional characters. A close examination shows that there is no relationship of affinity between them, but only a resemblance through formal analogy.

"The parts which seem, at first glance, in each to be identical, prove not to be homologous upon investigation. Anomia has really very close relations with Pecten, and is connected to the latter by the curious genus Hemipecten of Reeve. The perforations in one of the valves of Anomia is chiefly a greater extension of the auricular sinus in Pecten; and when the very young fry of this genus shall have been carefully observed, we believe they will be found spinning a byssus, which passing through this in the first instance, before a portion of it becomes attached, eventually becomes detached with a part of the adductor muscle, and forms the opercular process."

Lacaze-Duthiers,[3] in an elaborate memoir on Anomia, refers to

[1] At one time Vogt and Agassiz believed the dorsal and ventral plates of the Brachiopoda to be right and left, like the bivalved shell of the Lamellibranch!

[2] British Mollusca. Vol. II., p. 322.

[3] Annales des Sciences Naturelles, 1854. 2d Series, v., p. 35.

these statements of Forbes and Hanley, and expresses his belief in their correctness. In speaking of their peculiar asymmetry induced by this byssal modification, he aptly calls them the Pleuronectes among Mollusks.

In the year 1847, Steenstrup presented similar views before the Royal Danish Academy.[1] And in the same year, during the meeting of the Scandinavian Naturalists in Copenhagen, he made a similar communication, which was published in their Report for that year. On both occasions he militated against the suggestions of Owen, Agassiz, Deshayes, and other naturalists, who considered Anomia as a connecting link between the Lamellibranchiates and the Brachiopods. He showed that Anomia was not so abnormal as was generally supposed, and that the foramen in Anomia had no correspondence to the opening of the valve in Terebratula, but, on the contrary, was homologous to the notch in Pedum, Pecten, and certain other bivalve Mollusks, and that the plug in Anomia was simply a calcified byssus, and that it passed through this notch and held the shell fixed to some object. He showed also that the muscle attached to this plug was a foot muscle, corresponding to the muscle which goes to the sheath of the byssus in certain other Lamellibranchs; and concluding with the statement that the Terebratula and all the Brachiopods might necessarily be considered as not only widely removed from the Lamellibranchiates, *but as having no sort of relation to the Mollusca at all.*

Last year, in a brief examination of the early stages of Anomia, I had the pleasure of amply confirming the predictions of Forbes and Steenstrup, namely, that the plug in Anomia represented simply a modified byssus.

The following extract is taken from my short paper on the Relations of Anomia.[2] "The smallest specimens examined are quite orbicular, the upper or left valve is very tumid near the nucleus, the lower, or right valve is flat, and somewhat smaller than the upper valve. The foramen, or sinus, is not closed, but opens on the anterior border of the shell. The chief point of interest, however, is seen in the nucleus, or that portion of the shell first formed, when the animal was free and roving. This early condition of the shell is distinctly marked at the beak in both valves. It is yellowish in color, and marked with numerous, very regular concentric lines of growth, while the remaining portion of the shell is colorless, or white, with

[1] See the Proceedings for that year, pp. 74, 75.

[2] Proc. Boston Soc. Nat. Hist. Vol. XIV., p. 152.

irregular lines of increment. The nucleus is oblong oval. The umbones are nearly central, though nearer the anterior margin, and the shell is more globose behind. Both valves of the nucleus appear equally convex, and no sign of a sinus or perforation is visible in either valve. On the free edge of the right valve, directly under the umbo, a distinct notch is seen, the lines of growth indicating it, and showing that the edge of the shell is not absorbed to form this notch. It will be noticed that this marginal notch appears in that valve which is below, and which afterwards presents the opening for the passage of the byssal plug.

"The condition of the shell at this time clearly indicates that the animal is not only already attached, but has fallen to one side, and while in this position has added a few more lines of increment to its larval shell, as no sign of this notch is seen on the left or free valve. Soon, however, the peculiar and rapid secretion of a different shell growth takes place; the lines of increment are no longer regular, nor so con-

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

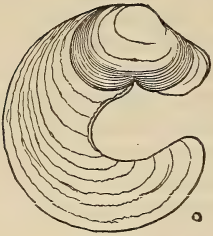


Fig. 5.

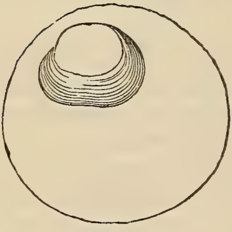


Fig. 6.

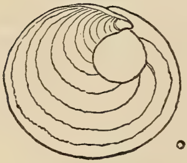


Fig. 1. Right or lower valve of Anomia, showing notch in ventral pallial margin, caused by byssus. Diameter one sixty-fourth inch.

Fig. 2. Left, or upper valve of Fig. 1.

Fig. 3. Foramen commencing to form. The black portion shows proportions of left valve.

Fig. 4. A more advanced stage of right valve with foramen almost completed.

Fig. 5. Left, or upper valve of Fig. 4. Diam. one thirty-second inch.

Fig. 6. Showing still later stage, with foramen completed, and nucleus still visible.

spicuous, and the shelly matter is white. The left valve adds concentric layers around its entire margin, not excepting the hinge margin. The lower valve appears to grow from its posterior and lower half, the successive accretions being produced around the byssus. This growth for a while seems to take place exclusively from the posterior half of the shell, limited in front by the byssus, and even after this growth has increased to twice the diameter of the embryo shell, only a slight increase is noticed on its anterior margin, this latter addition being slightly reflected. The left or upper valve grows more rapidly, so that its margin overlaps the right valve at all points. As the animal increases in size, the foramen increases also, and its earlier boundaries are consequently absorbed.

"It will be seen by reference to the figures, that the growth of the perforated valve is first posterior and downward, from the posterior half of the shell; it then grows forward, avoiding the byssal plug, and by successive additions surrounds the byssal plug, and ultimately reaches the umbones of the larval shell, and even beyond and behind this region.

"From these facts it is obvious that at an early stage the animal is free, and for a time locomotive; that it has an elongate, oval, bivalve shell, with close and regular lines of accretion, and that during the latter stage of this growth it becomes attached by a byssus passing from between the valves of the shell, as in Mytilus; that before the growth of the larval shell is completed it drops over to one side, since one valve only shows the notch upon its margin, and that so soon as this growth ceases, a new growth takes place, looser in texture, and white in color, as above described."

The figures are here given which accompanied the paper from which this extract is taken. At another time I hope to meet with living examples of Anomia in this early stage. The specimens from which the above studies were made, I found upon dried sea weed, but the shells told the story plainly enough, as will be seen by the figures.

Let us again revert to Steenstrup's views regarding the affinities of the Brachiopods. In the Proceedings of the Royal Danish Academy for the year 1848, pp. 88, 89, Prof. Steenstrup again refers to the supposed deviations of Anomia from the Lamellibranch, and showed that they were not only closely related to the other Monomyarians, but had no sort of approximation to Terebratula, or the other Brachiopods. In that meeting he indicated what he considered the true place to which the Brachiopods should be assigned.

Having shown that they were isolated from the Lamellibranchs, he there said if the Brachiopods were rightly looked upon, they would, according to his opinion, not find their place in the Molluscan series at all, but in the series of annulated animals, and just in the class of Annelids. In this class, however, he might not range them as a particular order, but as a link, or row of particular families, which one after the other came near to the now living Serpulæ, going slowly, without any abruptness, over to them. Steenstrup believed that if the relationship existing between the shells of Serpulæ and the tests of Thecidia, Crania, etc., was a natural one, then the type of the animal of Serpula might be recognized in the Brachiopoda.

At that time, Steenstrup believed that the Hippurites were Annelids too. This view he informs me he has since abandoned, though he regards them as a very alienated type from the Lamellibranchs. It seems strange, that in all the elaborate memoirs on the Brachiopods, no allusion has been made to Steenstrup's views on the subject. These allusions to the affinities of the Brachiopods in a language of which I was entirely ignorant, never came to my knowledge until nearly two years after my first views of the Annelidan affinities of the Brachiopods were published in "Silliman's Journal." These views he presents every year to the students at the University at Copenhagen, for which he tells me he has been highly blamed, but to which he still adheres.

In a letter to me he writes: — "You remember that Seneca says, we ought always to go 'Non pecorum modo, quo itur, sed quo eundum est.' As to the last half of this sentence I must be quite silent, but as to the first half I shall add that I have been highly blamed, that I did not follow the common 'quo itur' path."

Conclusion and Recapitulation.

The Mollusca have always proved a stubborn group to define, and simply because certain forms were placed with them, by general consent, which did not belong there. Milne Edwards first broke the spell by rendering the affinities of the lower classes less antagonistic by separating the Mollusca into two great divisions, the Mollusca and Molluscoidea. This act was promptly adopted by Prof. Dana as before alluded to in the first part of this paper.

However vague and ill-defined the Vermes may be, there seems to be no wider gap between their extreme forms than between Amphioxus and Man, or the Lerneans and Hymenoptera, or between Aspergillum and Loligo. Were it not that Protula and Autolytus increased by transverse division, one might look at low worms with these anomalous features of reproduction, as remotely separated from the Chætopodous groups.

In considering the assemblage of remarkable characters in the Brachiopods, we must recognize in them a truly ancient type, and consequently a synthetic, or comprehensive type. Thus while we do not find them in all their characters resembling any one group of worms, I have endeavored to show that all their features, to a greater or less degree, are shared by one or the other of the various groups of the Vermes, with one or two features shared by the Arthropods.

It is important to remaık in this connection that most of the ancient groups differ from present groups with which they are associated. Thus the Trilobites are widely unlike modern Crustaceans, Milne Edwards and Van Beneden suggesting their affinities with the Arachnids. Tetrabranchiate Cephalopods are widely separated from the Dibranchiate Cephalopods. Crinoids are widely unlike modern Echinoderms. In other words, among the Mollusks, Echinoderms and Crustaceans are ancient types widely different from the modern types with which they are correlated.

So in worms we should expect to see ancient types, while presenting a high organization, yet differing from present groups to which they are unquestionably related. And from the high complication of structure of the Brachiopods, Tetrabranchiates, and other ancient types, it would seem that in their culmination in ancient times they had the same relation to animals living then as the higher groups of present times bear to their associates. As to the more ancient forms of Brachiopods, it is probable with them, as with other groups, that their lower members were soft bodied, and the argument that has been urged, as militating against Darwin, that animals of high complication of structure occur in the older groups, becomes valueless, when we consider that the lower forms of their respective groups are more often soft bodied, and that complicated forms of earlier times, were also culminating forms of pre-existing groups. In the light thrown upon the history of man by the wonderful discoveries in Archæology, where we meet with traces of an ancient civilization, with complicated language and manners, we can surely believe in savage hordes pre-existing, from which this ancient civilization has been evolved.

The Tunicates, Amphioxus, and many important groups, which have taught us so much regarding the affinities of classes supposed to be widely separated, had no hard parts to preserve, and nothing by which we could make out their structure. Even the worms, with the exception of the Chætopods, have left us nothing, and the last named group are known to us only by their tracks, spines, and tubes left in the rocks. Even the hard leathery peduncle of the fixed Brachiopods has, in one or two instances only, been preserved.[1]

The earliest forms of Brachiopods thus far met with, are those with thin, diaphanous shells (as in the Lower Lingula Flags), and even before these forms existed we can legitimately conceive the primary existence of certain Brachiopods, with the peduncle endowed with high functional importance, and the anus terminating posteriorly, as in those Annelids, like Lysilla, where the caudal portion is apodous, scarcely annulated, and devoid of setæ. Later appeared Brachiopods with an anterior termination of the intestine, as in Phoronis and certain sipunculoid worms, and finally the peduncle became attached, and the anus obliterated.

In regarding the relations of the Brachiopoda, let us suppose that nothing was known of such a form as Lingula, and that the only forms of which we had any knowledge, were the short and wide forms, like Chonetes. It would certainly be considered a wild supposition to suggest the possible existence of a Brachiopod, in which the shell should be translucent and elastic, four times as long as wide. A peduncle partially annulated, nine times as long as the body, capable of sharp vermian contortions, having a rapid circulation within, incased in a sand tube, with the animal living free in the sand, and having a limited power of locomotion. Surely it would tax the powers of the imagination more to conceive this form than to simply endow a sedentary Annelid, like Protula, with the cephalic collar extending beyond the arms instead of surrounding the base, and secreting a dorsal and ventral plate, with the anus terminating at the side instead of behind.

The presence of prominent dorsal and ventral plates enclosing the arms from which the arms in some cases are protruded and the consequent developement of special muscles to move these plates, form the only marked differences between the Brachiopods and the Worms. In the Gephyreans as in the common Sipunculus, for example, where the anterior portion is highly contratile, ponderous retractor muscles are developed with widely expanded bases, as in the Polyzoa and in many Brachiopods.

[1] In the Museum of the Geological Survey of Canada is a specimen of *Eichwaldia subtrigonalis* Billings, from the Black River Limestone, Lower Sil., showing the silicified peduncle nearly as long as the shell, photographs of which Mr. Billings sent me.

In most cases the Brachiopods are fixed, and it is well known that with the radical change in the habits or conditions of any group, a corresponding change is noticed in their structure. Thus among the Crustaceans the feature of attachment is accompanied with many changes in the structure of the animal which mask their proper affinities, as in the Cirripeds, and notably in the Lerneans. Similarly in certain low worms, internal parisitism is generally accompanied with a loss of gills, setæ and cilia.[1]

On the same grounds, we should naturally expect to see great and striking differences in those worms which are attached. Consequently those Annelids which are fixed, while in most respects resembling the free Annelid, yet differ from them in being edentulous, the mouth or head, in some cases, supporting a crown of cirri, oftentimes springing from two cephalic lobes, which may be developed into a closely twisted spiral. There is also a marked degree of cephalization, the anterior rings forming a thorax, and supporting branchiæ, while the caudal region is often apodous, and without setæ, and in some cases not even annulated, and often separated from the thorax by a deep constriction.

So in the Brachiopods, while in every feature of their internal structure betraying their annelidan affinities, and while the errantian forms with their long vermiform and annulated peduncle, their locomotion by means of setæ, and their power of fabricating a sand tube, unite them clearly with the fixed and highly cephalized Chætopods; yet in those groups that are attached, a remarkable concentration is seen, and many features are presented which have heretofore obscured the affinities of the group.

To sum up the whole then. — Ancient Chætopod worms culminated in two parallel lines, on the one hand, in the Brachiopods, and on the other, in the fixed and highly cephalized Chætopods. The divergence of the Brachiopods, having been attained in more ancient times, a few degraded features are yet retained, whose relationships we find in the lower Vermes; while from their later divergence the fixed and cephalized Annelids are more closely allied to present free Chætopods.

And so we must regard the Brachiopods as *ancient cephalized Chœtopods*, while Serpula, Amphitrite, Sabella, Protula and others, may be regarded as *modern* (later) *cephalized Chœtopods.*

[1] Rolleston. Forms of Animal Life.

The following characters of the Vermes, mainly compiled from Rolleston's "Forms of Animal Life," are here given, with the characters of the Brachiopods in parallel columns.

Vermes.	*Brachiopoda.*
Bilaterally symmetrical, depressed or flattened, or circular, never flattened laterally.	Bilaterally symmetrical, depressed or flattened, or circular, never flattened laterally.
In many cases, above and below similar, or these regions distinguished with difficulty.	In many cases, above and below similar, or these regions distinguished with difficulty.
Most free, some attached.	Some free, most attached.
Locomotor muscles closely connected with integumentary system, not only on ventral, but on dorsal and lateral aspects of body wall.	Locomotor muscles closely connected with integumentary system not only on ventral, but on dorsal and lateral aspects of body wall.
In some (Annulata) annulated externally, and divided internally by dissepiments, in others not divided.	Never annulated externally, except the peduncle. A single dissepiment in Lingula.
Two layers of muscles in body walls.	Two layers of muscles in body walls.
Digestive canal straight, or seldom convoluted.	Digestive canal straight, or seldom convoluted.
Suspended in perivisceral cavity by partial dissepiments consisting of delicate tissue.	Suspended in perivisceral cavity by bands consisting of delicate tissue.
Peculiar depuratory apparatus, characteristic of the entire sub-kingdom. This apparatus in the Annulata taking the shape of bilaterally symmetrical tubes, opening externally, and communicating with the perivisceral cavity by ciliated infundibuliform orifices.	Peculiar depuratory apparatus, characteristic of the entire class. This apparatus taking the shape of bilaterally symmetrical tubes, opening externally, and communicating with the perivisceral cavity by ciliated infundibuliform orifices.
Nervous system consisting at most of simple œsophageal collar, to which a few accessory ganglia, or chain of ganglia, may be appended.	Nervous system consisting at most of a single œsophageal collar.
In some the bilateral elements of the nerve chain widely diverging.	The bilateral elements of the nervous system widely diverging.
Generative products in most, set free in perivisceral cavity.	Generative products set free in perivisceral cavity.

Possessing chitinous outgrowths, either as scales or plates, hairs or spines, the latter being secreted by setigerous follicles.	Possessing chitinous and calcareous outgrowths, as scales or plates, and chitinous outgrowths, as hairs or spines, the latter being secreted by setigerous follicles.
Cuticle perforated by minute pores.	Cuticle perforated by minute pores.
Perivisceral cavity lined in some cases by delicate ciliated membranes.	Perivisceral cavity lined by delicate ciliated membranes.
An extensive vascular system, containing a colored fluid representing the pseudo-hæmal system. The corpuscular nutritive true blood is contained usually in the perivisceral cavity alone, and in a few instances is found penetrating the pseudo-hæmal system.	An extensive vascular system, which may represent the pseudo-hæmal system. The corpuscular nutritive true blood is contained in the perivisceral cavity alone.
Embryos distinctly transversely segmented. In some cases attached by caudal portion at a later stage.	Embryos distinctly transversely segmented. In most cases attached by caudal portion at a later stage.
In some groups intestine having no anal outlet.	In some groups intestine having no anal outlet.
Sedentary Annelids.	
Usually having body divided into regions, the thoracic and caudal.	Having body divided into two regions, the thoracic and caudal.
Springing from the head, in many, two arms, often twisted into a closely wound spiral, and sustaining ciliated cirri.	Springing from the head two arms, often twisted into a closely wound spiral, and sustaining ciliated cirri.
Encircling the head, or base of arms, a flaring membrane split upon the sides, and notched, in the dorsal and ventral median line.	Encircling the head and arms, a flaring membrane split upon the sides, and often notched in the dorsal and ventral median line.
Mouth unarmed.	Mouth unarmed.
Mostly fabricators of sand tubes which invests the body.	One, *Lingula pyramidata*, fabricates a sand tube, which invests the body.
Gephryreans.	
Never definitely segmented. Anus opening anteriorly in many.	Never definitely segmented. Anus, when present, opening anteriorly.

I desire to express here my deep gratitude to John E. Gavit, Esq., who has constantly aided me in getting material together in our Eastport dredgings, who has freely placed at my disposal his extensive microscopical apparatus, and who has, by timely suggestions, aided me in many ways.

My thanks are also due to Dr. J. R. Nichols for the constant use of a Smith & Beck Binocular; to Dr. Elliott Coues, U. S. A., through whose attention and kindness I was enabled to study living Lingula on the coast of North Carolina; and to Prof. J. W. Dawson, for specimens of Rhynchonella, and for the loan of a stout dredge; and to Dr. P. P. Carpenter for accompanying me to the mouth of the St. Lawrence, and for aiding me in dredging for Rhynchonella. I am also under obligations to Prof. A. E. Verrill, Prof. A. Hyatt, Thomas Bland, Esq., and Edward Burgess, Esq., for many favors.

To the Editors of "Old and New" I am indebted for the use of the engraving which adorns the title page; and to Mr. C. A. Walker for the pains taken in engraving my hasty drawings.

EXPLANATION OF PLATE I.

Figures 1 to 7, inclusive. *Lingula pyramidata* Stimpson, natural size, from life.

Figure 1. Representing two specimens as they appear partially protruding from the sand, showing the sand disturbed by them about their burrows.

Figures 2, 3, 4, 5 and 6, different specimens in various positions after having been removed from the sand in which they were found; Figure 3 showing the animal while in the act of occillating the dorsal plate; Figure 4, with peduncle straightened.

Figure 7. Representing bottom of earthen bowl, in which eight specimens had been kept alive in sand; the sand covering the bottom of the bowl an inch and a half in depth, above which the Lingulas protruded, and below which they would partially disappear with a quick jerk when alarmed. On removing the sand they presented the appearance as here given. Sand tubes had been made by them, adhering to the bottom of the bowl, quite unlike those made by them when free in the sand. Into these tubes the Lingulas had partially receded, as represented by the figure; *a.* represents a deserted sand tube.

Figure 8. *Protula media* Stimpson, natural size, reduced from a drawing made by Mr. Emerton, kindly loaned by Prof. Verrill.

Figure 9. Showing thorax and left arm enlarged from same drawing; the pectinated character of cirri are not fully shown. This drawing is inaccurate in not showing the calyx or membrane encircling the base of cirri, and in not properly showing the pectinated character of the cirri. The correct and beautiful drawing of Mr. Emerton's will be published by Prof. Verrill in the Proceedings of the Connecticut Academy of Sciences.

Figure 10. *Serpula crater*, from Claparède.

The last three figures are given to show the distinct separation of thorax and caudal portion.