BRACHIOPODA

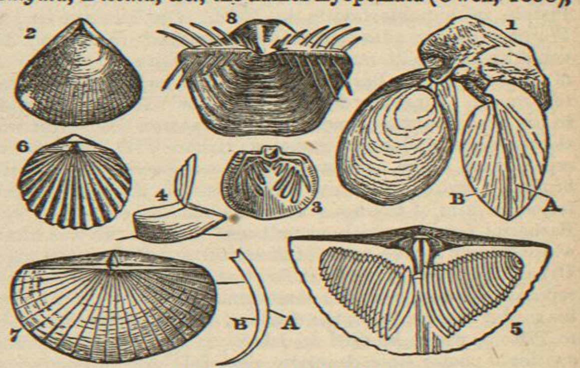
THE BRACHIOPODA constitute an important and well-defined class of Invertebrates, but the exact position the group should occupy in that division of the animal kingdom is still a matter upon which anatomists have not entirely agreed. For many years the species composing the class were referred to the genus *Anomia* of the Lamellibranchiata, but, as was judiciously observed by Edward Forbes, "a close examination shows that there is no relationship between them, but only a resemblance through formal analogy." Milne-Edwards separated the Mollusca into two great divisions, Mollusca and Molluscoida, and in the last he placed the Brachiopoda, Polyzoa, and Tunicata, an arrangement that has been followed by many naturalists. Although the greater number of zoologists have admitted the close connection existing between the Polyzoa and Brachiopoda, considerable doubt has been expressed with respect to the affinities and position of the latter in relation to the Tunicata; moreover, a strenuous effort has been made within the last few years by Steenstrup, Morse, Kowalevsky, A. Agassiz, and others, to demonstrate that the affinities of the Brachiopoda and Polyzoa are with the Worms, and that they should form classes of Annulosa, and be placed close to the Annelids.

According to Agassiz, the transition between such types as Pedicellina to Membranipora and other incrusting Polyzoa is readily explained from the embryology of *Thecidium*, and, in fact, all incrusting Polyzoa are only communities of Brachiopods, the valves of which are continuous and soldered together, the flat valve forming a united floor, while the convex valve does not cover the ventral one, but leaves an opening more or less ornamented for the extension of the lophore. Both Gratiolet and Hancock have expressed the opinion that the Tunicata are in no way related to the Brachiopoda, and that we cannot place these last and the Polyzoa along with the Tunicata in the same division. Gratiolet and some others have considered the Brachiopoda to be allied to the Crustacea, while even the asteridian affinities of the class have been hinted at by King.

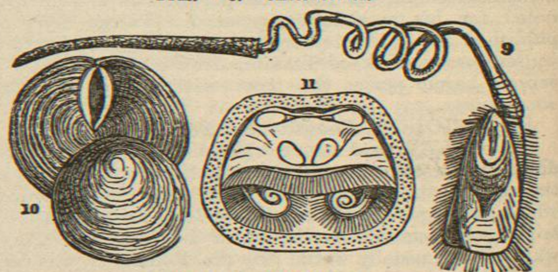
No doubt can be entertained, after perusing the admirable memoirs by Morse and Kowalevsky on the embryology of *Terebratula*, *Terebratulina*, *Argiope*, and *Thecidium*, that the genera composing the class and *Amphetrite* possess many important features in common, but almost any Invertebrate groups might be annelidilized by overrating certain points in their affinities. Mr Dall thinks that the general conclusion with reference to the affinities of the Brachiopoda will be something like this. There is much reason for supposing that all the Molluscs and Molluscoids came from the stock out of which the Worms have developed. Indeed, as Huxley has said, they are only isomerous Worms with many special modifications. It is natural, therefore, that the oldest and lowest forms should retain many of the characteristics of the oldest and most simple Worms, especially those which have been modified by a tubular habit. But, on the whole, the modifications are so important that we may continue to consider (if in the specializing tendency of present study we can retain any general divisions of Invertebrates) that the Molluscoids and Molluscs do form two groups somewhat aside from others, and somewhat more nearly related to each other than to the divisions external to them. Therefore, although it may turn out that the Brachiopoda constitute a class close to the Annelids, it cannot be denied that they possess many molluscan characters that cannot be overlooked, and are, under any circumstances, entitled by their importance and numerous distinctive features to constitute a well-defined and separate class.

The name BRACHIOPOD (βραχίων, an arm, πούς, ποδός, a foot) was proposed for the class by Cuvier in 1805, and by Dumeril in 1809, and has since been very extensively adopted. Blainville in 1824 proposed as a substitute for the Cuvierian name that of Palliobranchiata (*pallium*, a mantle; *branchiæ*, gills), on account of the respiratory system being combined with the mantle on which the vascular ramifications are distributed. Prof. King has always adopted the latter name, and perhaps rightly objects to Cuvier's on the ground that it is a misnomer, for the two variously curved and cirrated brachial or labial appendages, improperly designated as arms or feet, were subsequently found not to subserve the function of locomotive organs. **Name.**

Before describing the various parts of the animal and its shell, it may be as well to mention that it had been many times suggested by Owen, Bronn, Huxley, Gill, and others, that the class could be advantageously divided into two primary groups. Thus, for the first division, including *Lingula*, *Discina*, &c., the names Lyopomata (Owen, 1858), **Two divisions.**



Figs. –8.—Clistenterata.



Figs. 9–11.—Tretenterata.

Fig. 1.—*Waldheimia craneum.* A, ventral, B, dorsal valve
Fig. 2.—*Rhynchonella psittacea.*
Figs. 3 and 4.—*Thecidium.*
Fig. 5.—*Spirifer.* Dorsal valve, showing calcareous spiral coils.
Fig. 6.—*Orthis calligramma.*
Fig. 7.—*Leptæna transversalis.* A, ventral, B, dorsal valve.
Fig. 8.—*Productus horridus.*
Fig. 9.—*Lingula pyramidata (after Morse)*
Fig. 10.—*Discina lamellosa.*
Fig. 11.—*Crania anomala.* Interior of dorsal valve, showing muscular impressions and labial appendages.

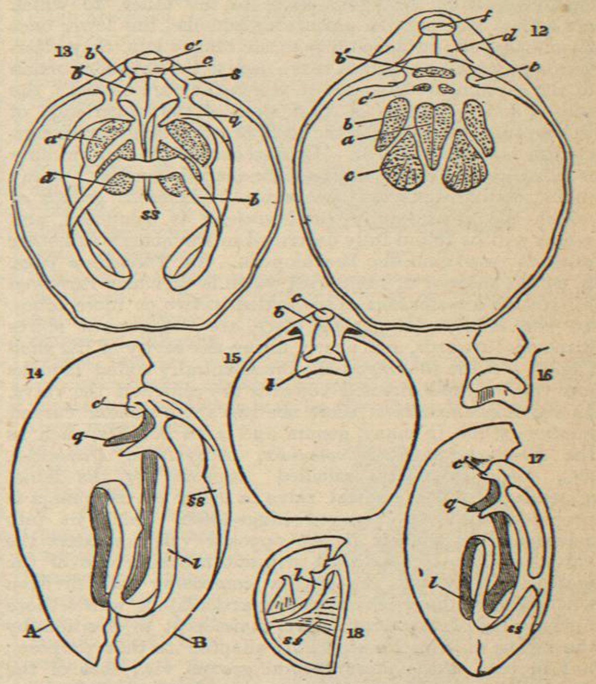
Pleuropygia (Bronn, 1862), Inarticulata (Huxley, 1869), Lyopomata (Gill, 1871), have been made use of; while for the second division, comprising *Terebratula*, *Rhynchonella*, &c., the names Athropomata (Owen, 1858), Apygia (Bronn, 1862), Articulata (Huxley, 1869), Arthro-

pomata (Gill, 1871) have been proposed. Prof. King, considering these names to be objectionable, and in some cases inadmissible on certain grounds, in 1873 substituted the name *Tretenterata* for the first group, the intestine being provided with an anal aperture, while the second group, to which he gives the name of *Clistenterata*, would embrace animals that are destitute of that organ; but it must also be remembered that the presence or absence of an anal aperture has been ascertained in only three or four recent genera, and that we are compelled, in a measure, to take for granted that what we find to be the case in *Lingula* and *Terebratula* is also so in the many extinct families and genera of which the animal cannot be examined.

With the character above enounced, we generally find structural modifications of the hinge and other differences in the animal, and especially so in what relates to the muscular system. In the opinion of Prof. King the absence of an anal vent in the Clistenterata makes them inferior to the aniferous Tretenterates.

The animal of the Brachiopod is in all cases protected by a shell composed of two distinct valves; these valves are always, except in cases of malformation, equal-sided, but not equivalved. The valves are, consequently, essentially symmetrical, which is not the case with the Lamellibranchiata or Conchifera,—so much so, that certain Brachiopod shells received the name *Lampades*, or lamp shells, by some early naturalists; but while such may bear a kind of resemblance to an antique Etruscan lamp, by far the larger number in no way resemble one. The shell is likewise most beautiful in its endless shapes and variations. In some species it is thin, semi-transparent, and glassy, in others massive. Generally the shell is from a quarter of an inch to about four inches in size, but in certain species it attains nearly a foot in breadth by something less in length, as is the case with *Productus giganteus.* The valves are also in some species very unequal in their respective thickness, as may be seen in *Productus Llangollensis*, *Davidsonia Verneuilii*, &c., and while the space allotted to the animal is very great in many species, as in *Terebratula sphæroidalis*, it is very small in others belonging to *Strophomena*, *Leptæna*, *Chonetes*, &c. The ventral valve is usually the thickest, and in some forms is six or seven times as great as the opposite one. The outer surface of many of the species presents likewise the most exquisite sculpture, heightened by brilliant shades, or spots of green, red, yellow, and bluish black. Traces of the original colour have also been preserved in some of the fossil forms; radiating bands of a reddish tint have been often seen in well-preserved examples of *Terebratula hastata*, *T. saculus*, *T. communis*, *T. biplicata*, and of several others. Some specimens of *T. carnea* are of a beautiful pale pink colour when first removed from their matrix, and E. Deslongchamps has described the tint of several Jurassic species.

The valves have been distinguished by various names, but those of *dorsal* and *ventral* are in most general use. The ventral valve is usually the largest, and in many genera, such as *Terebratula* and *Rhynchonella*, has a prominent beak, with a circular or otherwise shaped perforation or foramen at or near its extremity, partly completed by one or two plates, termed a deltidium. Through the foramen passes a bundle of muscular fibres, termed a peduncle, by which the animal is in many species attached to submarine objects during at least a portion of its existence. Other forms show no indication of ever having been attached, while some that had been moored by means of a peduncle during the early portion of their existence have become detached at a more advanced stage of life, the opening becoming gradually cicatrized, as is so often seen in *Strophomena rhomboidalis*, *Orthesina anomala*, &c. Lastly, some species have adhered to submarine objects by a larger or smaller portion of their ventral valve, as is the case with many forms of *Crania*, *Thecidium*, *Davidsonia*, &c. Some *Cranias* are always attached by the whole surface of their lower or ventral valve, which models itself and fills up all the projections or depressions existing either on the rock, shell, or coral to which it adhered. These irregularities are likewise, at times, reproduced on the upper or dorsal valve. Some species of *Strophalosia* and *Productus* seem also to have been moored during life to the sandy or muddy bottoms on which they lived, by the means of tubular spines of greater or lesser length. The interior of the shell varies very much according to families and genera. On the inner surface of both valves several well-defined muscular vascular and ovarian impressions are observable; they form either indentations of greater or lesser size and depth, or occur as variously shaped projections. In the *Trimerellidæ*, for example, some of the muscles are attached to a massive or vaulted



Figs. 12–18.

Fig. 12.—*Waldheimia flavescens.* Interior of ventral valve. *f*, foramen; *d*, deltidium; *t*, teeth; *a*, adductor impressions (= occlusors, *Hancock*); *c*, divaricator (= cardinal muscles, *King*, = muscles diducteurs principaux, *Gratiolet*); *c'*, accessory divaricators (muscles diducteurs accessoires, *Gratiolet*); *b*, ventral adjustor (= ventral peduncular muscles, or muscles du pedoncule paire superieure, *Gratiolet*); *b'*, peduncular muscle.
Fig. 13.—*Waldheimia flavescens.* Interior of dorsal valve. *c*, *c'*, cardinal process, *b'*, *b'*, hinge-plate; *s*, dental sockets; *l*, loop; *q*, crura; *a*, *a'*, adductor impressions; *c*, accessory divaricator; *b*, peduncle muscles; *ss*, septum.
Fig. 14.—*Waldheimia flavescens.* Longitudinal section of valves: A, ventral, B, dorsal valves; *l*, loop; *q*, crura; *ss*, septum; *c*, cardinal process.
Fig. 15.—*Terebratula vitrea.* Interior of dorsal valve. *l*, loop; *b*, hinge-plate; *c*, cardinal process.
Fig. 16.—Loop of *Terebratulina caput serpentis.*
Fig. 17.—Longitudinal section of *Terebratella dorsata.* (References as in fig. 14.)
Fig. 18.—Longitudinal section of *Magas pumilus.*

platform situated in the medio-longitudinal region of the posterior half or umbonal portion of both valves. In addition to these, there exists in the interior of the *dorsal* valve of some genera a variously modified, thin, calcified, ribbon-shaped lamina or skeleton for the support of the labial or brachial appendages; and so varied, yet constant in shape to certain species is this laminal apophysis, that it has served as one of the chief characters in the creation of both recent and extinct genera. The apophysis is more or less developed in some genera than in others. In certain forms, as in *Terebratula* and *Terebratulina*, it is short and simple, and attached to a small divided hinge-plate, the two riband-shaped laminæ being bent upwards in the middle (fig. 15) The cardinal process is prominent, and on each side of the hinge-plate are situated the dental sockets; the loop in *Terebratulina* becomes annular in the adult by the union of the oral processes or crura (fig. 16). In *Waldheimia* it is elongated and reflected; the hinge-plate large, with four depressions, under which originates a mesial septum, which extends more or less into the interior of the shell (figs. 13 and 14). In *Terebratella* the loop is attached to the hinge-plate and to the septum (fig. 17). In *Megerlia* it is three times attached, first to the hinge-plate, and then to the septum by processes from the diverging and reflected positions of the loop. In *Magas* the apophysary system is composed of an elevated longitudinal septum reaching from one valve to the other, to which are affixed two pairs of calcareous lamellæ, the lower ones riband-shaped; attached first to the hinge-plate, they afterwards proceed by a gentle curve near to the anterior portion of the septum, to the sides of which they are affixed; the second pair originate on both sides of the upper edge of the septum, extending in the form of two triangular anchor-shaped lamellæ (fig. 18). In *Bouchardia* the septum only is furnished with two short anchor-shaped lamellæ. Many more modifications are observable in different groups of which the great family *Terebratulidæ* is composed, and which will be found fully described in Davidson's and other authors' works on the Brachiopoda. In *Thecidium* (figs. 3, 4) the interior of the dorsal valve is variously furrowed to receive a testaceous ridge folded in two or more lobes. In the family *Spiriferidæ* there are two conical spires directed outwards, and nearly filling the cavity of the shell (fig. 5); while in *Atrypa* the broad spirally coiled lamellæ are vertical, and directed towards the centre of the valve. In the *Rhynchonellidæ* there are two short slender curved laminæ, while in many genera and even families, such as the *Productidæ, Strophomenidæ, Lingulidæ, Discinidæ*, &c., there exists no calcified support for the labial appendages. The ventral valve in many of the genera is provided with two curved hinge-teeth, which fit into corresponding sockets in the opposite valve, so that the valves cannot be separated without breaking one of the teeth. Nearly all the genera composing the division Clistenterata have their valves articulated while those forming the Tretenterata have theirs kept in position by the means of muscles especially adapted to that purpose; but in one of the most natural groups, viz., that of the *Productidæ*, we find genera presenting both conditions.

The intimate structure of the shell has been minutely investigated by Dr Carpenter, Prof. King, Dr Gratiolet, and several others, and been found to be distinct from that of the Lamellibranchiata and Gasteropoda. Dr Carpenter informs us that there is not in the shell of the Brachiopoda that distinction between *outer* and *inner* layers, either in structure or mode of growth, which prevails among the ordinary bivalves; that it seems obvious, both from the nature of the shell substance and from the mode in which it is extended, that the whole thickness of the Brachiopod shell corresponds with the outer layer only of the Lamellibranchiata; and that he has occasionally met with a second layer in recent *Terebratulæ*, within the earlier portion of the shell, but confined to only a part of the surface instead of extending beyond it. In some families composing the Clistenterata it consists, according to Prof. King, of three divisions, the innermost and middle ones, which constitute the entire thickness of the valve, being calcareous with a prismatic or fibrous structure, while the oute divisions would consist of a very thin membrane. The innermost and intermediate divisions are in some families traversed by minute tubular canals, which pass from one surface to the other, for the most part in a vertical direction, and at tolerably regular intervals, but just before terminating near the outer surface of the epidermis their orifices suddenly become dilated, the lower half of the canals being often considerably smaller in diameter than the upper half. The canals are occupied by cæcal processes proceeding from the mantle or the fleshy covering of the animal. Their function is, according to Dr Carpenter, branchial or subservient to respiration; but if there exists an outer epidermis, as described by King, which covers their expanded terminations, there would be no communication between the surrounding sea water and the mantle. In the *Rhynchonellidæ* and in some other families the shell structure would, according to Dr Carpenter, consist of flattened prisms of considerable length, arranged parallel to each other with great regularity, and obliquely to the surface of the shell, the interior of which is imbricated by their outcrop. In certain genera, such as *Lingula* and *Discina*, no canals traverse the shell from the inner to the outer surface. The shell structure, according to Dr Gratiolet, would consist of two distinct elements, that is to say, a corneous or horny animal substance, and a testaceous one; these occur in alternate layers of unequal thickness. The testaceous layers recall the structure observable in the *Terebratulidæ*, being traversed by numerous canals of extreme or microscopic minuteness. As Mr Woodward observes in his excellent manual of the Mollusca, Prof. Huxley has suggested that the cæca are analogous to the vascular processes by which in many Ascidians the *tunic* adheres to the *test*, the extent of which adhesion varies in closely allied genera. It seems, however, strange that these tubular perforations should not have been essential to the species of every family composing the class if they are really subservient to respiration. The subject will therefore demand further consideration.

Soft parts of the animal.

The anatomy of the Brachiopoda has been the subject of elaborate investigations by Cuvier, Vogt, Huxley, Hancock, Gratiolet, Woodward, Deslongchamps, King, and others, while of late years much light has been likewise thrown on the embryology and early stages of the groups by Steenstrup, Lacaze-Duthiers, Morse, F. Müller, Oscar Schmidt, M'Crady, Kowalevsky, and others. Some differences in opinion, it is true, have been and still are entertained with respect to the exact function to be attributed to certain parts of the animal, but on all essential questions there is a pretty general agreement.

According to Morse the Brachiopoda are reproduced by eggs, generally kidney-shaped and irregular, which are discharged from the anterior margin of the shell, and drop just beyond the pallial membrane, hanging in clusters from the setæ. Some uncertainty has prevailed as to whether there is a male and female individual. Lacaze-Duthiers and Morse state that the sexes are separate, and describe them as such in *Thecidium* and *Terebratulina*, and the French zoologist goes so far as to suggest that a difference is even observable in the shell, but the statemen requires verification. Prof. Morse describes the embryo o *Terebratulina* with great minuteness during its six stages of development. It is divided into two, three, or four lobes clothed with vibratile cilia, and before becoming attached swims or whirls head foremost by means of vibratile cilia which cover the body. The same distinguished American zoologist describes with equal care the formation of the shell from its first stage of development to the adult condition. Lacaze-Duthiers alludes to two and four eye spots in the embryo of *Thecidium*, and states that the animal appears to be in some measure sensible to light.

The mouth conducts by a narrow œsophagus to a simple stomach which is surrounded by a large granulated liver. Owen's "hearts" have been found to be oviducts, while the true heart consists of a pyriform vesicle appended to the dorsal surface of the stomach. The digestive organs and viscera, as well as the muscles, which take up only a small place in the neighbourhood of the beak, are separated from the great anterior cavity, and protected by a strong membrane in the centre of which the mouth is situated. The nervous system consists of a principal ganglion of no great size.

Both valves are lined by a delicate membrane termed the pallium or mantle; it secretes the shell, and is generally fringed with horny bristles or setæ. It is composed of an outer and inner layer, between which are situated the blood channels or lacunes; in fact, all the internal parts of the shell are lined by the inner layer of the mantle, with the exception of the spots where the muscles attach themselves to the shell. The outer layer lines closely the inner surface of the valves to which it adheres, and in those species in which the shell is traversed by canals there exist, on the surface of the mantle facing the inner surface of the valves, corresponding short cylindrical membranous projections or lacunes, which insert themselves into the small tubular orifices that traverse the shell. The cæcal prolongations do not exist in those genera, such as *Rhynchonella*, where the shell is deprived of tubular perforations. The inner layer is rather thicker than the opposite one, and is covered with vibratile cilia. As stated by Nicholson and other anatomists, the blood channels form a remarkable system of more or less branched tubes, anastomosing with one another, and ending in the cæcal extremities. This, which has been termed by Huxley the arterial system, communicates with the perivisceral cavity by means of two or four organs, which are called pseudo-hearts, and which were at one time supposed to be true hearts. Each pseudo-heart is divided into a narrow, elongated external portion (the so-called "ventricle"), which communicates, as Hancock has proved, by a small apicial aperture with the pallial cavity; and a broad, funnel-shaped so-called "auricle," communicating on the one hand by a constricted neck with the so-called "ventricle," and on the other by a wide patent mouth with a chamber which occupies most of the cavity of the body proper, and sends more or less branched diverticula into the pallial lobes (Huxley). The channels vary in their dispositions and details in different genera, and as they project to some small extent, leave corresponding indentations on the inner surface of the shell, so that their shape and directions can very often be traced on fossil and extinct genera as well as if the animal was still in life; this may be seen in the numerous illustrations appended to Davidson's and other authors' works treating of fossil Brachiopoda. There are usually four principal arterial trunks in each lobe of the mantle; the two central ones run direct to the front, near to which they bifurcate, while the outer ones give off at intervals on the side facing the lateral margin of the valves a series of branches which bifurcate several times. It has been observed by Hancock that the inner lamina of the mantle, and more particularly that portion of it forming the floor of the great pallial sinuses, will undoubtedly assist in purifying the blood. In 1854, in his review of Davidson's great work on British fossil Brachiopoda, Oscar Schmidt called attention to an important anatomical omission, namely, the existence of a vast number of microscopic, flattened, calcareous, denticulated plates or spiculæ on certain parts of the surface of the mantle, and destined, no doubt, to stiffen and protect the portions that contain them; and it was, moreover, observed by Hancock, and afterwards by Deslongchamps, that these calcareous plates are not to be found equally distributed over all the surface of the mantle, but only in those portions in connection with the great lacunes or veins, the labial appendages, and the perivisceral cavity. These spiculæ do not appear to be present in every species, and are totally absent in *Lingula*, *Rhynchonella*, and others. Deslongchamps observes that if we examine the genera *Kraussina, Terebratula, Terebratulina, Megerlia*, and *Platydia*, we have a series wherein the number and consistence of the calcareous portions increase in a very rapid manner, and that the spicules l over each other several times, leading the observers by insensible degrees to *Thecidium*, in which the spiculæ are soldered together, and incrust the mantle to such an extent that it is no longer distinct from the shell itself.

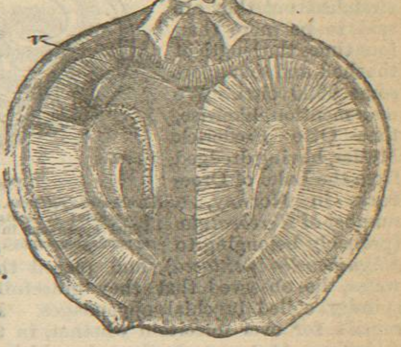


Fig. 19.
Waldheimia flavescens. Interior of dorsal valve, to show the position of the labial appendages. (A portion of the fringe of cirri has been removed to show the brachial membrane and a portion of the spiral extremities of the arms.)

The brachial appendages are a pair of singular organs eminently characteristic of the Brachiopoda; they often are more correctly termed *labial* appendages on account of each member being a prolongation of the lateral portion of the lips or margin of the mouth. The Lamellibranchs or Conchifera have analogous appendages, but very much less developed. They assume different shapes in different genera, and are supported, or otherwise, by the more or less complicated skeleton already described. The labial appendages, whatever may be the shape and convolutions they may assume, fill the larger portion of the cavity of the shell in front of the visceral chamber; they are formed of a membranous tube, fringed on one side with long flexible cirri, and occupy almost the whole of the pallial cavity, but were not capable of being protruded in those families in which they were folded back upon themselves and supported by a calcareous skeleton as in *Waldheimia, Terebratella, Megerlia*, &c. Barrett, who has examined the animal of *Terebratulina caput serpentis* in life, states that it showed more of itself than *Waldheimia cranium*, which might be supposed from the labial appendages being in the first very slightly supported by a small loop. Barrett observed, likewise, that it protrudes its cirri further, that the cirri on the reflected part of the brachial appendage are shorter than on the first part, and were

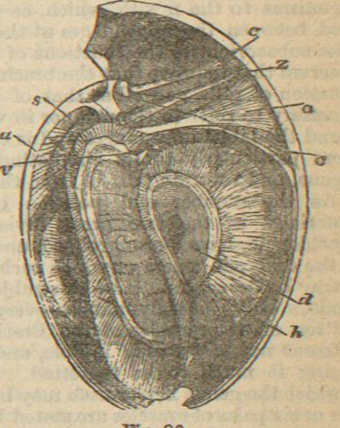


Fig. 20.
Waldheimia flavescens. Longitudinal section with a portion of the animal. *d, h*, brachial appendages; *a*, adductor; *c, c'*, divaricator muscles; *s*, septum; *v*, mouth; *t*, extremity of alimentary tube. The peduncular muscles have been purposely omitted.

almost constantly in motion, and often seen to convey small particles to the channel at their base, and that the cirri are bent up when the brachial appendages are retracted, but are generally uncoiled and straightened when the shell is opened, before which the animal has often been observed to protrude a few of its cirri, and move them about to ascertain if any danger threatened. In *Rhynchonella*, where the elongated spiral labial appendages are slightly supported only at their origin by two short calcareous processes, they can at the will of the animal, according to Owen and Morse, be unrolled and protruded to some distance beyond the margins of the valves, and when forcibly stretched out they are said to be more than four times the length of the shell, and to support some 3000 cirri. We may mention, likewise, that Otto Frederick Müller, having dredged from the Lake of Droeback, in Norway, a number of *Terebratulæ* (probably belonging to *Rhynchonella psittacea*), and placed them in a glass of water, he observed that they gracefully extended their spirally coiled brachial appendages. It must, however, remain for ever uncertain whether, in the extinct genera *Spirifera*, *Atrypa*, and others, in which the spirally coiled fleshy labial appendages were supported throughout their entire length by a calcified skeleton, the animal could protrude them beyond the margin of the valves. In some families—*Rhynchonellidæ*, *Productidæ*, and others—these organs are spiral and separate; in many the separation is only at their extremities. There can be very little doubt that these elegant organs, provided as they are with cirri and cilia, are not only instrumental in conveying microscopic organisms to the mouth, which, as seen in fig. 19, is situated between the appendages at their origin, but are likewise subservient to the functions of respiration. Hancock observes that to prove that the brachial organs subserve the function of gills, as well as that of sustentation, it is only necessary to refer to the manner in which the blood circles round the labial appendages and is carried to the cirri, but more particularly to its circulating through these latter organs, and returning direct from them to the heart.

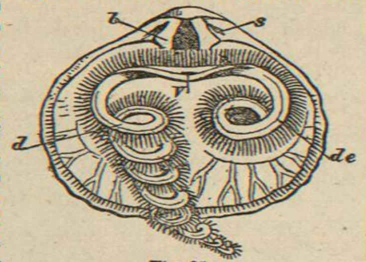


Fig. 21.
Rhynchonella psittacea. Interior of dorsal valve. *s*, sockets; *b*, dental plates; V, mouth; *de*, labial appendage in its natural position; *d*, appendage extended or unrolled.

As the number and position of the muscles differ materially in the two great divisions into which the Brachiopoda have been grouped, and to some extent also in the different genera of which each division is composed, it may be desirable to treat this subject under two separate heads. Unfortunately almost every anatomist who has written on the muscles of the Brachiopoda has proposed different names for each muscle, and the confusion thence arising is much to be regretted. In the Clistenterata, of which the genus *Terebratula* may be taken as an example, five or six pairs of muscles are stated by Hancock, Gratiolet, and others, to be connected with the opening and closing of the valves, or with their attachment to or movements upon the peduncle. First of all, the adductors or occlusors consist of two muscles, which, bifurcating near the centre of the shell cavity, produce a large quadruple impression on the internal surface of the small valve (fig. 13, *a*, *a'*), and a single divided one towards the centre of the large or ventral valve (fig. 12, *a*). The function of this pair of muscles is the closing of the valves. Gratiolet, who has likewise described with great minuteness the muscles of the Brachiopoda, informs us that those which close and open the valves were the only ones known to Pallas, but that he defined their position and functions clearly. The same was done by Blainville and Quenstedt, but the absence of good figures caused much uncertainty to prevail. This

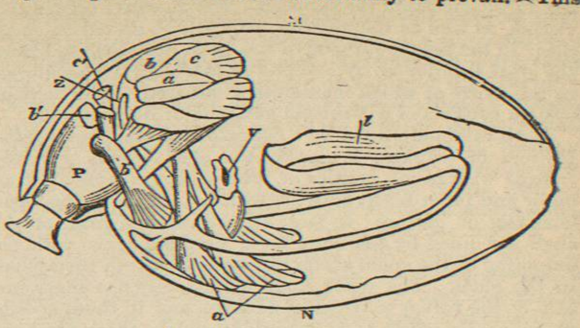


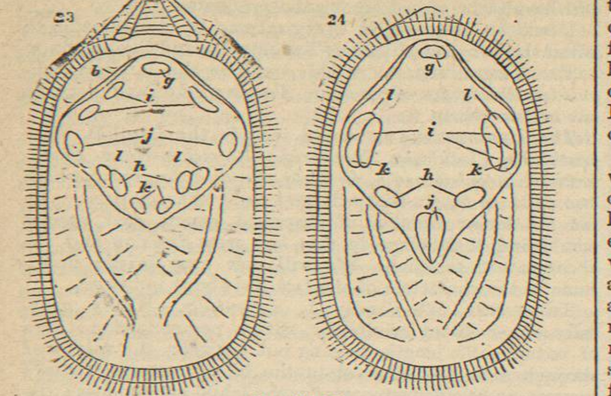
Fig. 22.
Waldheimia flavescens. Diagram showing the muscular system (*after Hancock*). M. ventral, N, dorsal valve; *l*, loop; V, mouth; Z, extremity of intestine; *a*, adductor; *c*, divaricators; *c'*, accessory divaricators; *b*, ventral adjustors; *b'* peduncular muscles; *b''*, dorsal adjustors; P, peduncle.

deficiency was subsequently supplied by Hancock and Gratiolet's admirable illustrations. Two other pairs have been termed *divaricators* by Hancock, or *cardinal muscles* ("muscles diducteurs" of Gratiolet), and have for function the opening of the valves. The divaricators proper are stated by Hancock to arise from the ventral valve, one on each side, a little in advance of and close to the adductors, and after rapidly diminishing in size become attached to the cardinal process, a space or prominence between the sockets in the dorsal valve. The *accessory divaricators* are, according to the same authority, a pair of small muscles which have their ends attached to the ventral valve, one on each side of the median line, a little behind the united basis of the adductors, and again to the extreme point of the cardinal process. Two pairs of muscles, apparently connected with the peduncle and its limited movements, have been minutely described by Hancock as having one of their extremities attached to this organ. The *dorsal adjustors* are fixed to the ventral surface of the peduncle, and are again inserted into the hinge-plate in the smaller valve. The *ventral adjustors* are considered to pass from the inner extremity of the peduncle, and to become attached by one pair of their extremities to the ventral valve, one on each side of and a little behind the expanded base of the divaricators. The function of these muscles, according to the same authority, is not only that of erecting the shell, they serve also to attach the peduncle to the shell, and thus effect the steadying of it upon the peduncle. Gratiolet describes the peduncle with great care, and states it to be composed of two portions—1st, of a horny sheath formed of concentric epidermic layers, very analogous to that which Vogt has described in *Lingula*; and 2d, a fibrous stem enveloped by the sheath. This stem, composed of tendinous fibres, is fixed by its free extremity to different submarine objects; the other extremity passes through the foramen, and is ended by a bulbous projection.

Such is the general arrangement of the shell muscles in the division composing the articulated Brachiopoda, making allowance for certain unimportant modifications observable in the animals composing the different families and genera thereof. Owing to the strong and tight interlocking of the valves by the means of curved teeth and sockets, many species of Brachiopoda could open their valves but slightly. In some species, such as *Thecidium*, the animal could raise its dorsal valve at right angles to the plane of the ventral one (fig. 4).

In the Tretenterata, of which *Lingula* and *Discina* may

be quoted as examples, the myology is much more complicated, and anatomists have differed considerably in their respective views concerning the function of some of the muscles. They have been carefully described by Owen, Vogt, Hancock, Gratiolet, Woodward, and others, and more



Figs. 23, 24.
Lingula anatina. 23, interior of ventral valve; 24, interior of dorsal valve (*after King*). *g*. umbonal muscular impressions (open valves); *h*, central muscles (close valves); *i*, transmedial or sliding muscles; *b*, parietal band; *j*, *k*, *l*, lateral muscles (*j*, anteriors; *k*, middles; *l*, outsiders), enabling the valves to move forward and backward on each other.

recently by King, whose views seem to carry with them a greater degree of plausibility. Of the shell or valvular muscles he makes out five pairs and an odd one, and individualizes their respective functions as follows:—Three pairs are *lateral*, having their members limited to the sides of the shell; one pair are *transmedians*, each member passing across the middle of the reverse side of the shell, while the odd muscle occupies the umbonal cavity. The *central* and *umbonal* muscles effect the direct opening and closing of the shell, the *laterals* enable the valves to move forward and backward on each other, and the *transmedians* allow the similar extremities (the rostral) of the valves to turn from each other to the right or the left on an axis subcentrically situated, that is, the medio-transverse region of the dorsal valve. It was long a matter in discussion whether the animal could displace its valves sideways when about to open its shell, but this has been actually observed by Professors Semper and Morse, who saw the animal perform the operation. They mention that it is never done suddenly or by jerks, as the valves are at first always pushed to one side several times and back again on each other, at the same time opening gradually in the transverse direction till they rest opposite to one another and widely apart. Those who have not seen the animal in life, or who did not believe in the possibility of the valves crossing each other with a slight obliquity, would not consent to appropriating any of its muscles to that purpose, and consequently attributed to all the lateral muscles the simple function of keeping the valves in an opposite position, or holding them adjusted. We have not only the observations of Semper and Morse, but the anatomical investigations of King, to confirm the sliding action or lateral divarication of the valves of *Lingula*.

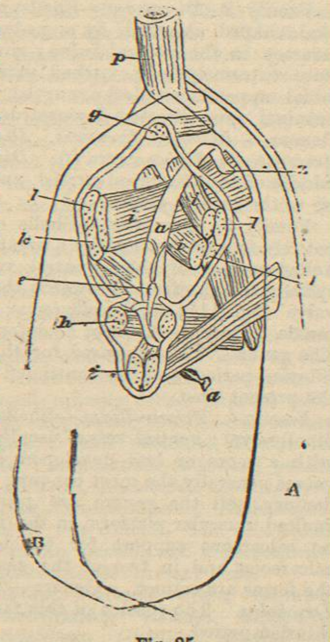


Fig. 25.
Lingula anatina. Diagram showing the muscular system (*after Hancock*). The letters indicate the muscles as in figs. 23 and 24. A, dorsal, B, ventral valve; *p*, peduncle; *e*, heart; *a*, alimentary tube; *z*, anal aperture.

In the Clistenterata, where no such sliding action of the valves was necessary or possible, no muscles for such an object were required, consequently none took rise from the lateral portions of the valves as in *Lingula*; but in an extinct group, the *Trimerellidæ*, which seem to be somewhat intermediate in character between the Tretenterata and Clistenterata, have been found certain scars, which appear to have been produced by rudimentary lateral muscles, but it is doubtful (considering the shells are furnished with teeth, though but rudely developed), whether such muscles enabled the valves, as in *Lingula*, to move forward and backward upon each other. We do not yet possess any reliable observations as to the manner in which *Discina* opens its valves, but Mr Barrett, who observed *Crania* in life, informs us that the valve opens by moving upon the straight hinge, without sliding the valve. There are muscles connected with other portions of the animal in both groups, such as the *parietal* muscles, strongly defined in the Tretenterata, and distinctive peculiarities of the peduncle, but the limited space at our disposal will not admit of entering upon further anatomical details.

Ranges of depth.

The Brachiopoda all inhabit the sea, and are supposed to have attained their full growth in a single season. A vast amount of important and accurate information has been collected during the past ten years with respect to the geographical distribution of recent species, as well as to the marine depths they inhabit or prefer. This important knowledge is mainly due to the numerous well conducted and equipped dredging expeditions carried on by private individuals and by the Governments of the leading maritime states. It would not be possible to give here the names of all those naturalists who have contributed to this portion of our information, but we cannot pass over those of Edward Forbes, J. G. Jeffreys, W. B. Carpenter, W. H. Dall, W. Thomson, E. Suess, A. Adams, H. Cuming, &c. Previous to these investigations the data we possessed with respect to the habitat and ranges of depth were in most cases vague and unsatisfactory. It has been ascertained that the Brachiopoda are much localized, and usually occur in great numbers in their favourite haunts. Jeffreys does not believe that the habitat of any Invertebrate animal is affected by bathymetrical conditions, and that the same species will occur at various depths. We can say nothing certain with respect to the ranges of depth at which the extinct species lived, but some idea as to their probable depths can be surmised from a study of the recent species. As far as our present information will carry us the Tretenterata do not appear to have been found at a greater depth than 1360 to 2000 fathoms. *Lingula* abounds in particular haunts at about half the tide-mark, and partly buried in mud, or at depths varying from three or four inches from the surface of the sea to seventeen fathoms. Prof. Morse describes a species which he found in vast numbers in a sand shoal at low water; the peduncle, six times the length of the shell, was partly encased in a sand tube (fig. 9). He observed likewise that this species (*Lingalu pyramidata*) had the power of moving over the