

On the Structure and Development of Argiope.

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With Plates 39 and 40.

The two species of *Argiope*, which I have studied at the Zoological Station Naples, occur at a depth of about 70 metres in the Bay of Naples. They differ considerably in their appearance. The shell of *A. neapolitana* (fig. 9) is of a uniform brownish white color, studded with numerous white spots, due to the presence of the canals which perforate the shell. The ventral shell is heart shaped, its posterior end is pointed, forming the beak, the anterior end is broad and has a median depression. The greatest length of this shell is from 2.5 to 3 mm, the greatest breadth which is about one third of the length from the anterior border is about the same. The aperture through which the stalk passes is not completed by the ventral shell, but the anterior side is formed by the posterior border of the dorsal shell. The remaining three sides of the aperture are formed by the ventral shell, the posterior by the posterior apex, and the sides by the inner borders of two triangular areas which belong to the same shell but are bent under to lie in the same plane as the dorsal shell (fig. 17 *tr*). The apex of this triangular area bears a tooth-like process which fits into a socket on the dorsal shell. There is a slight median ridge which runs from the posterior of the ventral shell for about two thirds of its length on its inner side, dividing the shell into two equal halves (fig. 17 *vr*).

The dorsal shell is not seen when the animal is in its natural position. It is not so vaulted as the other, but in outline it resembles it, only instead of ending in a point, the posterior third is cut away. The posterior border may be divided into three parts, the central third forming the anterior border of the aperture through which the stalk passes,

is slightly produced. The two outer thirds lie against the anterior border of the triangular areas of the ventral shell. The body of *Argiope* lies almost entirely in the dorsal shell whose internal skeleton consists of three triangular plates: one median, the other two lateral and paired (fig. 16). The lateral parts of the skeleton consist of two triangular plates, which have two faces and three borders. The plates pass from the junction of the outer third with the central third of the posterior border of the dorsal shell, parallel with the margin of the shell to about the middle of the lateral border (figs. 16 and 18 *sk*). Thus of the two faces, one looks inward, the other outwards. Of the borders one looks towards the median line, another looks towards the ventral shell and the third forms the attachment of the plate to the imperforate valve. It is at the angle formed by the first and third of these borders that the notch occurs, into which the teeth of the perforate valve fit. Although these plates do not form a continuous support in front, there are traces of them in the anterior border, in the form of small teeth (figs. 16 and 18). The third part of the internal skeleton also consists of a triangular plate, its two faces look laterally, its posterior border is deeply curved and serves to support the anterior part of the alimentary canal. The mouth is situated just behind the apex of this triangle, where the posterior border joins the upper. This latter border slopes gradually away towards the anterior margin of the shell, and is cut into a series of sharp teeth in *Argiope neapolitana*, although in *A. cuneata* it is quite smooth. This median septum divides the lophophore into two lobes (fig. 11 *sm*).

The shell of *A. cuneata* is about 1.5 times as broad as long; there is no median depression on the anterior border (Fig. 10). The posterior border is nearly straight, sloping very gradually towards the aperture for the stalk, there is no pointed beak. The shell is radially ribbed, and the ribs are of a bright yellow color while the depressions between them are a light brick red, the same color as the eggs and larvae. The ribs are usually six or eight and lie symmetrical on each side of a median groove, the ribs of both shells correspond, the margins of the shells are not entire as in *A. neapolitana* but slightly crenate, the projections corresponding with the ribs.

The internal skeleton consists like that of *A. neapolitana* of a median ridge on the posterior two thirds of the ventral shell and of three plates on the dorsal shell. The anterior border of the median one forms a much greater angle with the plane of the shell than is the case with that of *A. neapolitana*, it is also without teeth. In old specimens this plate is supported by two lateral wings. The lateral plates which support

the lophophore are perforated by two large holes, these are also found in the other species, but are there quite small. The shells of both species are slightly transparent so that the outline of the lophophore and the red ovaries and larvae can be indistinctly seen through them. Both shells are marked by faint lines which run parallel to the margin.

In its minute structure the shell of *Argiope* consists of a number of very fine calcareous spicules supported in an organic network. The spicules are not very regularly arranged but they have a general antero-posterior direction, and are oblique, their inner end being nearer to the edge of the shell, their outer to the beak. Their inner extremities are rounded somewhat enlarged and overlap each other like the slates on a roof (fig. 14); they are much larger at the centre than at the margin of the shell. On the outer side of the shell is a layer, in thickness about one eighth of the whole shell, where the proportion of calcareous matter to organic is enormously increased. The spicules are here nearly square and packed against one another like bricks. I have unfortunately been unable to see KING's paper¹ but I believe this layer must agree with the second layer discovered by him, and mentioned in the recent paper of VAN BEMMELEN².

Outside this is the third layer or periostracum. This is a thick structureless cuticle: it completely covers the whole shell, and in the fresh state adheres very closely to it. The cuticle does not stain (figs. 1 and 15 *cu*).

When sections are made through the decalcified shell, the organic basis or network is seen to consist of numerous very fine homogeneous fibrils. The meshes of the network have the same shape as the spicules they contain and so in longitudinal sections they appear elongated and oblique, in transverse or horizontal sections as irregularly square (fig. 15 and 19). These organic fibrils are in connection on their inner side with the mantle which lines every part of the shell. They stain very readily with Borax Carmine or Haematoxylin.

In the decalcified sections there is a considerable space between the periostracum and the shell. This may be partly due as VAN BEMMELEN suggests to the disappearance of KING's second layer, but it is, I believe, chiefly caused by the evolution of gas forcing the cuticle away from the shell.

The shell is pierced by very numerous canals which run completely

¹ On the Histology of the Test of the Class Palliobranchiata. Trans. of the Roy. Irish. Acad. Vol. XXIV. 1867.

² Untersuchungen über den anatomischen und histologischen Bau der Brachiopoda Testicardinia. Jenaische Zeitschrift f. Naturwissenschaft. XVI. 1883.

through the calcareous part, but their outer end is covered by the cuticle. They are of uniform diameter in the first part of their course through the first layer, but when they reach the second layer of KING, they expand and end in funnel shaped mouths (figs. 1 and 15 *mp*). The distribution of these canals is very uniform, they mostly lie on lines concentric with the free edge of the shell. Their course is usually perpendicular to the surface of the shell, though occasionally they have an oblique direction. They are as a rule single but in the posterior part of the perforate shell, where it is unusually thick, I have seen branched canals. Similar branched canals are described for *Terebratula caput serpentis*, and the canals of *Crania* branch at their outer extremities.

The minute structure of the internal skeleton is like that of the inner layer of the shell, there are no canals present, but in *Argiope* (*Cistella*) *lutea*, a species 'considerably larger than those of the Mediterranean', W. H. DALL¹ states that canals are present in the substance of the internal skeleton.

The mantle which lines the internal surface of each shell is formed by two evaginations of the body wall. Although the body of *Argiope* occupies a much greater part of the mantle cavity than is usual with *Brachiopoda*, still it lies almost wholly within the dorsal shell, consequently nearly the whole of the ventral and a considerable portion of the dorsal shell, that is the part not occupied by the body, are lined by the mantle. Since the mantle is formed by a duplicature of the body wall it is necessarily double and in some places there are prolongations of the body cavity in which the generative organs lie, in other places the two layers have fused.

At the edge of the shell the mantle becomes thickened and forms a number of ridges which are covered by a high epithelium; the nuclei of these cells stain very clearly. From some sections which I have prepared, I believe, that the ridges of the opposite shells interlock and thus close the mantle cavity in a very complete manner. Elsewhere the inner surface of the mantle is covered by a flat epithelium not very well defined, beneath this lies a number of granular branched connective tissue cells. On the outer surface the mantle is in direct connection with the organic basis of the shell. No setae occur on the mantle of *Argiope*.

Into each of the canals which pierce the shell, the mantle sends a diverticulum. This is a hollow tube which fits exactly into the calcareous

¹ Report on the *Brachiopoda* obtained by the United States Coast Survey Expedition, in Charge of S. F. DE POURTALÈS, with a Revision of the *Craniidae* and *Discinidae*, by W. H. DALL, 1871.

canal but, unlike that, is closed at its outer end. The walls of the tube consist of a structureless membrane which stains well and appears to consist of the same tissue as the organic network of the shell. The fibres of the latter in the neighbourhood of the tube fuse with it. The outer end of the tube is slightly enlarged and the outer wall which closes it is much thicker than the lateral walls. There appears to be a close connection between the top of these papillae and the periostracum, for in many cases when the latter was torn away elsewhere it remained attached to the summit of the papillae. The periostracum passes unchanged over the summit of the papillae but a number of fine lines appear to pass from the underside of the periostracum to the top of the papillae (fig. 15).

Within these papillae lie freely a number of round bodies, which stain deeply especially at their circumference. These bodies are generally aggregated in small clusters, two or three such aggregations often being found in one papilla. These bodies agree very exactly with the blood corpuscles which are seen in sections of the blood vessels running in the mantle. In many cases I have been able to see that the cavity of the papillae is in communication with that of the blood vessels and in some sections I have seen a bundle of corpuscles lying half in the blood vessel and half in the lumen of the papilla, therefore I believe the bodies in the papillae to be simply blood corpuscles and that the lumen of the papillae are in direct communication with the blood system.

There has always existed a great deal of doubt as to the nature and function of the mantle papillae. VAN BEMMELEN has seen the bodies described lying in the papillae, and has come to the conclusion that they are the deeply stained nuclei of flat epithelial cells lining the cavities. It not difficult as far as *Argiope* is concerned, to demonstrate that this is not so. In this Brachiopod the papillae are unusually large; in longitudinal sections it is seen that the bodies are very irregularly scattered, sometimes the canal is choked with them, sometimes there is only one hundle which may lie at either end or in the middle, in other cases there are none; in transverse section it is seen that the corpuscles lie in the centre and do not line the walls. Furthermore no trace of cells can be seen lining the canals (fig. 15 *mp*).

HANCOCK¹ has noticed the resemblance existing between these bodies and the blood corpuscles, but as he did not believe that the papillae possessed any respiratory functions, he concluded that the bodies

¹ On the organisation of the Brachiopoda. Phil. Trans. Vol. CXLVIII. Part II. 1858.

had nothing to do with blood corpuscles but performed some other function possibly a secretory one. This view that the papillae are not respiratory is, I believe, correct. The wall of the outer end, where the blood comes into closest contact with the external medium, is somewhat thickened, the papillae are everywhere covered by a thick layer of dense periostracum; they occur very uniformly distributed in both shells, being as numerous where one shell is lying imbedded in the object on which the *Argiope* rests, where no gaseous change could take place, as in the other free shell. These facts argue greatly against the view of respiration being carried on by the mantle papillae and to some extent support the view which I have adopted as regards these organs. I believe they exist for the purpose of conveying nutriment to the shell. It is not possible to see the blood flowing in these canals, but I believe it passes in and out, bringing nourishment to the organic network which surrounds every calcareous spicule, very much as the blood is forced in and withdrawn from the tentacles of *Phoronis*. By counting the number of papillae in a given area of young and old shells VAN BEMMELEN has shown that the growth of the shells does not take place by Intussusception, but the increase must occur at the edge. Thus the function of the old papillae is more closely connected with the nutrition than with the growth of the shell. But that this must be an important function is shown by the size of the shell, often many times the size of the body and by the proportion of the organic to the inorganic constituents.

One fact which seems at first opposed to this view, is that no papillae are found in the internal skeleton. But these are thin and delicate and, it is quite reasonable to suppose, may be nourished by the numerous blood vessels, running in the mantle which everywhere covers them. And in *Argiope* (*Cistella*) *lutea*, where the skeleton is probably much coarser, DALL states expressly that the internal skeleton is punctate.

The shell of *Argiope* can only be opened a very little way, without tearing the tissues of the body wall. When we open the shells wide, the body can be seen lying almost entirely in the dorsal shell and covered for the greater part by the lophophore. The posterior end of the intestine will probably be seen protruding through the torn body wall towards the ventral shell (fig. 11). The ovaries will be seen lying a pair in each shell, those of the dorsal shell, with some branches of the liver, are seen through the semi-transparent lophophore.

The lophophore lies entirely in the dorsal shell, it forms a great part of the body wall of the animal. The shape is an oval, the border running parallel with the margin of the shell, except at the anterior median

portion where there is a narrow deep indentation dividing the lophophore nearly into two equal halves; this is caused by the triangular septum mentioned above. These halves correspond with the two arms of other Brachiopods. The lophophore is attached anteriorly and anterio-laterally to the mantle lining the shell, postero-laterally it is attached to the free edge of the triangular plates; in the median posterior portion, it is continuous with the remaining body wall. In the median line it is attached on each side to the free edge of the septum. The lophophore carries round its margin a number of tentacles; the number increases with the age, but is usually from 70 to 100. Within the bases of the tentacles, a lip runs entirely round the lophophore, forming a groove (figs. 2 and 15); the mouth lies in the posterior median portion of this groove. The remainder of the lophophore is composed of a membrane which covers some of the viscera; the centre of each half of this membrane is rather thickened and presents in the fresh state an ill defined whitish patch. The tentacles usually lie pointing towards the centre of each half, but they are often curved and sometimes coiled like a corkscrew. I have never seen the tentacles protruded through the open shell in the natural state, but when the animal is killed by immersion in weak acetic acid, it always protrudes its tentacles. On the lophophore of one *Argiope*, I found a semi-parasitic Copepod which Dr. GIESBRECHT informs me, belongs to an entirely new genus which has affinities with the Lichomolgidae.

The shape of the body cavity is very complicated; at the posterior end it is nearly square, more anteriorly invaginations at the side take place to form the brood pouches, these gradually become deeper, and the posterior part of the lophophore appears in the dorsal wall of the pouch (fig. 7). Finally the pouches meet in the median line and then we have two portions of the body cavity, one lying in the ventral shell, which is soon obliterated by the fusion of its walls; the other lying in the dorsal shell. This is enclosed on one side by the lining of the shell, on the other by the lophophore; it soon becomes divided into two lateral halves by the appearance of the triangular septum (fig. 3).

Around the edge of the lophophore between the base of the tentacles and the origin of the lip, there runs a canal in the substance of the lophophore (figs. 2 and 15 *ca*). This is larger at its outer end but disappears in the centre by the fusion of the inner wall to the outer. In the posterior median line this inner wall passes in on each side to form one of the mesenteries supporting the alimentary canal. Thus the cavity in the lophophore communicates with part of the body cavity. From

the peripheral canal a branch passes off into each tentacle. The mass of the lophophore consists of a homogeneous, clear, supporting substance which is also found greatly developed in the stalk, at the origin and insertion of the muscles, and in other parts of the body wall. A few granular cells are found in this substance. The membrane which is formed of this homogeneous material is covered within and without by a layer of flat epithelium cells. Fig. 13 represents a transverse section through a tentacle and fig. 15 a longitudinal section through the base of another, showing the ciliated groove, formed by the lip and the tentacle, and the attachment of the lophophore to the mantle. From these figures it is seen that the greater part of the tubular tentacle is composed of the homogeneous supporting substance; lining this internally is a layer of flat epithelium cells. In the canal a number of muscular fibres (fig. 13 and 15 *mf*) are seen in section, these lie chiefly on that side of the tube which is nearest the centre of the lophophore. The supporting substance is covered outside also with a layer of epithelium which on one side is flat and non-ciliated, on the other three sides very high and ciliated. These latter sides are the inner and the two lateral. At the base of the tentacles on the inner side the columnar epithelium becomes very high and then becomes very low again, thus an epithelium cushion is formed, which is continuous all round the ciliated groove on the outer side. The remaining epithelium of the groove is cubical and ciliated except just at the edge of the lip where again it becomes very high. The other side of the lip is covered with non-ciliated cubical cells which gradually pass into the flat epithelium covering the disk of the lophophore. In the living animal the cilia can easily be seen in motion; those at the base between each tentacle are particularly large and powerful. It will be seen that this arrangement of cilia is adapted to bring any floating particles of food into the ciliated groove and when once there, they are no doubt driven by the action of the cilia towards the mouth, which as is stated above opens into this groove. I have been unable to detect any blood corpuscles in the tentacles, and I believe the sole function of the lophophore is to set up a stream by means of its cilia, and so to bring diatoms and other articles of food to the mouth, and that it has no respiratory function whatever. Indeed it is difficult to imagine how an interchange of gas could take place through the thick, dense layer of supporting substance.

The protrusion of the tentacles is probably brought about by forcing in a perivisceral fluid, but their retraction and coiling movements are probably occasioned by the muscular fibres which lie in their interior.

The mouth is a transverse slit in the median posterior part of the ciliated groove: it leads into a somewhat narrow oesophagus which lies against the posterior curved border of the triangular septum (fig. 1). At the bottom of this border, the oesophagus turns toward the posterior end of the animal and immediately enlarges into the stomach. This is globular in shape and receives upon each side the opening of the liver (fig. 5). The stomach narrows posteriorly and passes into a conical intestine which bends towards the ventral shell between the two brood pouches and ends between the ocluser muscles. There is no anus. The walls of the alimentary canal are of nearly the same thickness throughout, being only a little thinner in the stomach and a little thicker in the posterior part of the intestine where the lumen begins to disappear. They are lined throughout by cilia, continuous with those of the ciliated groove. On the outside the alimentary canal is enclosed by a membranous sheath which is prolonged into numerous strands and mesenteries; these pass into the body wall lining the shell and serve to support the structure. Within this sheath is a basement membrane and within this a thick layer which stains deeply and appears to be composed of muscular fibres. The inside is lined by very high epithelium cells which bear the cilia.

The inner coat of the oesophagus and stomach is sometimes broken up into broad ridges, by narrow depressions, but this is not always the case.

The alimentary canal is connected with the posterior ridge of the septum and with the dorsal shell by a number of connective tissue strands. Similar strands are also found on the ventral side of the canal; these unite to form a double mesentery which passes from the canal to the body wall. More posteriorly the double mesentery fuses to form a single band which lies in the median line and is at first connected with the body wall behind the sub-oesophageal nerve ganglion, but afterwards it unites with that part which covers the median ridge of the ventral shell (fig. 6 and 7 *m*). This corresponds with the mesentery of HUXLEY. In the anterior part where the mesentery is double, each sheet is continuous with the inner wall of the lophophore, so that the cavity of the lophophore opens into that part of the body cavity which lies between these two membranes. The other mesentery serving to support the intestine corresponds with HUXLEY's gastro-parietal band. It stretches from the line where the lophophore fuses with the mantle, to the side of the intestine, dividing the body cavity into two parts. In the half next the shell, the ova and part of the ocluser muscles lie, in the other the branches of the liver (fig. 6 *gp*).

Anteriorly this mesentery splits into two layers, one passing to fuse

with the body wall between the oclusor muscles and the ovary, the other to the outside of the ovary which thus lies between the two layers. It does not extend farther anteriorly than the stomach, being stopped by the liver, or very far posteriorly, where it forms a curve to allow the tendons of the oclusor muscles to pass to the ventral shell. The ileo-parietal band of HUXLEY is but very slightly represented in Argiope and can hardly be considered to afford any support to the intestine. It lies in the same plane as the gastro-parietal and is seen in fig. 8 where the inner lip of the opening of the segmental organ is seen to be connected with the wall of the intestine. Besides the mesenteries which are named there are numerous irregular connective tissue strands which serve to connect the alimentary canal with the walls of the body. In their minute structure the mesenteries consist of a median layer of homogeneous substance coated upon each side by flat cells whose nuclei stain deeply.

The liver consists of two branched glands lying one on each side of the alimentary canal, in that part of the body cavity which is enclosed on one side by the lophophore, on the other side by the dorsal shell anteriorly, and by the gastro-parietal band posteriorly (fig. 3 to 6 *H*). It is visible in the fresh state through the lophophore, the branches are thick, rounded at their ends, and not more than six or seven in number: they lie nearly all in one plane. The greater part of the liver lies in front of the mouth. The stem of the liver is thick with a broad lumen; it opens on each side into the stomach by a wide mouth. The lumen is continued until the end of each branch. The secreting surface of the tubules is increased by their inner walls being raised into a number of wedge-shaped ridges, so that in transverse sections the lumen has the form of a star. The cells lining the tubules are often very much vacuolated, and their nuclei lie in their outer ends; in the fresh state they have a brown color. The secretion they form is thrown out into the lumen which in many cases is quite full of it.

Like other recent observers, I have been unable to find any thing corresponding to a central circulatory organ, or to the system of arteries and «accessory pulsatile organs» described by HANCOCK. The blood is contained in a number of vessels which run irregularly in the tissues of the body, but which chiefly lie in the mantle and that part of the body wall lining the shell. It is not possible to make out very distinct walls to these vessels, which appear to be mere slits in the tissue; they communicate, as was mentioned above, with the papillae of the shell, and are especially numerous at the posterior end of the ventral shell, and in the angle formed by the posterior border of the triangular septum and

the dorsal shell. The blood corpuscles are large in comparison with the other cells of *Argiope*, which like all Brachiopod cells are extremely small. They stain deeply at their circumference and appear to possess no nuclei, and usually lie together in small clusters. Although owing to the presence of the shell it is impossible to observe the blood circulating, we must conclude that it does so by the contractility of the vessels, since there is no central propelling organ.

I have mentioned above the arguments which exist against the view that the function of respiration is carried on either by the tentacles of the lophophore, or by the papillae of the shell. I believe that respiration takes place in the mantle lining the shell, especially the perforate shell where a large area is constantly exposed to the currents of water which are set up by the action of the ciliated tentacles. The mantle is penetrated by a network of vessels, in which the blood is separated only by a very delicate sheet of tissue from the water, and I believe there cannot be much doubt that the amount of oxygen required by such a very inactive animal as *Argiope* can thus be easily obtained. This view is also supported by the fact that in *Lingula* respiration is carried on by the inner lining of the mantle which bears the well known respiratory ampullae.

The muscles of *Argiope* consist of four pairs; of these two pairs are connected with the movement of the shell upon the stalk, the other two with closing and opening the shell. Each of these last is composed of two parts and is usually considered to represent two distinct muscles, thus making the number six, which number was described by HANCOCK as typical of the Testicardinate Brachiopods. In describing the muscles I have adopted the nomenclature proposed by HANCOCK. Of the two pairs of adjustors which are both inserted into the peduncle, one pair arises from each shell (fig. 12 *d.ad.* and *v.ad.*). The pair arising from the dorsal shell has its origin opposite the commencement of the intestine, and the muscles of this pair are close to each other, one on each side of the median line; they pass down and are inserted by a tendinous cord which passes directly into the substance of the stalk. The adjustors of the other shell have their point of origin a little nearer the posterior border of the shell and area rather larger, they also are inserted into the stalk in a similar manner. The principal function of these muscles is without doubt to raise and lower the animal upon its stalk. HANCOCK suggests that they also serve to rotate the animal by the muscles of each side alternately contracting, but as the origins of the muscles are so close to one another and also their insertions, and as the muscles are parallel, I do not think this suggestion very pro-

bable, as far as Argiope is concerned. The oclusor muscles have two points of origin upon each side of the median line of the dorsal shell, one in front of the other. They correspond with the two parts of the muscle which were termed by HANCOCK the oclusor anterior and posterior. Their origin is external to that of the adjustor muscles, and their anterior limit passes far into the two anterior lateral divisions of the body cavity formed by the septum (fig. 12 *oc.m.*). The muscles of each side which are at first quite distinct soon unite into a common tendon which takes an obliquely downward direction, passing close under the central nervous system; and here it is connected with the homogeneous substance supporting the chief ganglion on each side of the oesophagus, and is inserted by an expanded extremity in the ventral shell just to one side of the median ridge. The insertion is a little anterior to the posterior limit of the intestine which lies between the two tendons. The division into two parts, of the divaricators, is much less marked than is the case with the oclusors. These muscles arise, one upon each side of the median line in the posterior part of the ventral shell, a little behind the insertion of the oclusors, they pass straight across and their tendons are inserted into the most posterior part of the dorsal valve in the middle line (fig. 12 *d.m.*). The axis upon which the shell turns passes through the teeth and sockets mentioned in the description of the shell, and this lies in front of the insertion of the divaricator muscles; hence a contraction of these muscles has the effect of opening the shell.

In Argiope all the muscles are unstriated. The fibres are somewhat flattened or oval in transverse section; they are quite free from each other; there appears to be no interfibrillar substance; and they stretch the whole length from their origin till they fuse with the tendon. A transverse section through their point of origin shews that the fibres arise in regular rows, the long diameter of the section of each fibre in one row making an obtuse angle with that of the neighbouring fibre in the next row. An oval nucleus lies upon some part of the length of each fibre. At the point where the muscle arises from the shell there seems to be a special development of the homogeneous supporting substance mentioned in the description of the lophophore. The muscle fibres after a longer or shorter course all pass into a tendon, which in the fresh state is white and glistening. In section the tendons appear homogeneous or faintly striated in the longitudinal direction: they either end in the stalk which is composed of a similar tissue, or in the homogeneous supporting substance which is developed at some places in the body wall, and which histologically very much resembles the tendon.

HANCOCK in his great work on the Brachiopoda states that all the muscles are unstriated with the exception of the posterior Ocluser, which is striated. This is confirmed by VAN BEMMELEN who suggests that in this arrangement of a muscle with a double origin (the fibres of one part being striated, and of the other unstriated) and a single insertion, we find a provision for the voluntary and involuntary closure of the shell. In *Argiope* I can see no trace of striation in the posterior half of the Ocluser muscle which exactly resembles the remaining muscles.

The peduncle of *Argiope* appears to be an unusually large development of the homogeneous supporting substance which occurs so frequently in the body of Brachiopoda. It is in close organic connection with both shells (fig. 1 *P*) and its free end is very irregular, being produced into papillae, which enter any depressions occurring on the rock upon which the animal lives. Externally it is coated by a layer of cuticle, within this is a layer of cells, the epidermis. The remainder of the peduncle consists of the homogeneous basement which stains well, and which contains three different elements. The first of these are a number of branched, granular, nucleated cells whose branches form a network in which the supporting substance lies. The second consists of numerous fibres which take a longitudinal course in the centre of the stalk; their lower end is very fine, and is often crumpled as if the stalk had shortened. The remaining structures met with in the stalk consist of some very peculiar oval bodies, these seem to be crammed with round cells somewhat resembling the blood corpuscles. These bodies are often connected with the lower end of a fibre. They are irregularly distributed but occur chiefly near the circumference. It is possible that they are connected with the secretion of the cement which glues the *Argiope* to its support.

Owing to the small size of *Argiope*, it is impossible to dissect out the nervous system, so I have been obliged to study it solely by means of sections. The central nervous ganglion is sub-oesophageal and lies in the epidermis. It is situated in that part of the body wall which lies immediately posterior to the base of the tentacles which overhang the mouth (fig. 1 *sg*) just where the body wall turns forward to form the mantle lining the ventral shell. The ganglion consists of two parts. The anterior is a well marked elevation, formed by a ridge of the homogeneous supporting substance, so often mentioned, which is covered by a layer of nervous cells and fibres. The posterior is simply a narrow band of nervous tissue, not very conspicuous. The ganglion extends the whole breadth of the body wall, which in this situation is not very great, having

been reduced by the lateral invaginations which form the brood pouches. The posterior band of nervous cells gives off a branch on each side which passes to supply the oclussor muscles, entering them where their tendon has fused with the supporting substance beneath the ganglion; it also gives off laterally two branches which pass to the mantle of the ventral shell. The main ganglion gives off two branches which enter the lophophore, one on each side, and which, I believe, run entirely round the edge of the lophophore beneath the ciliated epithelium cushion at the base of the tentacles, thus forming a circum-oesophageal ring. At each end the principal ganglion divides into two branches; one of these passes backward in the body wall in the line of attachment of the gastro-parietal band into which some small branches pass. The other branch circumscribes the oesophagus, the nerves being imbedded in the supporting substance of the lophophore, above the oesophagus they come to the surface again and enter an elongated ganglion which lies in the ectoderm just anterior to the base of the lip which overshadows the mouth. This ganglion is very small in comparison with the sub-oesophageal.

The ganglion consists chiefly of unipolar ganglion cells whose processes pass into the long fine fibres which compose the nerves.

The nerve cells lie upon a thick cushion of supporting substance and the nerves are very usually imbedded in the same tissue.

VAN BEMMELEN also describes a nerve which coming from the supra-oesophageal ganglion, also supplies the lophophore. I have not been able to find this branch in *Argiope*.

Although I have not been so fortunate as to find a male *Argiope*, yet I have no doubt that this genus like the other members of its class which have been described, is dioecious. In those *Argiopes* which I have examined, I find no trace of a testis, and in the allied genera *Thecidium*, LACAZE-DUTHIERS¹ describes the male genital gland in a position similar to that occupied by the ovary in *Argiope*, and I have myself seen the testes of *Megerlea* in the same position.

The ovaries of *Argiope* are of a bright brick red color resembling the red rays on the shell of *Argiope cuneata*. There are found two lying in the body cavity of the dorsal shell and two in that part of the body cavity which is produced into the mantle lining the ventral shell. The latter pair are not always developed in *Argiope neapolitana*. The ovaries of the dorsal shell are at their anterior end enclosed on one side by the body wall lining the shell and on the other by a mesentery which is

¹ Histoire de la Thécidie. Annales des Sciences Naturelles. 4^{me} Sér. T. XV. 1861.

attached at both ends to the body wall (fig. 4 *ov*), but a little below the origin of the adjustor muscles and the entrance of the liver into the stomach; this membrane becomes broader, its inner end becomes attached to the lateral walls of the stomach, its outer to the line of attachment of the lophophore and thus it forms the gastro-parietal band. This as was mentioned above divides the body cavity into two halves, in the ventral half the liver lies, in the other the ovaries and the greater part of the muscles. The two halves communicate below. The ovaries of the ventral shell lie, one in each half of the body cavity, which is here divided into two lateral portions by the presence of the median ridge spoken of in the description of the shell. These parts of the body cavity communicate with each other and with the remainder, at the posterior extremity.

Each ovary appears to be formed of a membrane continuous with the body wall: this bears on each side a number of ova which vary greatly in size. The membrane is covered with epithelium continuous with that of the body cavity, except where the ova occur and these seem to be as VAN BEMMELEN suggests modified epithelium cells. Each ovum is surrounded by a very delicate capsule in which nuclei occur. At the most anterior end the ova are very small, but gradually become larger as they approach the posterior; they are usually more or less round unless they exist in great numbers when they become angular by mutual pressure. They are very granular and stain well except the nucleus which only stains faintly or not at all, the nucleolus again staining deeply. Both these structures are very large, the nucleolus being sometimes of such a size that the nucleus assumes the shape of a new moon.

When the eggs are ripe they drop off into the body cavity, the capsule apparently bursting. In the body cavity they are taken up by the inner end of the oviduct and thus pass into the brood pouch.

The oviducts open internally by a funnel shaped mouth which looks towards the dorsal shell (fig. 8 *od*). The outer lip of the mouth is continuous with that part of the body wall which forms the inner boundary of the brood pouch, the inner lip is bent towards the middle line and is continuous with a connective tissue band which passes to support the posterior end of the intestine. This represents the ileo-parietal band of HUXLEY; it is very slight. The oviduct then runs round the ventral wall of the brood pouch and opens into this pouch by a small mouth close under the posterior border of the lophophore.

The walls of the oviducts consist of a connective tissue basement, lined by glandular cells which contain brown concretions; hence it is very probable that they act as secretory organs in addition to their

function of discharging the eggs. The lining layer of cells is ciliated. The cilia of the funnel take up the eggs which also pass along the oviducts by the action of cilia and then enter the brood pouch where the early stages of their development up to the formation of the free swimming larva take place.

The brood pouches (figs. 2, 7, and 8, *bd, p*) are invaginations of the lateral body wall; they lie behind the posterior border of the lophophore. A similar pouch, in which the eggs undergo their early development, is described by LACAZE-DUTHIERS in *Thecidium*, but here it is median and unpaired.

MORSE¹ has described in *Terebratulina* the escape of the egg from the mother, but he is not certain whether fertilization takes place before or after this occurrence. In *Argiope* it must of course take place while the egg is still connected with the mother, but it is doubtful whether in the brood pouch or in the body cavity, but the facts that the outer opening of the oviduct is very small and that the cilia work outwards, point to the former place. Brachiopods generally live together in colonies and the spermatozoa are probably discharged by the male into the water, and some of them reach the female in the streams of water set up by the ciliated tentacles.

When taken out of the brood pouch the eggs and young embryos only live a few hours, so that one's observations were necessarily confined to these stages which were existing in the *Argiope* at the time the shell was opened. To render these observations complete required a greater quantity of material than was at my disposal.

Like KOWALEVSKY², I have unfortunately not succeeded in seeing the segmentation of the egg, however once I found two ova which had divided into two segments, and one of the cells of one of them showed traces of a secondary division (figs. 21 and 22). The next stage consisted of a blastosphere; the cells here like those of the egg and of the embryos are crowded with granules, of a deep brick red color and very small. These characters render it very difficult to observe the outlines of the cells or their nuclei.

The cells at first are very cylindrical and the segmentation cavity consequently small, but when the blastosphere is mounted in glycerine,

¹ Embryology of *Terebratulina*. Memoirs of the Boston Society of Natural History. Vol. II.

² Observations on the Development of Brachiopoda. Moscow 1874. — Also: Observations sur le Développement des Brachiopodes. Analyse par M. M. OEHLERT et DENIKER. Archives de Zoologie Expérimentale et Générale. 2^{me} Sér. Tome I.

the cells become flatter with a better defined outline, and soon they break from one another and then have an oval form with a large nucleus (fig. 23).

The blastosphere becomes slightly flattened at one pole and here an invagination takes place (fig. 24). The invaginated layer forms three cavities, namely in the centre the mesenteron, and two lateral cavities which form the future body cavity. The cavity of the mesenteron is small and that of the body is very small. The blastopore closes, it is nearer the anterior than the posterior end of the embryo, but whether dorsal or ventral, I could not determine. The three cavities formed by the invaginated layer at first communicate at the end near the blastopore, they subsequently become shut off from one another. The central cavity forms the alimentary canal; throughout the larval life it is without a mouth or anus. The walls of the two lateral cavities form the muscles and other mesoblastic structures; the splanchnic and somatic walls are frequently in contact so that the body cavity is obliterated in many places, the latter does not become spacious till the adult condition is attained. The mesentery is formed by the approximation of the mesoblastic walls, before and behind the digestive tube; in the latter situation it must be subsequently absorbed as it is not present in the adult *Argiope*, although a dorsal mesentery is found in *Waldheimia* and *Rhynchonella*.

While these internal changes have been going on the embryo has divided into two segments. The anterior is connected with the walls of the brood pouch by a fine filament, and it remains so until the free swimming larva is ready to leave the mother (fig. 25).

Soon after the appearance of two segments, the anterior is again transversely constricted, and the larva now consists of three segments, the posterior being somewhat longer and narrower than the other two (figs. 26). About the same time four eye-spots appear on the anterior segment, these are minute aggregations of cells of a deep red color; the pigment spots are symmetrically arranged. The number is typically four, but in rare cases six eye-spots are present. Soon after the first appearance of the second segment, four bundles of small bristles appear on its edge.

Fig. 33 represents a longitudinal section through a larva shortly after the appearance of the second segment. It will be seen that this second segment is produced by a fold of the epiblast which extends round the whole larva; this contains near its edge a small spherical collection of mesoblast cells, which secrete the setae. This fold of epiblast soon commences to grow down over the posterior segment, it con-

sists of two layers of epiblast which are in contact except just at the edge where in four places of the circumference they are separated by the collection of cells secreting the setae. The outer layer of the fold consists of flat epithelial cells, the inner like the cells covering the third segment, of columnar cells (figs. 34 and 35). The alimentary canal extends through all three segments, the mesoblast lies between this canal and the epiblast, in many places its walls are in contact, but at the posterior end a small part of the body cavity is seen (fig. 33 *bc*). On the dorsal side the alimentary canal lies directly against the epiblast, the mesoblast has not yet grown in between them (fig. 34). This larva gradually becomes the free swimming »umbrella« larva by the following changes: the anterior segment becomes more and more constricted off from the remainder of the body, till it is only connected by a comparatively fine stalk; this gives it great freedom of movement. Its shape also alters considerably, assuming the shape of umbrella and is covered all over with very fine cilia; round the edge it bears a row of very large, powerful cilia which until the animal begins its free swimming existence, lie against the upper side of the head (fig. 29 and 30). The four eye-spots lie on the anterior end, those on the ventral side being slightly more posterior and slightly farther apart than the two others. The part of this segment bearing the eye-spots appears to correspond with the anterior segment of Thecidium as described by LACAZE-DUTHIERS. The folds which are formed by the second »segment« grow down over the third, until the latter is almost completely enclosed. Upon one side, which is, I believe, the ventral, the fold comes further than on the other sides and laterally it does not come quite so far as in front or behind. Thus the edge of the fold forms two bays laterally upon the sides of which the setae are carried. The setae have by this time grown to such a length, that when they lie in their natural position, pointing towards the axis of the larva, they completely cover in the posterior end of the third »segment«. They are pointed and each bundle has from fifteen to twenty setae (figs. 28 to 30).

That portion of the third segment which is uncovered by the fold of the second, now becomes marked off by a constriction, and soon within the epiblastic layer of cells, a small mass of the homogeneous supporting substance begins to appear (fig. 28 and 35 *IV*). This will form the stalk of the adult animal. KOWALEVSKY has figured the posterior »segment« as coated with cilia, I have not been able to see these.

The internal changes consist of the formation of two lateral bundles of muscle fibres at the expense of the mesoblastic cells (figs. 34 and

35 *mf*), these run from the small mass of homogeneous substance at the posterior end of the larva to the origin of the fold; some fibres also pass down between the two layers of the fold and are inserted into the oval mass of cells which secrete the setae. These muscles probably become the adjustors of the adult.

In the head segment, into which the alimentary canal extends but a very slight distance, there is a small clump of cells, without the large granules characteristic of the other cells: this may possibly be a nerve ganglion (fig. 35 *l, g*).

When the larva has reached the stage just described, the filament connecting it with the walls of the brood pouch breaks, and the larva escapes from the shell of the mother. In the water it swims rapidly to and fro, by the aid of the cilia, especially those long ones upon the edge of the anterior segment, sometimes it stops and revolves rapidly on its long axis. Frequently it stands on its head for a considerable length of time. It is extremely contractile and seldom retains the same shape for any length of time; its head segment is turned rapidly from side to side, and on approaching any object, the body is often much shortened and the setae are protruded in every direction. The length of the free swimming larva fully extended is about $\frac{1}{3}$ mm, though it frequently contracts to $\frac{2}{3}$ of this.

The setae have probably a defensive function; the color is also probably protective: when the larvae are fixed upon a piece of red coralline upon which they usually come to rest, it is very difficult to distinguish them.

After swimming about for a few hours the larva fixes itself on a piece of rock or some other object, by means of a secretion apparently supplied by the posterior segment.

I have not been able to follow the metamorphosis of the larva into the adult; the following description is taken from KOWALEVSKY's article mentioned above.

When the larva is fixed, the fold which previously covered the third »segment« gradually turns forward and grows over the head »segment«; so that the columnar cells previously inside become the outer layer. This fold forms the mantle and it begins to secrete the shell. The head becomes spherical, and the eyes persist. The digestive canal becomes round and is produced into the head segment, this part probably forming the oesophagus. The lophophore begins to appear as four projections directed inwards, on a thickening of the dorsal lobe of the mantle near its border. This thickening soon takes the form of a ridge;

the number of tentacles gradually increase to ten. The setae drop off though in some cases they disappear before this stage is reached. The youngest Argiope I have seen is represented in fig. 31. Here the number of tentacles has increased to twelve, the head »segment« has disappeared and with it the eyespots, two lateral diverticula of the stomach have appeared to form the liver, the body cavity is still entirely filled up by the viscera, the shells have already attained a considerable size and are pierced by about twenty canals. The lophophore has still the form of a complete circle, the median indentation has not yet appeared, the tentacles all point to the centre of the circle. The mouth appears by an invagination. The later stages are unimportant.

From this description it will be seen that there is in Argiope no median dorsal tentacle such as BROOKS¹ has described in the Development of Lingula.

Since the view that Brachiopoda must be classed with Molluscs, has been abandoned we have had four views put forward upon the affinities of this class. MORSE² and KOWALEVSKY have independantly maintained that Brachiopoda form an order of Vermes closely allied to the Chaetopoda. BROOKS has adopted the view which was put forward by HUXLEY and HANCOCK of the relation between Brachiopoda and Polyzoa, and he considers the latter to possess points of resemblance with the Veliger larva of Molluscs. VAN BEMMELEN has urged, partly upon histological grounds their relationship with Chaetognatha. Finally CALDWELL³ in a very suggestive paper appears to class Polyzoa and Brachiopoda with Phoronis, and he publishes two diagrams which represent the body plan of these three forms.

MORSE has given in parallel columns a list of the resemblances existing between Brachiopods and Chaetopods, but as BROOKS has already pointed out, many of these points of resemblance are superficial while the remainder apply equally to other classes such as Molluscs, Echinoderms, Ascidians.

KOWALEVSKY's chief arguments for placing Brachiopoda among the Vermes, is the so-called segmentation of the larva, and the presence

¹ On the Development of Lingula. Chesapeake Zoological Laboratory. Scientific Results of the Session 1878. Baltimore. — Also: Archives de Zoologie Expérimentale et Générale. T. VIII. 1879—1880.

² On the systematic Position of the Brachiopoda. Boston 1873.

³ Preliminary Note on the Structure, Development, and Affinities of Phoronis. Proc. of the Royal Society. 1882.

of setae. I do not consider the »segments« of the larva to have the value of true metameres, they are simply the result of the formation of the shell from the central region of the body, thus necessarily dividing the body into three parts, viz., one lying before the shell-forming region, the shell-forming region itself, and a third part posterior to it. In the larva there is no trace of segmentation of the mesoderm, and none of the organs shew the least trace of serial repetition; and with the exception of the second pair of oviducts in *Rhynchonella* there is no trace of segmentation in any adult Brachiopod. BALFOUR has already pointed out that the formation of the segments at the cephalic end of the body, as in Cestodes »renders it probable that they are not identical with the segments of a Chaetopod«. The larva differs from the characteristic Chaetopod larva in the following particulars. 1) The alimentary canal is not curved, nor divided into three regions, neither mouth nor anus is present; 2) the body cavity is but very slightly developed, it is not traversed by muscular strands, there is no connection between the nerve ganglion and the alimentary canal; 3) there is no provisional renal organ.

Finally as is shewn in fig. 35 we must consider the full grown larva of *Argiope* to consist of four regions and not of three like the larva of a Chaetopod, and these four regions do not correspond with the four described by LACAZE-DUTHIERS in the larval Thecidium.

In the adult structure there is no resemblance in any system of organs between the two classes except the possession of setae, but these structures are not confined exclusively to the two classes in question.

BROOKS in his article upon the development of *Lingula*, has upheld the relationship between Brachiopoda and Polyzoa, which was urged by both HUXLEY and HANCOCK.

The most striking points of resemblance in the adult anatomy are the position of the chief nervous system and the possession of a lophophore. With regard to the first point, the nervous system of both classes consists like that of the majority of Invertebrates of a circum-oesophageal nerve ring upon which nerve ganglia are developed, the point of resemblance lying in the fact that the sub-oesophageal ganglion of Brachiopods is larger than the supra-oesophageal, while in the Polyzoa the latter is not developed or only to a very slight extent. The characteristic position of the chief nerve ganglia of Brachiopoda which remain in the ectoderm has no parallel in Polyzoa.

BALFOUR has in his Comparative Embryology already pointed out that the homology of the lophophores »is rendered very doubtful (1) by

the fact that the lophophore is prae-oral in Polyzoa and post-oral in Brachiopoda; and (2) by the fact that the concave side of the lophophore is turned in nearly opposite directions in the two forms«. The abstractors of KOWALEVSKY's article in the Archives de Zoologie are at some pains to show that BALFOUR's statement concerning the situation of the lophophore is incorrect. BALFOUR surmises that the ring of tentacles forming the lophophore »is possibly derived from the ciliated ring« of the larva, since he considers that the origin as stated KOWALEVSKY« does not fit in with the adult anatomy of the parts. It is difficult to understand how the lophophore does grow down over the body, but KOWALEVSKY's observation on the Testicardines are in a measure supported by those of BROOKS upon Lingula, who states that in a stage with eleven tentacles the plane of the lophophore is still almost parallel with that of the mantle lobes. BALFOUR acting upon his supposition states that the lophophore is post-oral, and although his idea as to the origin is incorrect still the lophophore remains a post-oral structure in as much as it is derived from a part of the body which is developed behind the mouth, although it subsequently turns forward.

With regard to the larval resemblances, there seem to be no points in common between the two classes; which they do not also possess in common with some other groups.

If we compare a free swimming Brachiopod larva with a free swimming Polyzoon larva, such as HATSCHEK has figured in his development of Pedicellina, which is probably more primitive than that of an Ectopreous form, we see that almost the only point of resemblance is the ciliated ring which occurs so widely amongst free swimming larvae. While the organs in which the respective larvae differ are numerous and striking, in one case the alimentary canal is curved and provided with mouth and anus which both open within the ciliated ring, in the other case it is straight without mouth or anus; again in the Polyzoon larva there is a well developed pair of excretory organs, in the Brachiopod there are none; then there is the hypothetical »dorsal organ« which HATSCHEK suggests is a bud, and which has no parallel in the Brachiopod larva; finally the Polyzoon larvae become fixed by their prae-oral extremity, the Brachiopods by their aboral extremity¹.

VAN BEMMELEN who is the first observer to study the structure of Brachiopods by modern methods, and whose article has been so fre-

¹ J. BARROIS. Métamorphoses des Bryozoaires. Annales des Sciences Naturelles, Zoologie. T. IX. 1879—80.

quently quoted above, begins his comparison between Brachiopoda and Chaetognatha with an enumeration of the histological resemblances. These have I believe but a very secondary classificatory value unless taken in conjunction with other morphological resemblances, and these are not very striking. The formation of the mesoblast is the same, but a similar formation of the middle layer is found in such diverse groups as Echinodermata, Enteropneusta, Chordata, and probably also in Peripatus.

The comparison between the three divisions of a Sagitta and the three divisions of a larval Brachiopod does not hold, since as was pointed out above, the larva really consists of four segments. VAN BEMMELEN states that this segmentation is indicated in the adult, by the gastro- and ileo-parietal bands, which are to be regarded as dissepiments; but this cannot be so, since these mesenteries are parallel with the antero-posterior axes of the body and intestine and not transverse to them. The comparison between the vasa deferentia and the segmental organs is a just one, but segmental organs of fundamentally the same type are very widely distributed throughout the animal kingdom. The same arguments apply to the dorsal and ventral mesentery, and to the nervous system which in both classes consists of a circum-oesophageal nerve ring bearing a supra- and sub-oesophageal ganglion with two large nerves springing from the latter.

Finally in Sagitta we find no representatives of the lophophore, shell, or stalk, which structures are all eminently characteristic of the Brachiopoda.

Recently CALDWELL has in a Preliminary Note on Phoronis urged »an entirely new view of the homologies of the body surfaces« in Brachiopoda. It is of course impossible to criticize this view fully, until the complete paper appears: at the same time I should like to point out that the facts mentioned above do not warrant the statements that »Brachiopoda are fixed by their ventral surface« and that »both valves of the shell are ventral«. These views of the body surfaces seem to be founded more upon a comparison instituted between Brachiopoda and Phoronis, than upon direct observation of the development of the former group. Furthermore in the Brachiopods that I have examined, I have found no trace of the persistence of the prae-oral lobe in the form of an epistome. The prae-oral lobe appears to disappear utterly. Finally the internal opening of the segmental organ lies upon the other side of the lateral mesentery *lm* in CALDWELL's diagram B.

In conclusion, I would say, that I do not consider the Brachiopoda

and Polyzoa so closely united as to form a natural phylum. I should propose to follow GEGENBAUR in making a primary class of the Brachiopoda, and though in their development and adult structure they are widely separated from both Vermes and Mollusca, of the two classes I would place them nearer to the former class than to the latter.

Naples, July 1883.

Description of Plates 39 and 40.

- alc* Alimentary Canal.
- bc* Body cavity.
- bdp* Brood pouch.
- br* Bristles.
- brc* Bristle-forming cells.
- bv* Blood vessel.
- ca* Canal running round the edge of the lophophore.
- cu* Cuticle.
- dad* Dorsal adjustor muscle.
- dm* Divaricator muscle.
- ds* Dorsal shell.
- e* Eye spots.
- em* Embryo.
- ep* Epiblast.
- gp* Gastroparietal band.
- hy* Hypoblast.
- in* Intestine.
- l* Lip of lophophore.
- lg* Larval ganglion.
- li* Liver.
- lo* Lophophore.
- m* Mesentery.
- mf* Muscle fibres.
- mo* Mouth.
- mp* Mantle papilla.
- ms* Mesoderm.
- ocm* Oclusor muscle.
- od* Oviduct.
- oe* Oesophagus.
- ov* Ovary.
- P* Peduncle.
- sg* Sub-oesophageal ganglion.
- sk* Skeleton supporting the lophophore.
- sm* Septum.

- st* Stomach.
sta Stalk connecting embryo with walls of brood pouch.
t Tentacle.
tr Triangular area.
vad Ventral adjustor muscle.
vr Ventral ridge.
vs Ventral shell.
I First larval segment.
II Second larval segment.
III Third larval segment.
IV Fourth larval segment.

- Fig. 1. A longitudinal median section through *Argiope neapolitana*, showing the form of the alimentary canal and its relation to the dorsal shell and septum. The peduncle and the sub-oesophageal ganglion are also shown. In this figure only the cuticle is drawn.
- Fig. 2. A longitudinal section of *A. neapolitana* taken about a quarter of the breadth from the side. This shows the attachment of the lophophore to the dorsal shell and to the internal skeleton, also the lateral invagination to form the brood pouch. The gastro-parietal band, the ovary, the ocluser and ventral adjustor muscles, and some branches of the liver are also seen. ZEISS a. a. Camera lucida.
- Fig. 3. A transverse section of *A. neapolitana* near the anterior end. This shows the two dorsal extensions of the body cavity separated by the dorsal septum, containing some branches of the liver. ZEISS a. a. Cam. luc.
- Fig. 4. A transverse section of the same, just behind the posterior border of of the septum, showing the oesophagus, liver and dorsal ovaries. The body cavity of the ventral shell is just commencing to appear, it contains the ventral adjustor muscle. ZEISS a. a. Cam. luc.
- Fig. 5. A transverse section of the same, more posterior. Here the entrance of the liver into the stomach is seen, and the strands connecting the alimentary canal with the ventral body wall; these fuse more posteriorly to form the mesentery. ZEISS a. a. Cam. luc.
- Fig. 6. A transverse section more posterior. Here the gastro-parietal band is seen, also the ovaries in the body cavity of the ventral shell. ZEISS a. a. Cam. luc.
- Fig. 7. This section still more posterior is cut slightly obliquely. It shows the lateral invaginations to form the brood pouch. On the left side, the body cavity of each shell is continuous, on the right, it is shut off by the growth of the lophophore. ZEISS a. a. Cam. luc.
- Fig. 8. A transverse section a little anterior to the peduncle. The posterior extensions of the brood pouches are seen and the inner funnel shaped openings of the oviducts, also the posterior end of the intestine. ZEISS a. a. Cam. luc.
- Fig. 9. *Argiope neapolitana*. Magnified about 4 times linear.
- Fig. 10. *Argiope cuneata*. Magnified about 4 times linear.
- Fig. 11. Semi-diagrammatic figure of the body of an *Argiope* lying in the dorsal shell, to show the form and relations of the lophophore. Some branches

of the liver and the ovaries can be seen through the semi-transparent disk of the lophophore.

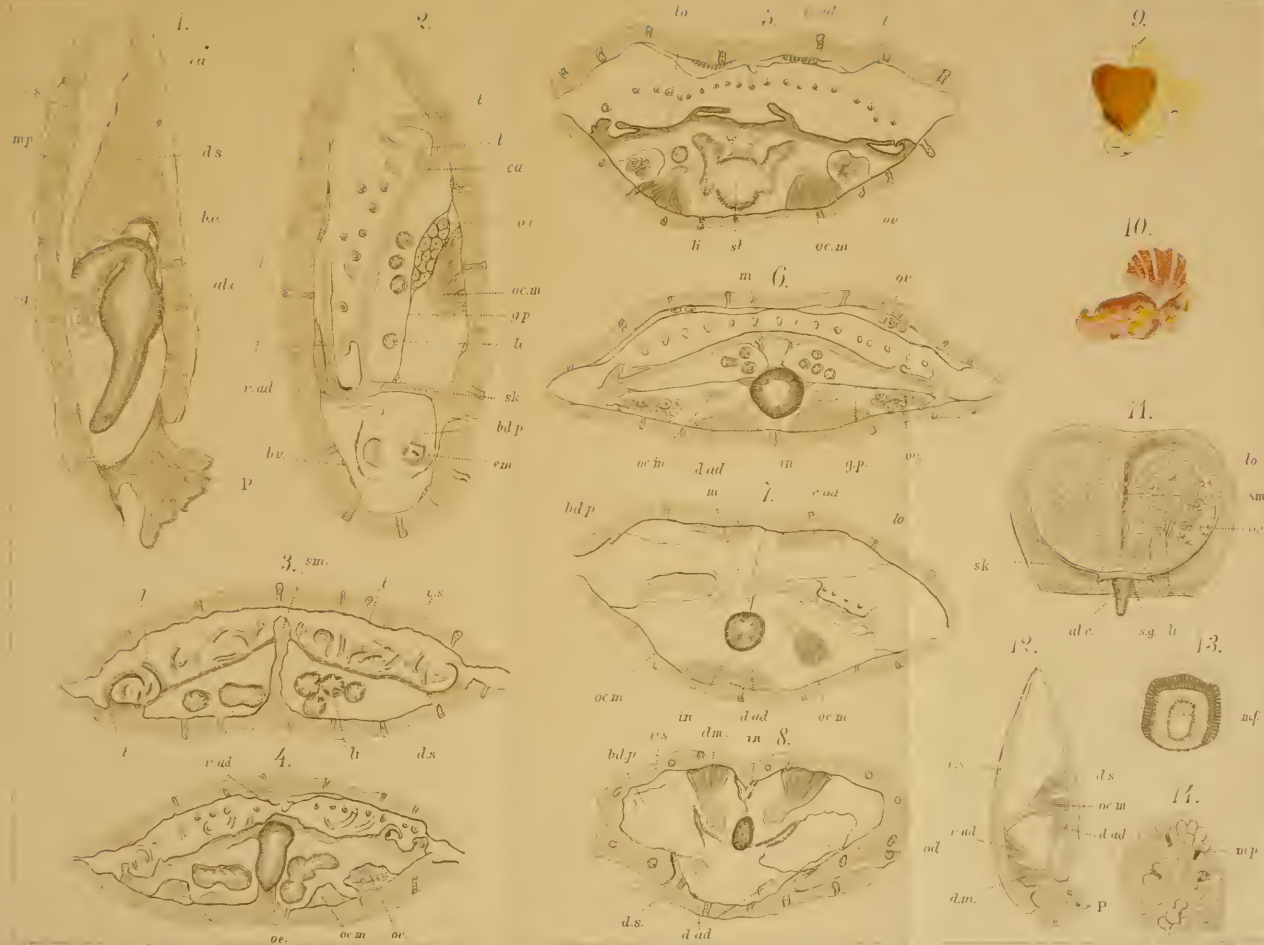
- Fig. 12. Diagrammatic view of the muscles of *Argiope*.
- Fig. 13. Section of a single tentacle showing the ciliated epithelium on three sides, and the central canal containing muscle fibres. ZEISS F.
- Fig. 14. View of the rounded inner ends of the calcareous spicules of the shell, with some mantle papillae. ZEISS A.
- Fig. 15. A section through the point of attachment of the lophophore to the mantle lining the dorsal shell. The mantle papillae are seen piercing the shell and are connected with cuticle upon the outer side. The ciliated groove formed by the lip and the tentacles is shown and the cushion of high epithelium cells. In this section the communication between the canal running round the edge of the lophophore and the canal in the tentacle is not shown.
- Fig. 16. View of the interior of the dorsal shell of an *Argiope neapolitana*, to show the arrangement of the internal skeleton supporting the lophophore.
- Fig. 17. View of interior of ventral shell of the same, showing the median ridge, and the triangular areas whose apices fit into notches in the dorsal shell and so form the hinge.
- Fig. 18. Lateral view of dorsal shell.
- Fig. 19. View of the organic fibres, in whose meshes the calcareous spicules of the shell lie.
- Fig. 20. Ovum.
- Fig. 21. Ovum of two segments.
- Fig. 22. Ovum of three segments.
- Fig. 23. Blastosphere; by the side are some cells of the blastosphere more highly magnified.
- Fig. 24. Gastrula.
- Fig. 25. Larva of two segments showing the stalk attaching it to the walls of the brood pouch.
- Fig. 26. Larva showing traces of three segments with eyespot and commencing bristles. The outline of the alimentary canal is seen faintly.
- Fig. 27. Slightly older larva.
- Fig. 28. Larva with the two kinds of cilia on the first segment. The second segment has already begun to grow down over the third which has constricted slightly into two parts.
- Fig. 29. Free swimming larva seen from the ventral side.
- Fig. 30. Free swimming larva seen laterally.
- Fig. 31. Young *Argiope*, the lophophore still circular, with twelve tentacles. The liver is growing out as two lateral diverticula of the stomach.
- Fig. 32. View of the ventral shell of the same.
- Fig. 33. Longitudinal section through a larva of about the same stage as fig. 27. This shows the alimentary canal extending through all the segments.

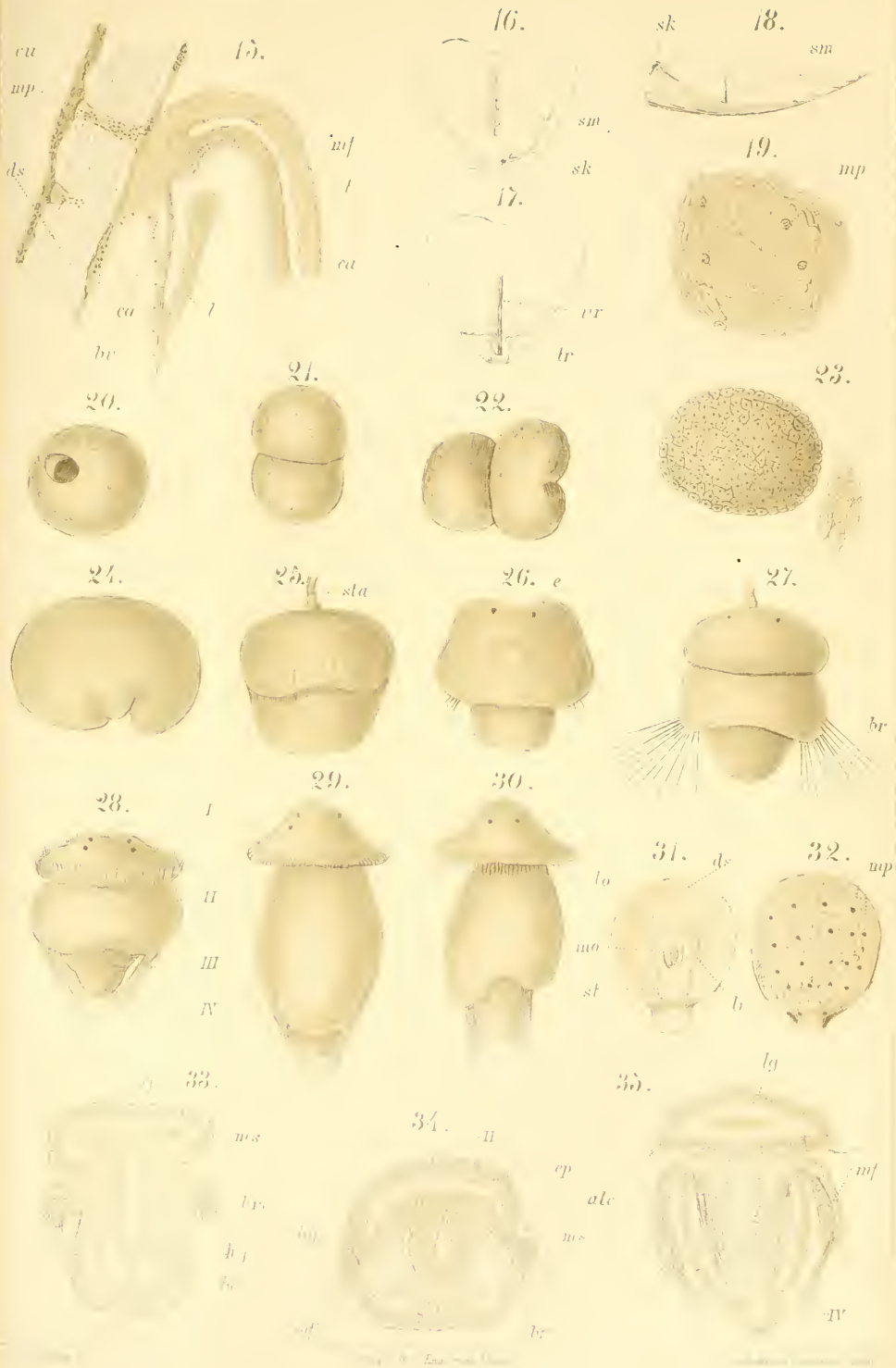
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The second segment is beginning to grow down over the third, it bears at its edge a cluster of cells which secrete the bristles.

Fig. 34. A transverse section through a somewhat later stage, this is cut somewhat obliquely. Above the fold of epiblast forming the second segment is seen. The alimentary canal lying near the dorsal wall, the bristle-forming cells, and some muscle fibres are also shown.

Fig. 35. A longitudinal section through a free swimming larva. Here the anterior segment is much constricted off from the others, posteriorly a portion is also separated off to form the future peduncle, muscles run from this to the base of the fold formed by the second segment, and some fibres pass to the bristles.





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