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Liverpool Marine Biology Committee.

*L.M.B.C. MEMOIRS*

*ON TYPICAL BRITISH MARINE PLANTS & ANIMALS*

*EDITED BY W. A. HERDMAN, D.Sc., F.R.S.*

II.

CARDIUM

BY

J. JOHNSTONE,

*Fisheries Assistant, University College, Liverpool*

(With 7 Plates)

PRICE TWO SHILLINGS

LIVERPOOL

T. DOBB & CO., PRINTERS, 229 BROWNLOW HILL

DECEMBER, 1899

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*L.M.B.C. MEMOIRS*

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II.

CARDIUM

## NOTICE.

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The Memoirs may be obtained, post free at the nett prices stated, from the Hon. Treasurer, Mr. I. C. THOMPSON, 53, Croxteth Road, Liverpool; Prof. HERDMAN, University College, Liverpool; or the CURATOR, Biological Station, Port Erin, Isle of Man.

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## EDITOR'S PREFACE.

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THE Liverpool Marine Biology Committee was constituted in 1886, with the object of investigating the Fauna and Flora of the Irish Sea.

The dredging, trawling, and other collecting expeditions organised by the Committee have been carried on intermittently since that time, and a considerable amount of material, both published and unpublished, has been accumulated. Thirteen Annual Reports of the Committee and four volumes dealing with the "Fauna and Flora" have been issued. At an early stage of the investigations it became evident that a Biological Station or Laboratory on the sea-shore nearer the usual collecting grounds than Liverpool would be a material assistance in the work. Consequently the Committee, in 1887, established the Puffin Island Biological Station on the North Coast of Anglesey, and later on, in 1892, moved to the more commodious and convenient Station at Port Erin in the centre of the rich collecting grounds of the south end of the Isle of Man.

In our twelve years experience of a Biological Station (five years at Puffin Island and seven at Port Erin), where College students and young amateurs formed a large proportion of the workers, the want has been constantly felt of a series of detailed descriptions of the structure of certain common typical animals and plants, chosen as representatives of their groups, and dealt with by specialists. The same want has probably been felt in other similar institutions and in many College laboratories.

The objects of our Committee and of the workers at our Biological Station have hitherto been chiefly faunistic and speciological. The work must necessarily be so at first when opening up a new district. Some of our workers have published papers on morphological points, or on embryology and observations on life-histories and habits; but the majority of the papers in our volumes on the "Fauna and Flora of Liverpool Bay" have been, as was intended from the first, occupied with the names and characteristics and distribution of the many different kinds of marine plants and animals in our district. And this faunistic work will still go on. It is far from finished, and the Committee hope in the future to add greatly to the records of the Fauna and Flora. But the papers in the present series are quite distinct from these previous publications in name, in treatment, and in purpose. They will be called the "L.M.B.C. Memoirs," each will treat of one type, and they will be issued separately as they are ready, and will be obtainable Memoir by Memoir as they appear, or later bound up in convenient volumes. It is hoped that such a series of special studies, written by those who are thoroughly familiar with the forms of which they treat, will be found of value by students of Biology in our laboratories and in Marine Stations, and will be welcomed by many others working privately at Marine Natural History.

It is proposed that the forms selected should, as far as possible, be common L.M.B.C. (Irish Sea) animals and plants, of which no adequate account already exists in any text-book. Probably most of the specialists who have taken part in the L.M.B.C. work in the past, will prepare accounts of one or more representatives of their groups. The following have already promised their services, and in some cases the Memoir is already far advanced. The

first Memoir appeared in October, the second is now published, the third and fourth will be issued early in 1900, and others will follow, it is hoped, in rapid succession.

Memoir I. ASCIDIA, W. A. Herdman, 60 pp., 5 Pls., 1s. 6d.

II. CARDIUM, J. Johnstone, 92 pp , 7 Pls., 2s.

III. ECHINUS, H. C. Chadwick, ... pp., 3 Pls., 1s.

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ARENICOLA, J. H. Ashworth.

ANTEDON, H. C. Chadwick.

OYSTER, W. A. Herdman and J. T. Jenkins.

As announced in the preface to ASCIDIA, a donation from Mr. F. H. Gossage of Woolton has met the expense of preparing the plates in illustration of the first few Memoirs, and so has enabled the Committee to commence the publication of the series sooner than would otherwise have been possible.

W. A. HERDMAN.

University College, Liverpool,

December, 1899.



# L.M.B.C. MEMOIRS.

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## No. II. CARDIUM

(THE COCKLE).

BY

JAMES JOHNSTONE,

*Fisheries Assistant, University College, Liverpool.*

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THE edible cockle (*Cardium edule*) is by far the commonest member of the genus *Cardium*, a group of eulamelli-branchiate Mollusca having a world-wide distribution and containing a great number (about 200) of species. The number of British species is, however, limited to ten, most of which (*C. echinatum*, *C. fasciatum*, *C. edule*, *C. minimum*, *C. norvegicum*, *C. nodosum*) are recorded as being present in the Irish Sea; of these the only abundant species is *C. edule*; *C. norvegicum* (*Lævicardium*) is fairly common, the others being only occasionally found. The different species seem to have a fairly well-marked bathymetrical range, but *C. edule* is found from between tide marks out to 1360 fathoms. Here and over the greater part of Europe *C. edule* is the only species of any economic importance; in Jersey, however, *C. norvegicum* is used for food, and in the Mediterranean various other species are eaten.

The edible cockle is gregarious all along the coast line where suitable bottoms exist, but the great cockling beds

are, as a rule, found only in sheltered waters, in shallow bays, and at the mouths of estuaries. There is great constancy in the characters of the cockles from the various parts of the Lancashire and Cheshire coasts, no well-marked varieties being found. The difference in size observed in specimens from various parts of this district are most probably due to the extent to which the beds have been fished or disturbed in late years. Generally the influence of some fresh water\* seems to be favourable in that cockles are more abundant in the neighbourhood of the mouths of rivers, but the largest specimens are found only in areas far removed from the influence of fresh water. Large cockles, with shells two inches in length, are found on some parts of the North Coast of Devon, in Barra, in the Western Hebrides, and in the Scilly Isles. In Barra these large cockles are sufficiently numerous to form the material for an important fishery. Such giant forms are not found on the Lancashire coast, where the average length is about one and a half inches. Here the marketable cockle has a minimum breadth of  $\frac{3}{4}$  inch, the size being fixed by the Sea-Fisheries Committee's Bye-law. With the exercise of proper care on the part of fishermen to take only well-grown animals, there can be no doubt that the Lancashire and Cheshire cockle fisheries might be more largely developed, since the physical conditions are so suitable.

The cockle inhabits the topmost layer of the sand, burying itself to the depth of an inch at most. It lies in an oblique position, and, when the bed is covered with water, with the siphons projecting slightly above the surface.

\* The influence of extreme salinity or freshness, as might be expected, is to produce well-marked variations in the character of the shell. See Bateson, *Phil. Trans. Roy. Soc.*, vol. CLXXX. B., pp. 297—330, 1889; and Forbes and Hanley, *History of the British Mollusca*, 1850, vol. II., p. 21.

An exceptional habit has been noted by R. D. Darbishire\* when the cockles become anchored by the byssus threads of *Mytilus* and grow and develop freely in the water. Only on the posterior margin of the shell, from which the siphons protrude, are there any other attached animals or plants. Among these are green or brown Algæ (*Sphacelaria*), Zoophytes (*Obelia*), small anemones (*Actinia*), and rarely, barnacles (*Balanus*). In some places the cockles commonly bear a tuft of algæ, and the position of the animal in the sand can be determined by the presence of this projecting tuft. The animal, as a rule, remains in nearly the same position, but is able to shift about by means of the strongly developed muscular foot. Where the sand is not much disturbed by the tidal current, as round the stake of a net for instance, the cockles are generally more abundant.

A current of water continually entering the mantle cavity by the lower, and passing out again by the upper siphon, bears the food supply in the form of suspended microscopic animals and plants. The cockle feeds on spores and other young stages of lower algæ, fragments of filamentous algæ, vegetable debris, Foraminifera, Diatoms, and probably also the smaller micro-crustacea. The animal exercises no selective action on the food taken in; all that is contained in the entering current of water, including a large quantity of sand and suspended inorganic matter, is carried in by the cilia of the labial palps and passed on into the stomach. The greater part, therefore, of the contents of stomach and intestine is sand and fine mud.

The chief enemies of the cockle are fishes and birds. They also are eaten by starfish and bored by dog whelks. They form an important food for many fishes, chiefly

\* Fauna of Liverpool Bay. Report I., p. 241.



plaice and dab. There is said to be enormous destruction by the larger sea-birds. According to the fishermen who gave evidence to the Commissioners of 1879, the decrease in some cockle beds may be directly attributed to the increase in sea-gulls due to the operation of the Sea-Birds Preservation Act. Whole cockle beds may be destroyed by a hard frost or by an encroachment of sand.

At the beginning of the year the reproductive glands are nearly ripe, and spawning commences at the end of February or the beginning of March. The spawning period is prolonged, and ends about June or July. The reproductive glands then pass into the "spent" condition and after a short time begin to ripen again. Eggs and milt are shed freely into the water, where fertilisation and development go on. The minute larva swims freely in the water for some time, then settles down in the sand as a small shelled cockle.

After a detailed account of the anatomy of the cockle as a typical Lamellibranchiate Mollusc, an Appendix follows, containing an account of the animal from the economic aspect, with special reference to the cockle fisheries in the Lancashire Sea-Fisheries district.

#### THE SHELL.

As in the case of most Lamellibranchs, the shell is equivalve, that is, the two valves are precisely alike in shape; it is inequilateral, the straight central rib or groove on each valve dividing it into unequal anterior and posterior parts; as regards the form and relative proportion of the two parts so delimited, and the ratio of length to lateral breadth or depth, great variability is found. The number of ribs varies from 20 to 24. The external surface is marked by a series of fine concentric grooves and ridges indicating the growth of the shell margin. Some of these



grooves are very prominent, and, in a full grown shell, 3 to 6 such can readily be observed which probably mark the limits of as many successive years of growth. Occasionally these grooves are very distinct. Looked at from the outside the margin is nearly even; on the inside it is deeply notched, the depressions corresponding in position with the ribs on the outside (see fig. 1, Pl. I., and fig. 10, Pl. II.).

The hinge line is gently curved, and the concavity of the shell is continued dorsally beyond the hinge into the umbo; along this hinge line is a series of double teeth on each valve which interlock when the valves are closed. On the right valve the central cardinal tooth has the form of a deep depression with sharp cusps arranged anteriorly and posteriorly. On the left valve this arrangement is reversed, there being a single median cusp with depressions in front and behind; similarly on the right valve each of the two lateral teeth (which are really anterior and posterior) consists of a prominent ventral and a smaller dorsal cusp with an elongated depression between. On the left valve this arrangement is reversed. The hinge ligament, which represents the dorsal uncalcified portion of the shell, lies posterior to the umbones and is external; it is hollow and arched, underneath it the dorsal margin of the valves do not come into contact when the shell is closed, and a median glandular fold of the mantle projects up into the cavity beneath the arch of the ligament, and is in contact with the internal surface of the latter. The ligament is very elastic and serves for the divarication of the valves when the adductor muscles are relaxed.

There is little pigmentation on the shell except at the posterior margin, where, particularly on its internal surface, it is tinted a chocolate brown or green. This pigmentation may extend on to the scar of attachment

of the posterior adductor muscle, which is often striped with brownish yellow and white. This posterior margin is much denser than any other part of the shell, and dissolves slowly in dilute acid, always remaining after the rest of the shell has disappeared; the organic matrix is more abundant here than at any other part.

The scars indicating the attachment of the muscles show plainly on the dry shell (fig. 10). The posterior adductor scar (*Add.p'*.) is large and usually pigmented. The anterior adductor scar (*Add.a'*.) is rather smaller, and is always unpigmented. Both approach very near the margin of the shell, and lie just beneath the hinge line. On the dorsal margin of the posterior adductor is a small oval scar (*Ret.p'*.), sometimes not very obvious. This indicates the place of attachment of the posterior retractor of the foot. Two scars are to be seen in a similar position over the anterior adductor scar. The more dorsal of these (*Ret.a'*.) is the scar of attachment of the anterior retractor pedis. The other (*Pro'*.) shows the attachment of the protractor pedis. The pallial line indicating the place of attachment of the radial series of muscle fibres serving for the retraction of the mantle edge runs parallel to the ventral shell margin, at a distance of about 8 mm., and is slightly indented in correspondence with the notches on the margin. There is no siphonal sinus, but at the posterior margin of the shell the pallial line becomes much broader as the retractor muscle of the mantle edge passes into the retractor of the siphons. A small scar hidden in the umbo serves for the attachment of a small bundle of muscle fibres attached to the dorsal margin of the wall of the visceropedal mass.

The shell in the region of the umbones is always thin, and the periostracum is worn off in the fully grown specimen. Towards the margin, and especially at the

posterior margin, it is much thicker, and both periostracum and organic matrix are present. The internal structure is very peculiar, differing from that of most lamellibranch shells, and corresponding closely to what Ehrenbaum,\* who has investigated various species of *Cardium*, describes as the gastropod type of shell structure. The calcareous substance is distributed in two ill-defined layers (fig. 29, Pl. V., *Sh.i.*, *Sh.e.*), which must be termed inner and outer shell layers since the terms prismatic and nacreous layers are not applicable here. The shell is composed of a great number of exceedingly thin laminae which lie, for the most part, parallel to the shell surface. But since the mantle edge is folded over the shell edge, each lamina begins as a curved plate, the convexity of which is turned towards the margin, and since the whole shell grows by the addition of successive laminae to those already formed, its most external layer is formed by the edges of the laminae coming out on the surface at an angle of from  $45^{\circ}$  to  $60^{\circ}$ . The deposition of calcareous matter seems to be effected principally by a rather wide zone of the external surface of the mantle, extending back from the margin. Hence the dorsal parts of the shell are thin, since there seems to be little, if any, formation of lime over the general mantle surface.

Each lamina has a very fine fibrous structure, the fibres lying longitudinally in the thickness of the layer. In any two successive laminae the directions of the fibres are at right angles to each other. Thus, starting from any one, in laminae 1, 3, 5, 7, the fibres are parallel to each other, but in laminae 2, 4, 6, 8, they are at right angles to the fibres in the first set. This is not easily observed in sections perpendicular to the surface of the shell and to the margin, owing to the excessive thinness of the laminae.

\* Zeitschr. f. wissensch. Zool. Bd. XLII., pp. 1—47, 1885.

In sections taken in a plane perpendicular to this, that is, perpendicular to the surface of the shell and tangential to a line of growth, it is evident that in the centre of the section the laminae must lie in planes approximately parallel to the surface, since, owing to their upward bending near the surface of the shell, they must lie at one point in planes perpendicular to that surface. So here the section is marked out into irregular areas representing small portions of the bent laminae. In any two such contiguous areas the directions of the fibres are at right angles to each other. Further, since the laminae are very thin, several are superposed in the thickness of the section, and in any one such area, by focussing, a system of parallel lines crossing each other at nearly a right angle may be easily seen.

The structure of the shell is greatly complicated by the sculpturing at the margin. Once the formation of the definitive ribs and grooves has been initiated, the deposition of successive laminae proceeds upon the surface so laid down, and so at the edge of the shell the surface of a lamina is a very irregular one. Further back from the margin, as one observes in a vertical section tangential to the edge, the laminae are very regularly crumpled, the contour of a single lamina being concentric with that of the internal surface of the shell at its extreme margin. It is obvious that this arrangement causes great irregularity in the appearance presented by a vertical section made with the intention of passing perpendicular to the shell edge, for it is difficult or impossible to make the section pass exactly through a rib or hollow without cutting, in some part, the margin of the rib where the planes of the laminae are approximately perpendicular to the surface and margin of the shell. This causes the coarse pseudo-prismatic appearance observed in a vertical section

perpendicular to the margin (fig. 29). These apparent prisms are, of course, the obliquely cut edges of the laminae.

The shell is everywhere penetrated by very fine tubes and irregular channels. These are more apparent in the vertical section taken perpendicular to the shell margin, where they seem to be cut, for the most part, transversely. In a section at right angles to this they are by no means so obvious. It is evident from this that the black appearance of these cavities is due not so much to pigment, as Ehrenbaum supposes, as to the air included in the process of preparation of the section. They are very regular, following the planes of deposition of the shell laminae.

The periostracum (*Epic.*, fig. 29) appears in section, not as a regular layer on the external surface, but rather in irregular fragments and patches.

#### GENERAL ORGANISATION, MANTLE AND FOOT.

In the ordinary cockle not preserved by any special method, the animal is completely retracted within the shell. The shell margins fit together very closely except at the posterior extremity where, in the relaxed condition, the siphons protrude. Even here on account of the contraction of the siphonal tubes, the mantle cavity is completely closed. In this condition it is difficult or impossible to open the shell without injury to the soft parts, and, when this is done, the animal is so much distorted owing to muscular contraction that the true relations of the parts are not evident. The animal is best prepared for dissection either by gradually adding a 4% solution of cocaine to the water in which the expanded animal lies, or by placing it at once in a 1% solution, and allowing it to extend, which generally happens in the course of an hour. The irritability of the siphons and

mantle edge is first lost; the foot never becomes quite insensitive. The animal is then killed in a 20% solution of formol, a small piece of wood having been previously placed between the edges of the valves to prevent the slow contraction of the adductor muscles which occurs after death. Only a slight amount of contraction takes place in the formol, the siphons and foot being generally moderately extended. If it is desired to prepare the animal for sectioning, both valves are removed by placing it in a 10% solution of nitric acid in 70% spirit; if for dissection, it is propped up on a couple of glass slides in a dish with the shell margin horizontal, and the acid solution poured in so as to cover one valve. Either of the two valves can be dissolved off in this way, the other being left to fix the animal in the dissecting dish. A great inconvenience is caused by the accumulation of carbon dioxide, resulting from the decomposition of the shell, within the cavities of the body. If the specimen is being prepared for sectioning, it is best to remove this gas by allowing it to remain for some days in 70% spirit containing a little ammonia.

Except at the margin, and for a reddish strip at the dorsal surface which is the pallial portion of Keber's organ, the mantle lobe is thin and transparent. Removal of this by cutting along the line *Mn'*, seen in fig. 2, exposes the gills and labial palps. The gills pass obliquely backwards from the dorsal surface of the body beneath the umbo at an angle of about 30° to the vertical axis of the visceropedal mass.

The labial palps are triangular in shape. Their shorter or anterior sides are attached to the body-wall, and their most anterior extremities pass into the upper and lower lips respectively. The dorsal margins are thin, smooth, and slightly uneven. The internal surface of the outer, and the external surface of the inner palps are marked



with deep grooves parallel to the anterior margins, and are ciliated. The other surfaces are smooth and non-ciliated. Cilia are present on all surfaces of the grooves and ridges. Each ridge is roughly quadrangular in section (fig. 24). The outer faces and the faces turned towards the apices of the palps are covered with long columnar cells bearing long cilia, and having abundant eosinophilous cells. The rest of the surface of the ridges and furrows is covered with cubical cells, carrying shorter cilia. The smooth surfaces of the palps have an epidermis of flat, almost squamous cells. Within the palp there is a very loose connective tissue, rather denser in the interior of the ridges and containing blood corpuscles in its interspaces.

The mantle lobe of each side (*Mn.*, fig. 4, Pl. II.) is inserted into the extreme dorsal margin of the body, and round the lower margin of each adductor; anteriorly the right and left lobes fuse together at the dorsal surface of the anterior adductor. Posteriorly there are two fusions; dorsal to the posterior adductor the mantle roofs in a portion of the mantle cavity which passes upwards over the adductor (*Mc.1*, figs. 3 and 6), and in which the terminal portion of the rectum and the anus lie. The first fusion forms the septum between the dorsal and ventral siphons. It is prolonged inwards from the mantle edge forming a horizontal shelf (*Mn.1*, fig. 3), which separates the cavity of the dorsal siphon (*Mc.2*, figs. 3 and 6) from the general mantle cavity (*Mc.3*, figs. 3 and 6). The second fusion forms the lower wall of the ventral siphon. Between the posterior margin of the mantle and fusion one, and between the first and second fusions, the mantle edges are prolonged outwards to form the siphons. In the full grown animal these have a maximum length, when extended, of about 1 cm. In the young cockle their length is relatively much greater.

The siphons differ slightly in structure; the dorsal, or exhalent one (*Si.d.*, figs. 2 and 3), is the shorter of the two. Its free edge is quite even and a small portion of the wall of the tip is exceedingly thin. This thin tip is contractile, and is generally closed forming a little cone at the end of the siphon. The tentacles, which are rather over 1 mm. in length when fully extended, are situated in an irregular ring at the base of this cone. Other and larger tentacles are borne on the wall behind this ring. At intervals the conical tip of the siphon opens and water and faecal matter are suddenly expelled. The ventral or inhalent siphon (*Si.v.*, figs. 2 and 3) remains permanently open. The free edge bears a great number of very delicate tentacles, smaller and thinner than those borne on the outer wall and differing slightly in structure. Behind this, as in the upper siphon, is a ring of tentacles with others scattered irregularly upon the wall. At the tip of both upper and lower siphons are a number of brown pigment spots which are the openings of little pigmented crypts or glands.

The mantle edge (fig. 23) is thrown into longitudinal folds extending along its entire length. There is an inner strong fold projecting into the mantle cavity, a smaller median fold, and an outer fold which dips into the grooves on the shell margin. On the surface applied to the shell, the epidermis consists of rather irregular cubical cells, except towards the extreme edge, where the cells become spindle shaped and are crowded with brownish pigment granules. Over the rest of the mantle edge (ventral and internal surfaces), there is an epidermis consisting of a very regular layer of cubical cells with very distinct nuclei and a strong cuticle. On the inner of the three folds mentioned above, and in the deep groove separating this from the small median fold, the cuticle



becomes very strongly developed. From it a cuticular structureless membrane passes off over the free edge of the shell forming the epicuticula or periostracum (*Epic.*). When the shell is dissolved off in acid, this cuticular investment is seen to be really continuous with the mantle edge, so that the latter is firmly attached to the outer surface of the shell.

On the inner surface is a ciliated zone which begins a little way back from the free edge of the inner fold, and ceases or begins to die out opposite to the line of attachment of the pallial muscles to the shell. Coincident with the distribution of the cilia is that of a zone of mucous glands opening on to this ciliated surface on the mantle margin. These glands are very similar to those which will be described as present on the ciliated tip of the foot (p. 17), but are, as a rule, unicellular, the body and conducting stalk being formed from a single cell. Occasionally several cohere together forming a structure of the same nature as those found on the foot, but they are very generally much smaller individually. Their stalks passing out through the epidermis give the latter an irregular appearance. The tips of these stalks project out among the cilia as prominent little knobs.

The pallial muscles (*Ret.m.*, fig. 23) have a narrow zone of attachment to the shell (*Ret.m'*., fig. 10). Here the epidermic cells disappear completely from the mantle surface. The muscle bundles, passing ventrally, parallel to the surface, are attached to the shell at a very acute angle. The bundles run along the outer surface for a short distance, then divide into two series. One of these continues to run along the outer surface, and terminates in the connective tissue in the outer and median folds, the other series, consisting of stronger bundles, crosses over to the inner surface and breaks up into smaller bundles,

and isolated fibres which terminate in the inner mantle fold.

Within the mantle there is, at the margin, a filling tissue composed of fine connective tissue fibres, in which run the muscle bundles and the trunks and finer branches of the pallial nerve plexus; passing inwards, this begins to include large irregular communicating spaces, and is soon reduced to a mere lining to the epidermal surfaces from which trabeculæ pass inward, forming a very coarse network. The trabeculæ consist of rather dense fibrous tissue with scattered nuclei. Far back from the edge this becomes reduced to little more than a layer of small nuclei and a few fine fibres. Delicate bridges of fibrous tissue unite the two epidermes, so that the whole cavity in the interior of the mantle lobe is divided into a system of inter-communicating spaces which are generally empty in sections, but are most probably blood sinuses. The inner epidermis is composed of flat squamous cells. Near the point of attachment of the mantle lobe to the body-wall the former becomes much thicker, and the spongy tissue in its interior attains a greater development.

If now, the mantle lobe being removed, the labial palps be cut away along their attached borders, and the gills be carefully removed by cutting close to their bases, the portion of the body lying between the adductors is laid bare. The base of the ctenidium (*Br'*., fig. 3) extends downwards obliquely from the region of the body extending up into the umbones, to the lower horizontal level of the posterior adductor. Here the bases of the right and left ctenidia become free from the body-wall, and continue to pass ventrally and posteriorly till their posterior extremities fuse with each other in the middle line, and with the horizontal shelf, referred to above, as formed by the extension inwards of the first fusion of the mantle lobes

between the siphons. At this point of conrescence of the two ctenidia, a peculiar little semicircular flap of membranous tissue projects downwards and forwards into the general mantle cavity.

This horizontal shelf is further prolonged anteriorly by the inner lamellæ of the internal branchiæ. Part of these inner lamellæ (*Br.I.2*, figs. 3 and 4) have the ordinary filamentar structure and are connected to the outer lamellæ of the same branchiæ by the inter-lamellar junctions. But the remainder of the inner lamellæ are simply membranous, and fuse with each other across the middle line of the body, and thus form the floor of the ventral supra-branchial chamber (*M.c.4*, fig. 4), which continues forward the cavity of the dorsal siphon. The outer reflected lamellæ of the external branchiæ, on the other hand, fuse with the body-wall just beneath the origin of the mantle lobes. It is evident from a consideration of fig. 4 that the inner and outer lamellæ of each external branchia must enclose a cavity, which is also continuous with the cavity of the dorsal siphon; this is the dorsal supra-branchial chamber (*M.c.5*, fig. 4). The ventral supra-branchial chamber is single and median. There are paired, right and left, dorsal supra-branchial chambers.

Since the inner lamellæ of the internal branchiæ do not fuse with the body-wall but with each other, the ventral supra-branchial chamber is incomplete anteriorly; the dorsal chambers end blindly in front. Evidently water entering the general mantle cavity by the ventral siphon or through the ventral opening of the shell has three courses open to it. It may pass forward between the labial palps into the mouth and so reach the dorsal siphon *per anum*; it may enter the ventral supra-branchial chamber through the space included between the posterior surface of the foot and the anterior margin of the fused inner lamellæ of the

inner branchiæ; or, finally, it may pass through the inter-filamentar gaps in the branchial lamellæ into either dorsal or ventral suprabranchial chambers and so into the dorsal siphon.

Two regions of the body can be distinguished (figs. 2 and 3, Pl. I.), the visceropedal mass (*Ped.1* and *Ped.2*) and the portion of the body lying behind this and in front of the posterior adductor. This latter portion contains the pericardium (*Per.*) and heart, and the renal organ (*Ren.*) with the terminal portion of the rectum. The visceropedal mass contains, besides the muscular foot, the greater part of the alimentary canal, the digestive gland, and the gonads. It is sharply marked off from the posterior region by the differentiation of a sub-epidermal muscular sheath, but the same epidermal layer covers both portions of the body.

The pericardium is situated dorsally, occupying the whole dorsal area between the visceropedal mass and the posterior adductor, beneath it is the renal organ, the ventral wall of which forms the roof of the ventral suprabranchial chamber.

The visceropedal mass is defined by the continuous muscular sheath (*cf.*, fig. 11) extending ventrally from the dorsal body-wall. In horizontal section it is elliptical. It consists of a proximal or vertical, and a distal or horizontal limb which, both in the contracted and relaxed condition, form an angle of about  $90^\circ$  with each other. The distal limb is directed forward, it is very much flattened laterally and has a deep groove, the pedal groove, (*By'*, fig. 3) running along its ventral edge from near the tip to a point beneath the axis of the vertical limb. About a third of the length of the distal limb, from the tip posteriorly, has an epidermis composed of short columnar ciliated cells which also form the lining to the pedal

groove. The rest of the epidermis of the visceropedal mass consists of short columnar, non-ciliated cells, with a continuous thick cuticle.

As on the internal surface of the mantle edge, this ciliated portion of the foot is also an area provided with unicellular mucus-secreting glands. These form a continuous dense layer beneath the ciliated epidermis, and are imbedded in the loose muscular sheath of this part of the foot. Each of these glands (figs. 21 and 22, Pl. IV.) consists of either a single cell or a group of from 2 to 6 cells aggregated together. Single-celled glands are uncommon, and are only found near the posterior limit of the glandular area. Towards the tip of the foot they are more complex; the largest groups measure about 0.3 mm., the stalks being about half that length. Such a complex gland consists of a group of cells forming a bulb with a long stalk. The limits of the separate cells are not always clearly distinguishable. The cell bodies consist of a reticulum, some of the bars of which are rather coarse; these are, however, continuous with a very fine meshwork, which apparently makes up the cell substance. This reticulum is continuous from cell to cell. Nuclei are not evident, but in every cell there is a nodal point at the intersection of several of the coarser bars of the reticulum; reticulum and nodal points, and the finest ground substance, stain a intense blue with haematoxylin. The stalk is non-tubular, has the same structure as the bulb, and breaks up at its free end into a small number of branches which penetrate between the epidermal cells and form little knobs among the cilia on the surface of the foot. The structure and staining reaction of these bodies, coupled with the habit which the very young cockle has of pulling itself along a smooth surface by causing the tip of its foot to adhere to

the surface, indicate their probable nature—that of a simple mucus-secreting apparatus.

The pedal groove itself is not a glandular structure, nor do the glands above described open on to its surface. Passing backwards from the tip of the foot the cilia disappear, and the groove is lined with an epidermis consisting of simple columnar cells. The groove becomes deeper, and may be thrown into longitudinal folds. Finally, it passes into a duct which runs upwards and backwards into the proximal limb of the visceropedal mass, and terminates in a swollen bulbous head, which lies on the right side of the caecal prolongation of the straight intestine (*By.g.*, fig. 3). A single delicate hyaline fibre may sometimes be seen projecting from the opening of this duct, and indicates, what the histological character of the gland in fact demonstrates, that the apparatus is a byssus secreting structure. Sections of the duct show only an epithelium consisting of short columnar, ciliated cells. Further up, the duct expands into a wide cavity (fig. 19) from which lateral diverticula are given off; these may branch again. Their lumina are always restricted. Each of these secreting alveoli (fig. 20) is lined with a epithelium of rather club-shaped cells which do not seem to bear cilia, but from between which a number of fine threads pass out into the lumen where they become agglutinated together, forming a filament. The filaments from the various alveoli unite together in the duct to form the single byssus thread.

That *Cardium* possesses a true byssus was demonstrated by Gosse,\* who shewed that in the young *C. aculeatum* this was actually functional. Carrier† and Barrois‡ have

\* Ann. and Mag. Nat. Hist. Ser. II., vol. XVIII., pp. 257—8.

† Arb. Zool.-Zoot. Institut, Wurtzburg. Bd. V., pp. 56—92, 1882.

‡ Comptes Rendus Acad. Sci. T. C., pp. 188—190, 1885.



also shown that in *Cardium* "*oblongum*," *C. echinatum*, and *C. rusticum* a rudimentary byssus gland, corresponding in all respects to the structure above described, is present. Finally, Gwyn Jeffreys\* mentions a case of *C. edule* itself in possession of a functional byssus.

Of the apertures of the body, the mouth (*M.*, fig. 3) is a wide slit lying between the visceropedal mass and the anterior adductor; the anus (*An.*) lies on the dorsal surface of the posterior adductor. The apertures of the gonad and renal organ are rather difficult to observe. They may be seen by folding back the internal branchia (see fig. 3). The ureter (*Ren'*., fig. 4) is a mere slit in the wall of the renal vestibule, and lies on the lateral wall of the renal organ just dorsal to the origin of the posterior retractor muscles of the foot. The external opening of the gonad lies in nearly the same position, but on the lateral and posterior wall of the visceropedal mass; it is slightly elongated and sometimes has tumid lips.

#### THE MUSCULATURE.

The muscles may be conveniently arranged into four groups: (1) the adductor muscles of the shell; (2) the extrinsic muscles of the foot; (3) the intrinsic muscles of the foot; and (4) the pallial muscles. The extrinsic and intrinsic pedal musculature form really one system. The pallial muscles may be divided into the pallial muscles proper and the muscles of the siphons.

(1) There are two adductor muscles of the shell (*Add.a.* and *Add.p.*, fig. 3), anterior and posterior. Each is a strong bundle inserted on the dorsal oblique surface of the shell near the margin, and running across in an exact transverse direction from valve to valve. Owing to the curve of the shell the scars of attachment (*Add.a'* and *Add.p'*.,

\* British Conchology, vol. II., p. 208.

fig. 10) are much larger than the areas of transverse sections of the muscles. The posterior muscle forms a thicker bundle than the anterior. In the extended condition of the animal, the structure of the muscle bundle is rather loose, being penetrated by blood spaces usually filled with corpuscles.

The force of contraction of the adductor muscles is very great. Plateau\* has measured this in terms of the weight required to force open the valves. Two hooks were inserted under the ventral edges of the valves. The hook sustaining the upper valve was fixed to a support. The other, which was carried by the lower valve, supported a scale pan. Weights were placed in the scale pan till the valves were separated to the extent of 1 mm. As the mean of eight such experiments it was found that the weight required was 1134 grms. And taking the transverse area of both adductors into account, this gives the force necessary to overcome the contraction per sq. cm. of the sectional area of the adductor muscles of *Cardium* as equal to the weight of 2856 grms. Plateau also made the converse experiment. An animal in a completely relaxed condition, with the shell gaping, was supported with the lower valve resting on a firm support. A loop was passed round the upper valve, from the lower end of which was suspended a scale pan. The mean weight required to overcome the elasticity of the hinge ligament was found to be 106 grms.

(2) The extrinsic muscles of the foot take their origin from the superficial muscular sheath of the visceropedal mass. The posterior retractors of the foot (*Ret.p.*, figs. 3 and 11) originate in the posterior margin of the proximal limb of the latter, and run backward as a short apparently single median bundle (*Ret.p.*, fig. 4), this bifurcates into

\* Bull. Acad. Roy. Sci. de Belgique. Ser. III., t. VI., pp. 226—259, 1883.



the right and left muscle bundles, which are inserted, one into each valve, at the dorsal margin of the posterior adductor scar (*Ret.p'*, fig. 10). There is a well-marked decussation of the fibres forming each muscle. That is, the fibres forming the left retractor originate in a flattened band, lying on the right side of the middle line, on the inside of the muscular posterior wall of the visceropedal mass, and *vice versa*. This crossing of the fibres is effected by two or three smaller inter-digitating bundles from each side, and is complete, none of the fibres remaining uncrossed. The band from which these muscles take the origin (*Ret.p.*, fig. 11) can be traced round the bend of foot into the ventral and lateral walls of the distal limb, after which its further course becomes very complex.

The anterior retractors of the foot lie through almost all their course in the interior of the visceropedal mass. Together they form a flattened band of fibres on the inside of the anterior wall (*Ret.a.*, fig. 11). At the upper level of the anterior adductor they come to the surface as two paired bundles which are inserted into the shell on the dorsal margin of the anterior adductor scar (*Ret.a'*, fig. 10). As in the case of the posterior retractors, a certain amount of crossing takes place, though this is not so evident as in the case of the other. Below the bend of the foot the further internal course of the fibres is difficult to make out.

The protractor muscles of the foot form right and left short bundles, which are inserted into the shell near the scars of attachment of the anterior retractors. Internally the fibres spread out in a fan-shaped sheet on the lateral dorsal walls of the proximal limb of the visceropedal mass, but there are no obviously distinct bundles, as in the case of the retractor muscles. Many of the fibres seem to pass

round and meet on the posterior margin, and the bundles may be regarded as being constituted by a break in the continuity of the circular muscular sheath of the proximal limb, the free ends being gathered up into two short bundles and attached to the shell. Judging from the direction of the fibres, the only effect of the contraction of these muscles will be to slightly rotate the whole visceropedal mass about its dorsal attachment on the shell, so that the term "protractor" is rather a misnomer.

The superior retractors of the foot (elevatores pedis, Pelseneer) form two paired muscle bundles, which are inserted one into each valve in the most dorsal part of the umbo. The scars cannot be easily seen without breaking the shell. Each bundle consists of fibres gathered up from the transverse and oblique musculature of the dorsal body-wall.

(3) The intrinsic muscles of the foot include all the pedal muscles, which are not inserted into the shell, but have their attachments within the visceropedal mass itself. There is a thick hypodermal muscular sheath (fig. 25) in which typically four muscle layers can be distinguished. Beneath the epidermis is a thin layer of fibrous connective tissue within which is a layer of muscle fibres running transversely round the foot. This is succeeded by a thick layer of obliquely running fibres, which passes into another layer of transverse fibres, and internal to all is an irregular sheath of longitudinal fibres. The precise arrangement is variable at different levels, and all the layers may not be present. The oblique and circular layers are always represented. Here and there in a transverse section through the proximal limb of the visceropedal mass, strong muscle bundles (*M.p.l.*, fig. 11) may be seen passing across between the lateral walls in a transverse direction. In the extended condition the structure of these is rather

loose, but the ends of each bundle are gathered up into a tendinous root, which penetrates the muscular layers of the body-wall, and has its attachment in the fibrous connective tissue which is present among the muscle fibres. These straight transverse bundles occupy the greater portion of the cavity of the proximal limb. Towards the axial portion they separate, leaving a space in which the convoluted and straight portions of the intestine are lodged. Between them penetrate the tubules of the gonads.

(4) The pallial muscles consist of the retractor muscles of the mantle edge and siphons and the intrinsic musculature of the siphons. The former (*Ret.m.*, fig. 3) form a radial series which extend round the mantle edge from adductor to adductor. They are inserted into the shell along the pallial line (*Ret.m'.*; *Ret.s'.*; fig. 10), and extend into the folds in the mantle edge where their distribution has already been described. Their length in the extended specimen is about 0.5 cm. Towards the posterior margin of the shell they become very much stronger in correlation with the development of the siphons, for the retraction of which they serve. In the walls of the siphons they form a dense longitudinal sheath which extends outwards to the tips. This sheath lies principally on the inner portion of the wall. Special circular and radial intrinsic fibres are present in the siphonal walls. The former are distributed in bundles lying just beneath the outer wall, and less evident bundles situated midway between outer and inner walls. The radial fibres pass across from inner to outer epidermis. The outer zone of the siphonal wall consists of connective tissue with included blood spaces.

## THE ALIMENTARY CANAL.

By far the greater portion of the alimentary canal lies entirely within the proximal limb of the visceropedal mass, and may be easily dissected in a specimen hardened with formol by removing the muscular body-wall of one side, cutting through the attachment of the transverse muscle bundles as close to the integument as possible. The attachments of these to the opposite wall are then cut through beneath the intestine and the bundles removed, the digestive gland and the gonad are picked away, and the stomach and intestine lie exposed to view.

The mouth (*M.*, fig. 3, Pl. I.) is at first a wide slit extending across the body between the anterior body-wall and the anterior adductor. It is bounded dorsally and ventrally by the prominent upper and lower lips, the outer extremities of which are produced laterally to form the dorsal and ventral labial palps respectively. The opening soon contracts, so that the perforation in the muscular body leading into the œsophagus is oval in form. The latter (*Al.c.1*) is a short tube passing backwards and slightly upwards towards the posterior and dorsal part of the visceropedal mass, where it expands into the stomach (*Al.c.2*), which forms a capacious sac, increasing in diameter from before backwards. The stomach is surrounded on all sides by the dark-green mass of the digestive gland (*D.g.*). This is really paired, and forms a thick lobe on each side. Each lateral lobe, however, expands over the dorsal anterior and posterior sides of the stomach, so that it seems to nearly envelope the latter. If the digestive gland is carefully picked away prior to laying bare the stomach, two ducts may be seen opening into the latter. One is small, and opens on the posterior and dorsal margin; the other is much larger, and opens into the stomach at its junction with the œsophagus; it

passes at first forwards and downwards, then comes round into the mass of the gland. A great number of smaller lateral ductules open into these principal ducts, and on them are arranged in clusters the secreting alveoli of the gland.

The epithelium of the stomach passes gradually into that of the ductules of the gland. The tricuspid body disappears; the long spindle cells become shorter, and a corresponding decrease in length of the cilia takes place. But the epithelium of the ductules (fig. 17, Pl. III.) always consists of spindle cells carrying cilia, and their walls are thrown into slight longitudinal folds; at the passage of the lumen of the ductule into that of a secreting alveolus a rapid transition from this ciliated epithelium into that characteristic of the alveoli takes place (fig. 15, Pl. III.).

The fixation and subsequent treatment of the digestive gland, so as to exhibit the nature of the secretory epithelium, is difficult, but good results are to be obtained by McMunn's method. A very small piece of the gland is rapidly removed from the living animal, and at once put into a 20% solution of commercial formaldehyde in water. The tissue is allowed to remain in this for about 24 hours, and is then transferred to 70% spirit and dehydrated, embedded and cut in the ordinary way. The sections are stained with Mayer's glychaemalum and eosin, or with Heidenhain's iron haematoxylin. With fixing reagents of less penetrative power the epithelium breaks up in the process.

The lumen of the alveolus is always a very restricted one, and is usually cruciform in transverse section. The spindle cells becomes cubical and the cilia disappear (fig. 15, Pl. III.). Then the cubical epithelium becomes replaced by four groups of large club-shaped cells (fig. 16, Pl. III.). In tangential sections of the alveolus these cells, which are then cut transversely, have very definite polygonal out-

lines. Their cell substance is coarsely granular, with many round clear spaces; the nuclei are placed at their lower extremities. Only four to six cells are found in each group. The groups are delimited by the arms of the cross-shaped lumen, which extend nearly to the walls of the tubule, and here at the thinnest portion of the wall the cells composing it are small and irregular, and have relatively large nuclei. If the section has been stained with Heidenhain's haematoxylin a very distinct basement membrane, staining dense black, can be seen investing each alveolus. The whole mass of the gland is bound together by fibrous connective tissue, in the interspaces of which are crowded corpuscles of various kinds.

The lining epithelium at the animal's mouth consists of elongated columnar cells bearing cilia, and supported on a rather distinct basement membrane. Passing inwards this epithelium is thrown into a close series of longitudinal folds, and the height of the cells diminishes. The cells have distinct striated free borders, the nuclei are situated about their middle, the lower ends are rather loose and seem separated from each other; rounded faintly granular eosinophilous cells are found here and there wedged in between the columnar cells.

As the œsophagus widens out to form the stomach these cells gradually elongate to form the epithelium lining the cavity of the latter. This gastric epithelium (fig. 18, Pl. III.) is of variable thickness, but the cells are always longer than in the œsophagus. A gelatinous looking substance—the “fleche tricuspide” (*F. tri.*, fig. 18)—lines a large portion of the stomach-wall, and underneath this the epithelium becomes much thicker, consisting of long spindle-shaped cells, the long oval nuclei of which occupy any position within a rather wide zone about their middle. The lower ends of these cells are



very distinctly rounded off, forming an uneven lower margin, which rests on a fibrous sheath consisting of several layers, and which passes into the loose connective tissue surrounding the digestive gland tubules.

The thickness and extent of the tricuspid body is variable, some portions of the stomach-wall being bare; the latter is thrown into folds and pads, into which the substance of the tricuspid body dips. In most parts this substance is closely adherent to the gastric epithelium, in other parts it is distinctly separated; where it lies in close contact with the epithelium the striated free border of the latter is very evident. Where it is separated the epithelium is seen to bear cilia which, at other places, must be embedded in its substance. It stains slightly with eosin. No obvious structure can be discerned in it except that in favourable preparations, delicate striæ, parallel to the surface of the epithelium, and other striæ perpendicular to the surface may be seen, which seem to indicate that it has been deposited round the cilia and in laminae, perpendicular to the surface of the epithelium. Where the tricuspid body is wanting the gastric epithelium is composed of much shorter spindle cells than are found elsewhere. The average length of the cells beneath the tricuspid body is 0.08 mm., on the rest of the stomach-wall 0.04 mm.

The whole posterior part of the stomach contracts to form the straight portion of the intestine (*Al.c.3*, fig. 3). This extends downwards nearly in the axial line of the proximal limb of the visceropedal mass. It is slightly curved, the concavity being anterior. The diameter, the average value is 1.25 mm., decreases from above downwards. At the lower end and on the anterior side, the spiral portion of the intestine takes origin, below this there is a short anteriorly directed caecum.

As the stomach contracts to form this division of the intestine, two folds of its wall (fig. 11, Pl. III.), which are anterior and posterior, are formed, and are continued down the straight intestine dividing the lumen of the latter into two longitudinal cavities, both of which communicate with the stomach by wide openings and with each other by a long wide slit. Of the two communicating semi-tubes so formed, the left (*Al.c.3'*) is the larger, and is exactly circular in transverse section; it lodges the crystalline style. The right semi-tube (*Al.c.3''*) is irregular in section, and forms the channel along which the ingested food travels. Morphologically, this is the portion of the intestine immediately following the stomach. The left semi-tube is a diverticulum of the stomach cavity—the pyloric caecum\* (sac of the crystalline style). Pyloric caecum and intestine are separate in some Lamellibranchs (*Pholas, Donax*), but in *Cardium* and others have fused together, the anterior and posterior folds being the remains of the primitively adjacent walls. At the tip of the straight intestine, in the short caecum already referred to, is a vestige of the originally separate condition of the two channels.

Three very distinct kinds of epithelium are present in the straight portion of the intestine. On the wall of the sac of the crystalline style there is a single layer of spindle-shaped cells (*Ep.I.1*, fig. 12, Pl. III.), having an average height of about 0.03 mm. These bear a very close set series of long and stiff cilia, having an average length of  $\frac{2}{3}$  that of the cells carrying them. The cell bodies are finely granular, with rather highly refractive free borders, the nuclei are situated at their lower extremities; the cells fit together very closely, except at their lower extremities,

\* Purdie, A. Studies in Biology for New Zealand Students. No. 3. Anatomy of the common Mussels. Wellington, 1887.



where large clear spaces are seen, which are either intercellular spaces or cell vacuoles, probably both. The epithelium in the intestinal division (*Ep.I.3*) is made up of much shorter cells, which bear short cilia. The free extremities of these cells fit closely together, but the lower ends are rather loose. Scattered abundantly throughout the epithelium are large, round, oily masses, staining faintly with eosin, and quite homogeneous in structure. Similar bodies can be seen in the tissue lying outside the epithelium. Here they are seen to be true cells, with the nucleus compressed against one portion of the cell wall and the greater part of the cell space filled up with an oily globule. In many the cell contents are very coarsely granular, and stain strongly with eosin. Others are finely granular, and all transition stages between the coarsely granular condition and the homogeneous appearance, which the bodies in the epithelium present, can be found. Similar oily globules can be found projecting into the lumen of the intestine, or even lying free in the cavity. Nuclei are not evident in these structures in the latter positions. The nuclei of the ordinary cells are found near their bases. Above each nucleus is a large clear cell vacuole, the occurrence and position of which seem to be fairly constant.

In the sac of the crystalline style and near the anterior fold is a very remarkable strip of epithelium (*Ep.I.2*), which extends all the way from the opening of the sac into the stomach to the point from which the spiral division of the intestine takes origin. This appears in transverse section as a crescentic area of the wall made up entirely of very long spindle cells. On the left side these long cells pass gradually into the epithelium lining the sac of the crystalline style. On the right side they are very sharply demarcated from the short cells lining the

intestinal division of the straight intestine. Their maximum length is about 0·2 mm. They are finely granular, with the nucleus at any level from near the free extremity to near the bottom of the cell. They bear a covering of very short cilia. Sometimes, at the middle of the free surface, there is a little groove in which the cilia are matted together. This is not constantly present, and it is probably due to the action of reagents.

The epithelium, of the intestinal portion especially, rests on a layer of dense connective tissue, which fills up the spaces between the epithelia forming the anterior and posterior folds, and is found in patches all round the intestine. This presents no very obvious structure. It seems to be largely fibrous, with nuclei scattered through it. It stains densely with haematoxylin. It includes large irregular spaces, evidently blood channels; in its substance are seen corpuscles of various kinds, blood corpuscles and corpuscles containing a greenish substance.

The crystalline style (*St.*, fig. 12, Pl. III.) completely fills the lumen of the left division of the straight portion of the gut. In sections made from hardened specimens, the style is usually seen to be retracted away from the wall of the sheath. But since, in such preparations, it may be observed that the superficial layer of the ciliated epithelium is in some parts torn away and adherent to the substance of the style, it is evident that this contracted condition is due to the process of embedding; and the same cause most probably gives rise to cavities sometimes observed in its marginal part. In hand sections of the animal, simply killed with formol and examined under a low magnification, the style appears perfectly homogeneous, and completely fills the sac.

No obvious structure is to be observed in the style except a very delicate concentric lamination. It is per-

fectly transparent, and seen singly, colourless; in mass the substance is very slightly yellowish. The length, when taken from full-grown specimens, varies from 20 to 26 mm. The diameter decreases from above downwards, and may be taken as about 1 mm. The proximal extremity always projects into the cavity of the stomach, and is opaque and slightly frayed; the distal extremity does not fill the lumen of the ventral portion of the sheath, but remains adherent to one portion of the wall. It is firm, somewhat elastic, but breaks easily.

Barrois,\* in an exhaustive memoir on the Morphology and Physiology of the Lamellibranch Style, gives an account of the chemical composition and reactions of the substance of which it is composed, which may be briefly summarized here. Barrois made his analysis and experiments on the crystalline styles of *Cardium edule*. The style has an average weight of 0.026 gm. It is a colloidal substance. A number placed together coalesce to form a transparent jelly, which takes the form of the vessel in which it is contained. Dried at a temperature of 120°, the mass contracts considerably in volume, but still remains perfectly transparent and somewhat moist. On ignition a small amount of inorganic ash remains. The fresh style is rapidly soluble in concentrated hydrochloric acid to a bluish solution; it is slowly soluble in water, forming a slightly opaque and viscous solution. Millon's reagent gives a red colouration in the warm. Treated with copper sulphate solution and caustic potash, a fine blue colouration is obtained. These reactions indicate the presence of an albuminoid substance.

When the solid styles are boiled with dilute sulphuric acid, and the acid solution neutralized and precipitated with alcohol, a solution in the latter solvent is obtained.

\* Revue Biologique du Nord de la France. T. I. and II., 1889—90,

This solution is filtered off from the flocculent precipitate, formed by the addition of the alcohol. It is evaporated nearly to dryness, and the dissolved matter again taken up by water; the aqueous solution so obtained reduces Fehling's solution. This series of reactions is characteristic of mucine and chondrine, since glycogen or other carbohydrates capable of yielding sugar on treatment with dilute acid, and consequently reducing Fehling's solution, are absent.

Further the addition of crystals of magnesium sulphate in excess to the aqueous solution of the styles, gives an abundant precipitate which contains practically all the proteid matter present in the solution. This behaviour with magnesium sulphate, which agrees with that of a globulin, and the reaction with dilute acid, indicate the nature of the substance. It is allied to, but apparently not identical with mucine.

Leaving out of account the older views concerning the function of the crystalline style, such as that of von Heide, that it was an accessory genital organ, or that it was a skeletal structure (Carus and Garner), or the representative of the radula of the Glossophora, and consequently a masticatory organ (Meckel), only two hypotheses as to its nature seem to survive modern investigation. Hazay\* as the result of a series of observations and experiments, concluded that it represented a store of reserve food material, resulting from the metamorphosed excess of food matters taken in during the warm season, and lodged in the pyloric caecum to be utilized by the animal during periods of hibernation. Practically the same conclusion was arrived at by Haseloff† from a series

\* Die Mollusken-Fauna von Budapest II. Biologischen Theil. Cassel, 1881.

† Ueber den Krystallstiel der Muscheln nach Untersuchungen verschiedener Arten der Kieler Bucht. Osterode, 1888.

of experiments carried out on *Mytilus*, from which it appears that not only is the style absorbed during the starvation of the animal by keeping it in filtered sea-water, but it is formed anew on abundant food being supplied. Haseloff inferred that the style "is the product of the chemical transformation of the excess of food material taken in by the animal, the change being effected by the agency of the digestive ferments." More lately, Woodward\* working on the same mollusc, was able to confirm Haseloff's experiments.

Barrois rejects the conclusion of Hazay and Haseloff, basing his objections chiefly on the chemical composition of the style which is very different from that of most reserve food materials, and on the unusual form in which the substance is stored up. In both these points it differs notably from all undoubted physiological reserves. In *Helix pomatia*, which undergoes a true hibernation, abundant reserve food material is stored up in the liver in the form of glycogen. This substance undergoes a gradual change into sugar in the course of the hibernation period, and ultimately disappears completely. Moreover, neither in *Mytilus* nor in *Cardium* taken during all times in the year was he able to observe any change in the volume of the style. Specimens of *Cardium* were placed in filtered sea-water and starved for eleven days. Only after the eighth day was any diminution in volume observed, and in general complete disappearance only occurred on the death and partial decomposition of the animal. The disappearance of the style during this experiment Barrois regards as due, not only to the solution of its substance in the stomach which goes on, as under normal conditions, but also to the profound bodily disturbance brought about by

\* On the Anatomy of Pterocera, with some notes on the crystalline style. Proc. Malacological Soc., London. Vol. I., pt. 4. 1894.

the experiment. At the same time, the secretion of the substance from the walls of the sac ceases, and the remains of the style are pushed into the stomach by the action of the cilia.

Barrois' own view, based chiefly on the chemical composition of the style, is that it is acuticular structure secreted by the wall of the sac, which acts as a lubricating material and invests sharp particles of sand, &c., with a viscous coating which prevents damage to the intestinal wall. As it is formed it is moved forward into the cavity of the stomach, where its free extremity is continually being worn away by the attrition of the food particles and the solvent action of the digestive fluids. The viscous fluid so formed also unites the food matter into a coherent bolus which easily traverses the intestine.

The view that the style is a cuticular structure secreted by the wall of the pyloric caecum seems rather difficult to reconcile with the appearance of that epithelium, for, with the possible exception of the longitudinal strip of elongated cells in the caecum, the wall of the latter does not present the appearance usually associated with a secretory surface. The compact layer of columnar cells, the refractile free border, and the dense layer of long stiff cilia contrast strikingly with the wall of the right division of the lumen of the straight portion of the gut, where secretion into the cavity of the intestine is most probably taking place, and is far more suggestive of a surface performing a mechanical function than of an actively secreting epithelium. And it seems unnecessary to locate the mucus-secreting epithelium in the wall of the crystalline style sac. All along the course of the intestine there is abundant evidence of some substance being poured out into the lumen, in the rounded homogeneous bodies found in the wall or projecting from the



wall into the cavity, or even free in the cavity of the intestine itself. Many of these are possibly migrating cells taking up food matters and again passing back through the intestine into the blood stream, but there can be little doubt that many are the products of secretion of cells in the intestinal wall itself or in the tissue lying round that wall. Masses of a dense tissue staining with haematoxylin in the same manner as the mucus-secreting cells in the foot and mantle are to be found along the whole length of the intestine.

The faecal matter is expelled from the intestine in the form of coherent strings, frequently of great length, in which the particles are certainly bound together by some viscous material. On Barrois' view this faecal matter ought to contain a substance chemically identical with the substance of the style, otherwise, transformation of the latter goes on in the intestine, and the substance of the style must function otherwise than as a simple lubricant. On the whole it would seem as if the presence of the style were associated with the ingestion of a large quantity of foreign matter, such as mud and sand, and the separation, to some extent, of the nutrient material therefrom. The substance of the style need not be regarded as physiologically a store of reserve material, but as a first separation out of some constituents of the food which are continuously lodged in a portion of the stomach by the action of the ciliated wall of the latter, and as continuously dissolved away.

A narrow slit on the anterior surface of the straight portion of the gut leads into the next division—the spiral portion of the intestine. This lies nearly in the axis of the proximal limb of the visceropedal mass, and anterior to the latter. It is twisted into a close spiral of five or six turns (*Al.c.4*, figs. 3 and 11) the planes of which are

nearly horizontal. At its upper extremity the coiling becomes rather irregular, and the tube passes into the succeeding coiled portion of the intestine near the axis of the latter. The crystalline style passes the opening of the spiral intestine, and its narrowed end is lodged in the short caecum already referred to. The anterior fold in the straight intestine continues on into the spiral portion, and passes into a thick pad, nearly filling up the lumen of the latter (*Ty.*, fig. 13, Pl. III.). This pad or typhlosole is formed by the same tissue which fills up the space in the anterior and posterior folds which divide the straight gut into right and left divisions. Owing to the presence of this typhlosole the spiral gut appears externally as a round tube, although in section the lumen is contracted and crescentic in form; the tissue filling the typhlosole is continuous with a narrow layer surrounding the gut and with the general connective tissue of the visceropedal mass.

After making about six turns the typhlosole disappears, and the intestinal tube passes into a loose coil of four or five turns, which may be described as the coiled portion of the intestine (*Al.c.5*, figs. 3 and 11), and which lies anterior to the spiral gut. The average diameter of this coil is from 0.6 to 1 cm. Its most anterior turn joins the spiral intestine; its most posterior one passes off into the rectum, which passes to the right side of the straight intestine, and runs up along the posterior part of the visceropedal mass (*Al.c.6*, figs. 3 and 11) to near the dorsal portion of the latter, where it pierces the muscular body-wall and enters the pericardium. After passing through the ventricle of the heart, the rectum runs along in the dorsal body-wall over the posterior adductor, and terminates in the anus (*An.*, fig. 3).

The histological character of the epithelium of the intes-



tine behind the typhlosolar portion resembles that described as present in the right division of the straight intestine. The wall may be smooth or thrown into three or four longitudinal ridges. The whole surface is ciliated. The oily eosinophilous globules already referred to are particularly abundant in the coiled intestine, and many may be found lying freely in the cavity. The average diameter of this portion of the intestine is about 0.5 mm.

Towards the anus the epithelium becomes arranged in a very peculiar manner (fig. 14, Pl. III.). Passing over the posterior adductor the wall becomes thrown into longitudinal folds, which, towards the anus, become more complex, secondary foldings being developed, and the bases being narrowed till some folds have, in transverse section, an almost dendritic appearance. Within they are filled up by the dense tissue already noted. A continuous sheet of connective tissue with a few muscle fibres surrounds the gut, but does not enter into the folds. Near the anus this dense filling tissue becomes restricted to the dorsal half of the intestinal tube, where it forms a crescentic pad lying on the epithelium beneath. This epithelium differs completely from that forming the ventral half. While the latter is thrown into complex foldings and bears long cilia which, on account of the proximity of the folds to each other, become matted together in the lumen, the upper epithelium is smooth, is non-ciliated, and consists of long clear spindle cells, with nuclei lying at their lower extremities, which form a sharp contrast with the cubical epithelium of the lower half. The transition from upper to lower epithelium is quite a sharp one. The tissue forming the pad lying on the upper half of the tube differs somewhat from the dense tissue lying outside the intestinal tube in its more anterior parts. Here it seems to consist of a dense mass

of cells, the bodies of which stain with haematoxylin, so that nuclei and cell bodies are not clearly distinguishable.

#### THE VASCULAR SYSTEM.

The pericardium (*Per.*, figs. 3 and 4) is a spacious sac which occupies the whole dorsal surface of the body between the posterior wall of the visceropedal mass and the posterior adductor. Its anterior wall is closely applied to the former. Its ventral wall rests on the upper surface of the renal organ. Dorsally and laterally the pericardial wall is also the body wall, and is thin and delicate, except in the median dorsal line where it is produced upwards into a strong ridge, and also on the lateral dorsal borders where the mantle lobes take origin. It is widest in front and contracts as it approaches the posterior adductor. It is nearly filled by the heart consisting of the median ventricle and the two auricles.

In the animal which has been killed after treatment with cocaine, the ventricle is usually fixed in the condition of diastole and then, together with the two auricles, fills almost the whole pericardial cavity. The ventricle (*Ven.*, figs. 3 and 4) is constricted medially, forming two rather well-marked lateral lobes. The walls are muscular but rather thin. Abundant muscular trabeculae run across the cavity in all directions. The rectum passes through its cavity, suspending the ventricle in the centre of the pericardium. The auricles (*Aur.*, figs. 3 and 4) are triangular in shape, the apices being attached to the ventricle, the bases to the bases of the ctenidia. Their walls are very thin, except at the apical portions, where they are thickened and composed of dense fibrous tissue; these portions project into the ventricle; the openings are horizontal slits bounded by the thickened tissue which forms a pair of

valves preventing the reflux of the blood into the auricles during the ventricular systole. On the floor of the pericardium, beneath the ventricle, are the openings of the reno-pericardial canals. On the anterior part of the floor are several openings which are the terminal portions of systems of tubules forming the paired pericardial glands. The tubules are lined with cells containing brownish-red concretions, and are distributed over a wedge-shaped area of the mantle extending, ventrally, from the most dorsal portion.\* The ventricle is prolonged backwards into a short narrow neck which still contains the rectum. A transverse membranous partition, beginning at the dorsal surface of this neck, extends backwards and downwards across its cavity, embracing the rectum, and ends so that its free edge lies near the ventral surface. This must form a valve preventing the reflux of blood into the ventricle from the posterior part of the body. Behind this valve the tube expands forming a "bulbus arteriosus" (*B.a.*, fig. 30) with thin muscular walls. This terminates in two lateral branches, the right and left posterior pallial arteries which diverge from each other and pass backwards beneath the posterior adductor. Here their walls become very ill-defined and communicate freely with a system of lacunæ between the bundles of the muscle. The arteries, which are now difficult to trace, reach the mantle margin and terminate in the sinuses there and in the walls of the siphons.

Anteriorly the ventricle passes into a single median vessel with well defined walls, the anterior aorta (*Ao.*, fig. 30); this pierces the posterior wall of the visceropedal mass, and travels along in the dorsal region of the latter, giving off, in its course, small vessels to the digestive gland. Near

\* Grobben, Dr. C. Die Pericardialdrüse der Lamellibranchiaten. Arbeit. Zool. Inst. Wien. Bd. VII. 1888.

the anterior margin of the visceropedal mass the aorta bifurcates; one vessel runs straight forward over the anterior adductor to the mantle lobes, forming the anterior pallial artery (*Art.p.a.*), the other passes straight downwards as the visceropedal artery. In its course this gives off a vessel from its anterior side which soon bifurcates, forming the right and left labial arteries (*A.lab.*). Still further down a large vessel is given off from the posterior side, the visceral artery (*Art.v.*), this runs back horizontally until it meets the straight portion of the intestine; branches are given off which supply blood to the rest of the gut. The main vessel is continued beyond this branch to the ventral surface of the foot as the pedal artery (*Art.p.*).

Only the above described vessels, constituting the arterial portion of the vascular system, have definite walls. The further course of the circulation lies in irregular lacunæ between the various organs, between muscle bundles, and in cavities in the connective tissues. The first focus of this system of venous channels is the renal sinus (*Sin.ren.*, figs. 4 and 30), an irregular blood space surrounding the tubules of the renal organ. Anteriorly this begins as a pair of blood spaces lying underneath the pericardium on each side of the middle line of the body ("venæ cavæ"). These unite into a large median cavity in the middle of the renal organ, from which the blood filters outwards round the system of tubules constituting that organ. Blood enters the renal sinus dorsally from the mantle lobes, and anteriorly from a vertical sinus in the posterior part of the visceropedal mass (*Sin.p.*, figs. 11 and 30). This communicates with the renal sinus through an opening in the muscular wall of the former, where the posterior retractor muscles of the foot take origin from the muscular body-wall. Here the arrange-

ment of the muscles is such as to constitute a valve regulating the flow of venous blood outwards from the visceropedal mass.

From the renal sinus the blood reaches the heart by passing through the gills. The precise path taken will be considered in connection with the structure of those organs and of the kidney.

#### THE RENAL ORGAN.

The renal organ is a single median structure. As seen from the ventral side it forms a crescentic mass with the convexity facing posteriorly, and the two horns, which are anterior, embracing the posterior retractor pedis (fig. 31, Pl. VI.). It forms part of the lateral and the whole ventral wall of that portion of the body lying between the visceropedal mass and the posterior adductor. Its posterior wall lies against the adductor. Its dorsal wall is applied to the ventral wall of the pericardium.

In front the renal organ consists of a single wide sac with a few secretory tubules opening into it along each side, but the diverging retractor muscles of the foot passing upwards through it on their way to their insertions in the shell, break up the posterior portion of this sac into three separate cæcal divisions (*Ren.*, fig. 7, Pl. II.). The median posterior division passes backwards between the diverging muscles, the right and left posterior divisions pass to the outside of the right and left muscles respectively. Each of these three divisions branches out behind the muscles into a great number of irregular secreting tubules, owing to which the mass of the organ is greatest at its most posterior part, that is, at the convex margin of the crescent.

It is, of course, not the actual renal sac, but the outer body-wall that is seen from the outside: between the renal

sac and the outer wall is the blood sinus surrounding the secretory tubules. The renal sinus communicates with the pedal sinus by perforations in the muscular wall of the visceropedal mass, as the pedal retractors originate from the latter. The muscles lie actually in the blood sinus. In front of them the sinus is a wide central cavity lying beneath the flattened renal sac, with renal tubules dipping into it on all sides except dorsally. The body-wall is gathered up into a pair of lateral folds, which take part in the formation of the bases of the ctenidia, and the blood from the central cavity filters through the spaces between the tubules into these lateral folds, and so into the gills.

The reno-pericardial canals (*Ren.per.*, fig. 4, Pl. II.) are a pair of large tubules which take origin on the lateral internal walls of the lateral posterior divisions of the renal sac. In sections they may be found on the part of the wall lying on the outside of each retractor muscle. They open into the renal sac by wide fimbriated mouths. Their walls near these openings are often peculiarly modified, and are produced out into several small diverticula, resembling the renal tubules. The canals pass downwards and forwards along the ventral wall of the renal sac, and come to open into the pericardium on the floor of the latter underneath the ventricle, by a pair of prominent slits. All along their course the tubules carry a lining of long cilia, and on the openings of the canals into the pericardium these are very prominent, especially in young specimens (0.5 to 1 cm.), where they sometimes form a ciliated fringe projecting into the latter.

The form and course of the renal tubules are very irregular, and in sections through the posterior margin of the renal organ it is at first sight difficult to distinguish between the tubules themselves and the blood sinus. This



can be done, however, by the character of the wall; the internal surface of the renal tubule (fig. 9) is formed by an irregular epithelium composed of large non-ciliated cubical cells with clear or very faintly granular contents. The cell walls are very definite; the nuclei lie at the bases on the lateral walls. The epithelium is supported on a sharply defined basement membrane, from which bridges of delicate fibrous tissue stretch across the blood spaces. The wall of the renal sac, other than that lining the tubule, has the same characters, except that the cells are smaller and more irregular.

#### THE BRANCHIÆ.

The general arrangement of the branchiæ (ctenidia) with respect to the other parts of the body, has already been described above. There is a single ctenidium on each side. Each of these organs consists of two branchial plates lying side by side in the mantle cavity, attached to a base containing blood vessels. Each branchial plate or branchia is again folded on itself so that it consists of two lamellæ. The lamellæ of the same branchia are bound together, but there is no connection between the two branchiæ except at the base of the ctenidium from which both take origin.

The base of the ctenidium (*Br'*, fig. 3, Pl. I.) is a ridge of the body-wall containing the blood vessels—the common afferent and efferent branchial vessels. The afferent vessel carries blood to both branchial plates, while the efferent vessel carries away the blood oxidised by contact with the water flowing through the mantle cavity. A flat band of muscle fibres runs along the ctenidial base from the posterior to the anterior extremities. The branchial nerve terminates in the posterior portion of the base.

The ctenidium of the left side is shown in fig. 2. The



inner branchia (*Br.I.*), which is the larger of the two, is narrowest behind where it fuses with the corresponding structure of the right side, and increases gradually in width towards its anterior margin which is attached to the body-wall, and is slightly overlapped by the labial palps. The outer branchia (*Br.E.*) is narrower than the inner, and is broadest at about midway between its two extremities. The two branchiæ of each side fuse together behind the visceropedal mass at their posterior extremities.

Each branchia consists of a large number of hollow filaments connected together at intervals. The direction of these filaments is at right angles to the ctenidial base. At the free ventral margin, where each branchia is folded on itself forming the two lamellæ, the filaments of the inner pass over with some modification in structure into those of the outer lamella. The whole ctenidium is cut obliquely to the base in fig. 4, and each of the two branchiæ is seen to be made up of a direct and a reflected lamella. For the greater part, these two lamellæ are intimately bound together: the precise nature of the connections is not, however, shown in the figure. In the inner branchia the external lamella (*Br.I.1*) which is inserted into the base of the ctenidium, is the direct one, and the internal lamella (*Br.I.2*) is the reflected one. Conversely in the outer branchia, the internal lamella (*Br.E.1*) is the direct one, and the external lamella (*Br.E.2*) is the reflected one. This difference in the disposition of the two branchia will be noticed, the inner lamellæ of right and left internal branchiæ fuse together in the middle line, and here the lamellæ (*Br.I.3*) are simply membranous plates, showing no sign of filamentar structure. These membranous portions of the inner lamellæ are continuous at the posterior extremities of the ctenidia

with the horizontal septum, which continues forward the fusion of the mantle edge between the two siphons, and consequently they form the floor of the ventral supra-branchial chamber which is a continuation forward of the cavity of the dorsal siphon. This ventral supra-branchial chamber is continuous with a series of cavities between the two lamellæ of the right and left inner branchiæ. The reflected lamellæ of the outer branchiæ, on the other hand, are filamentar in structure through all their width, and extend dorsally beyond the ctenidial base to be inserted into the body-wall in the angle formed by the latter and the mantle lobes. This dorsal extension of the reflected lamellæ of the outer branchiæ is common to a number of Eulamellibranchs, of which *Cardium* forms the type, and is the "appendice" of Pelseener, which is regarded by him as the beginning of a third lamella of the outer branchia.\*

The branchiæ of *Cardium* are of the "fluted or compound type," that is, each is thrown into a number of deep furrows and ridges, the direction of which is perpendicular to the base of the ctenidium. Two such ridges, with a furrow between, are represented in fig. 26—where the branchia is cut in a plane at right angles to the filaments. Each ridge consists of a group of from 20 to 30 filaments. One or two filaments may occupy the summit of the ridge, the bottom of the furrow is constituted by two filaments which have opened out and fused by their edges forming a membranous plate. In each branchia these ridges and furrows are symmetrically opposed to each other, ridge against ridge, and furrow against furrow. The supra-branchial cavity extends into the interior of each ridge.

Morphologically the branchia consists only of this

\* Bull. Sci. de la France et de la Belgique. Ser. III., t. XX., pp. 27—52, 1889,

double series of hollow filaments which were primitively vascular channels, the wall of the filament itself serving as the membrane through which the gaseous interchange between the blood and the surrounding water is effected. This simple arrangement is complicated here by the process of folding, which is described above, and further by a partial coherence of the filaments, which with the development of other vascular tissues, form two series of junctions within the branchia:—1st, a series of inter-filamentar junctions (*Br.j.1*, figs. 26 and 28, Pl. V.) joining the separate filaments in each lamella, and 2nd, a series of inter-lamellar junctions (*Br.j.2*, fig. 26) joining the two lamellæ of the same branchia. It will appear from a consideration of figs. 26 and 28 that this conjunctive tissue is not formed simply by the branchial filaments themselves, but also by vascular tissue developed from the base of the ctenidium. The whole of an inter-lamellar junction is constituted by this vascular tissue, the inter-filamentar junction, on the other hand, is formed both by the union of the adjacent walls of the filaments and by a separate vascular tissue. Wherever such an inter-filamentar junction occurs, the filaments taking part in it have split (fig. 28) and the adjacent edges of separate filaments have united. But underneath this place of union the vascular channel is completed by a sheet of connective tissue continuous with the tissue of the efferent or afferent vessels, as the case may be. If the whole lamella could be flattened out, it would appear as a trellis work of which the vertical bars would be formed by the filaments, the horizontal bars by the vascular inter-filamentar junctions. At intervals of every 40 or 50 filaments, vertical afferent and efferent vessels occur alternately, and between these vessels the blood circulates in the horizontal inter-filamentar junctions. But there must also be a

limited circulation of the blood through the filaments themselves.

There is a very regular segmental or repetitional structure in each branchia, which is due to the fluting and to the regular occurrence of the afferent and efferent vessels. At the base of each furrow is a vessel, the external wall of which is formed by the two flattened-out filaments already referred to. The rest of the vessel is formed from extra-filamentar tissue. Afferent and efferent vessels so formed alternate with complete regularity along the whole length of the branchia. There is this difference between the two series:—the afferent series (*Br.aff'*.) consists of a number of hollow plates extending uninterruptedly from the base to the ventral edge of each branchia, and also stretching across from external to internal lamellæ; each afferent vessel is thus common to the two lamellæ of the branchia; the efferent series consists of a number of nearly cylindrical vessels (*Br.eff'*.), one of which is present at the base of every alternate furrow. They must necessarily be double the number of the afferent vessels. The afferent vessels form the inter-lamellar junctions. It also follows from this arrangement that the suprabranchial cavity in the inter-lamellar space is divided up into a series of separate cavities having no connection with each other except at the base of the branchia.

Fig. 26 represents such a double segment in the internal branchia of one ctenidium. There are from 50 to 60 such segments in the length of the organ.

The separate filament (fig. 27) is in transverse section ellipsoidal in shape, the broader end is external, the more pointed end is internal. The outer surface is composed of large cubical cells, the inner surface of smaller cells. Within is an elongated cavity across which bridges of

delicate fibrous tissue pass from wall to wall, and which contains blood corpuscles. There are no skeletal structures.

In any section of the wall four cells are very obvious. Two of these are very large, one being situated on each lateral wall. Their nuclei are prominent but stain lightly. There is a very evident striated free border, and the cell bears a number of long and coarse cilia. The two other cells lie nearer the broad end of the filament, and resemble those described. The nuclei are, however, very large and stain intensely, so that they are very evident even under a low magnifying power. Between these two cells the outer wall of the filament is composed of cubical cells bearing short cilia. The inner surface consists of small cubical or even flattened cells.

Both the vertical afferent and efferent vessels and the inter-filamentar vessels have very thin walls composed of a flattened epithelium. Only a few fine trabeculæ cross the cavities of these vessels. It is obvious from a comparison of the area presented by this vascular tissue with the area of the filaments themselves, and from a comparison of the nature of the epithelia in each case that by far the greater part of the gaseous exchange in respiration must be effected through the wall of the vascular tissue proper and not through that of the filaments. The latter, in fact, form a mechanical tissue supporting the series of vascular channels, and by the action of their ciliated epithelium, causing the current of water from without to flow through the bars of the trellis work of each lamella into the supra-branchial cavities.

#### THE COURSE OF THE CIRCULATION.

The heart is a systemic one. Blood, with the waste products eliminated in the renal organ, and having under-

gone oxidation in the gills, is distributed through the body by two series of vessels; posteriorly it leaves the heart by the right and left posterior pallial arteries (*Art.pp.*, *Art.pp'*, fig. 30, Pl. V.), and reaches the siphons and the posterior mantle margin; anteriorly it traverses the aorta ( *Ao.*), which soon bifurcates; one branch, the anterior pallial artery (*Art.pa.*), passes over the anterior adductor and reaches the anterior mantle margin; the other branch descends the anterior part of the visceropedal mass as the visceropedal artery (*Art.vp.*). In its course this supplies blood to the labial palps through the right and left labial arteries (*A.lab.*), and again bifurcates, one branch, the visceral artery (*Art.v.*), penetrates the visceral mass and, passing first to the straight portion of the intestine, supplies the whole length of the latter, the other continues on to the bend of the foot.

Further than this, it is impossible to trace the afferent blood channels. Both in the mantle margin and in the visceropedal mass the arteries become lost in an irregular system of lacunæ, lying principally in the interspaces between the muscle bundles. This lacunar system represents the capillary and venous portions of the vascular system of a more highly organised animal, and it is here that the interchange between blood stream and tissues, in the metabolism of the latter, is effected. Two foci exist towards which the blood circulating in this lacunar system converges. From the anterior and posterior margins of the mantle lobes it flows in the ventral mantle edge towards the centre, then dorsally through the spaces in the interior of the thin mantle lobes towards the umbonal parts of the latter. Here there is a direct communication between the intrapallial lacunæ and the renal sinus, but the greater portion of the blood, after bathing the tubules of the pericardial gland, reaches the anterior corners of the auricles.



The second focus of the venous blood is the renal sinus, towards which all the blood circulating in the visceropedal mass converges. There are two large sinuses in the latter, an irregular sinus lying on the anterior margin and a posterior pedal sinus (*Sin.p.*) lying beneath the internal part of the posterior retractor muscles of the foot. As the latter are gathered up into the two compact muscle bundles which run upwards through the renal organ, they leave an opening in the muscular wall of the foot which leads into the two short longitudinal trunks, these, finally, open into the large central sinus in the middle of the renal organ (*Sin.ren.*, figs. 7 and 30).

From this central space the venous blood flows outwards, bathing the renal secretory tubules in its course, and enters two longitudinal vessels which run along the bases of the ctenidia. These are the common afferent branchial vessels (*Br.aff.*, fig. 30). From them a series of vessels, running perpendicularly to the bases of the ctenidia, enters each branchia—the afferent branchial vessels (*Br.aff'*., figs. 26 and 30). These communicate through the interfilamentar branchial junctions with a series of similarly disposed vessels—the efferent branchial vessels (*Br.eff'*., figs. 26 and 30), which fall into a pair of common efferent branchial vessels (*Br.eff.*), and these finally open into the auricles. From the auricles the blood enters the ventricle through the openings at the apices of the former, reflux being prevented by the action of the valves guarding these openings.

Menègaux\* bases a theory accounting for the protrusion of the foot, siphons, and mantle edges, on the anatomical relationships indicated above, *i.e.*, the presence of a valve

\* Recherches Sur le Circulation des Lamellibranches Marins. 296 pp., Besançon, 1890. Also Comptes Rendus de l'Acad. Sci., Paris. T. CVIII., pp. 361—364, 1889.



behind the ventricle and at the opening of the posterior pedal into the renal sinus. Since it has been proved that there is no entrance of water from without, either into the blood stream or into a closed water vascular system, the mechanism of the erection of the foot and siphon must be sought for in the intrinsic musculature of those parts or in arrangements whereby the blood pressure in localised regions of the animal's body can be varied at will. Since there appears to be no arrangement of muscles which can possibly bring about the protrusion of the siphons, the only other evident cause of this must be their distension with blood which is forced in from the heart through the posterior pallial arteries. The condition of "turgescence" in the siphons is probably initiated by the simultaneous relaxation of the constrictor muscle fibres at their bases, and of the retractor muscles. The lacunar spaces are thus enlarged and become distended with blood. The radial muscles and, to a certain extent, the constrictor muscles must function in preventing lateral expansion so that the blood pressure is distributed towards the tips of the siphons and is directed largely towards increasing their length. The valve behind the ventricle prevents the reflux of blood back into the heart. Retraction is abundantly provided for by the constrictor fibres of the siphonal walls and by the retractor muscle bundles.

Similarly the turgescence of the foot is initiated by the relaxation of the posterior and anterior retractores pedis. The entrance of the posterior pedal sinus into the renal organ is guarded by an arrangement of muscle fibres which is in effect a valve, and the closure of this is most probably the first effect of the relaxation of the posterior retractor of the foot, since in sections through this region, in an extended specimen, the opening is difficult to find.

Blood which is forced into the visceropedal mass by the increased action of the heart, is now retained there since there is no other exit than that into the renal sinus, and, as in the case of the siphons, an area of increased pressure is established. This, of itself, must tend to straighten out the two limbs of the foot, and this is in fact observed in cases of extreme distension. But the action of the intrinsic circular and transverse fibres also aids in the protrusion of the foot, since by their correlated contraction both diameters can be reduced and the increased pressure distributed towards the tip. Within the distal limb the courses of the intrinsic fibres are so various that no reliable deduction as to the result of their contraction can be made.

Retraction of the foot is provided for by the contraction of the posterior retractor pedis. This, first of all, opens the passage leading into the renal sinus and allows the blood in the foot to enter the latter space. Then both anterior and posterior retractors operate by their contraction in reducing the length of the proximal limb, and waves of contraction passing upwards from the tip chase the blood in the whole foot into the renal sinus. It does not appear from the disposition of the muscle, regarded here as the homologue of the "protractor pedis" in other Lamellibranchs, that its contraction can have any appreciable effect in the protrusion of any part of the visceropedal mass.

It follows from the above that in the condition of turgescence, the large blood spaces in parts of the body, other than the visceropedal mass, are relatively emptied of blood; and that conversely, in the contracted condition, those spaces are gorged. In sections made from the turgescient animal the empty condition of the renal sinus in particular is evident. In the contracted condition, blood

accumulates in the more dorsal intrapallial lacunæ and in the spaces round the adductors. The lacunæ in the contracted foot itself are only potential, and the circulation there must be largely confined to that taking place in the visceral artery and in the venous lacunæ round the intestine. This explanation of the condition of turgescence assumes that the quantity of blood contained in the body is sufficient to produce the distension of the parts in question. Fleischman has shown that this is the case for *Anadonta*, and the assumption may not unreasonably be made that it is the case also in *Cardium*.

#### THE NERVOUS SYSTEM.

The central nervous system in *Cardium* is constituted by the two separate, paired, cerebral ganglia, each of which represents the fusion of originally distinct cerebral and pleural ganglia; the single median pedal ganglion, formed by the fusion of originally lateral and paired pedal ganglia, and the single median parieto-splanchnic ganglion also formed from originally separate, right and left, ganglionic masses. There are two pairs of connectives, the cerebro-visceral connectives joining the cerebral and parieto-splanchnic ganglia, and the cerebro-pedal which connect the cerebral and pedal centres. The whole nervous system is bilaterally symmetrical.

The cerebral ganglion of each side (fig. 3, Pl. I., *Ga.c.*) lies quite superficially in the loose connective tissue between the bases of the labial palps, the anterior dorsal wall of the visceropedal mass, and the anterior adductor; and is easily exposed by removing the palps close to their attachments, and parting slightly the adductor from the adjoining body-wall. It is oval in shape and unpigmented. The right and left ganglia are joined together by the long cerebral commissure (*Com.*) which runs in the base of

the dorsal palp; four conspicuous nerves leave the ganglion on each side, and are easily observed.

The cerebro-visceral connectives (*Con.cv.*) run backwards and upwards in the loose tissue surrounding the ganglion; they pierce the muscular body-wall, and pass through the upper portion of the visceropedal mass embedded in the substance of the digestive gland. Leaving the latter they again pierce the posterior muscular body-wall near the external openings of the gonads, and slightly above the origin of the retractor muscles of the foot. Then they pass along the lower wall of the renal sinus to join the parieto-splanchnic ganglion.

The pedal connective of each side (*con.cp.*) runs downwards in the loose tissue round the ganglion for a short distance, then pierces the anterior muscular wall of the visceropedal mass, and passes vertically downwards on the internal surface of the latter to the pedal ganglion. The connectives are quite distinct, but lie close together in the middle line of the body; about half-way down in the course of each, a nerve is given off which passes backwards into the visceral mass.

A large nerve, the anterior common pallial nerve (*N.pa.*), leaves the anterior surface of each ganglion, and passes along the lower surface of the anterior adductor, and outwards from this on to the most anterior and dorsal corner of the mantle lobe. Just before leaving the adductor each pallial trunk bifurcates.

A very small nerve, the anterior adductor nerve (*N.add.*), leaves the ganglion near the origin of the anterior pallial nerve, and plunges into the posterior surface of the anterior adductor muscle.

Lastly, there is the strong cerebral commissure running over the dorsal wall of the mouth.

These are all the nerves that can be observed in the

course of dissection. In addition to these, several smaller twigs can be seen in sections, passing off from the ganglion into the surrounding tissue, some of these most probably innervate the labial palps.

The parieto-splanchnic ganglion (*Ga.sp.*, fig. 31, Pl. VI.) is best dissected by placing the animal (removed from the shell), ventral surface uppermost, and cutting through the wall of the lower siphon, the fused inner lamellæ of the internal branchiæ, and the horizontal shelf formed by the confluence of the two ctenidia and the septum between dorsal and ventral siphons. These parts are then folded back and the ganglion and its nerves are fully exposed.

This is the largest of the ganglionic centres, it is nearly square in shape. Indications of its origin from paired and lateral ganglia are seen in the two little anterior lobes, from which the connectives take origin. It is covered only by a single layered epithelium, and lies in a cavity; three nerves leave it on each side.

The cerebro-visceral connectives are the most delicate of the nerves leaving the ganglion. Each connective originates in one of the anterior lobes already referred to, and at once plunges into the renal sinus and passes through the latter, lying apparently free in the blood space. The further course has been described above.

The branchial nerves (*N.br.*) leave the ganglion from the anterior corners, and pass along in the wall of the afferent branchial vessels to the bases of the ctenidia. Where the latter become free from the body-wall the nerves bend round at a right angle, and pass backwards to the tip. Following Duvernoy and Drost\* I have termed these the "branchial nerves," though I have been

\* Drost, K. Über das Nervensystem u.d. Sinnesepithelien der Herzmuschel (*Cardium edule*), &c. Morphologisches Jahrbuch. Bd. XII., pp. 164—201; Taf x., 1886—7.

unable to demonstrate their actual endings in the tissues of the ctenidia.

The posterior common pallial nerves (*N.pp.*, fig. 31), are the stoutest of the nerves proceeding from the visceral ganglion. They leave the latter from its most posterior corners, and pass over the ventral surface of the adductor, reaching the mantle at the most lateral and posterior corners of the former. As they leave the muscle each nerve bifurcates; and the external branch, which is the largest, runs along the mantle edge as the external pallial nerve (*N.p.1*); the internal branch again divides, the outer of the two nerves so formed also runs in the muscular tissue of the mantle margin as the median pallial nerve (*N.p.2*); the inner one has its whole course in the thin tissue of the mantle within the line of insertion of the retractor muscles. This internal pallial nerve (*N.p.3*) is by much the most delicate of the three.

As each common pallial nerve passes over the adductor, two branches are given off from its external surface. These enter the wall of the dorsal siphon. Three other nerves leave the trunk after the branch forming the median and internal pallial nerves is given off. These enter the wall of the ventral siphon. Thus the two siphons are innervated by five nerves on each side, of which two enter the dorsal, three the ventral siphon. Anastomoses between the first three of these siphonal nerves are common, and gangliform enlargements may be observed at their points of origin from the mantle nerve or further out on their course.

The pedal ganglion (fig. 3, Pl. I., and fig. 33, Pl. VI.) is best exposed by removing the viscero-pedal mass, with the bases of the labial palps, and, therefore, the cerebral ganglia attached, and pinning it down in a dish with the anterior margin uppermost; the muscular body-wall is



then cut through in the middle line, and the two sides reflected outwards from below upwards, the attachments of the transverse muscle bundles being cut through as close to the body-wall as possible. The whole course of each cerebro-pedal connective is then exposed from the point where it perforates the muscular body-wall to its ending in the ganglion. The latter, with its nerves, is further exposed by picking away the transverse muscle fibres and the tubules of the gonad.

The ganglion (*Ga.p.*) is elongated in a transverse direction, and is rather oblong in shape. The cerebro-pedal connectives (*Con. cp.*) leave its upper and external borders. Half-way between the pedal and cerebral ganglia each connective gives off a small branch from its internal surface, which enters into the visceropedal mass.

Exclusive of the connectives four pairs of nerves radiate out from the ganglion. These enter into the surrounding tissue. One nerve, however, which is very thick, and which leaves the lower border of the ganglion, can be traced as far as the tip of the foot.

The pallial plexus is formed by the three pallial nerves described above. The anterior common pallial nerve, it has been stated, bifurcates on leaving the anterior adductor muscle; the inner of the two branches so formed gives off a very fine nerve on its internal side, and thus three pallial nerves, as in the case of the posterior common pallial trunk, are formed. These three nerves are, of course, identical with the three formed from the posterior trunk, and so each pallial nerve has a double origin, one extremity proceeding from the cerebral ganglion, the other from the visceral. At about the centre of the mantle margin, the middle and external nerves, which have hitherto kept widely apart from each other, come together and separate again, and at this point of contact a gangli-



form enlargement is formed. The external nerve gives off an abundant series of branches which pass outwards to the extreme mantle edge; between external and median, and to a less extent between median and internal nerves, there are numerous anastomosing branches. These anastomoses are particularly abundant in the neighbourhood of the branching of the common pallial trunks.

#### SENSE ORGANS.

The sensory structures in *Cardium* are:—(1) Sensory epithelial cells (Flemming's cells) in the integument; (2) visual organs borne by the siphonal tentacles; (3) a pair of otocysts in the proximal limb of the visceropedal mass.

(1) The sensory epithelial cells are found over the general body surface, but are more abundant on the mantle edge and on the siphons. On the latter they are present in groups in the depressions at the free extremities of the tentacles borne by the outer wall.\* They are either spindle-shaped cells with the nucleus at the middle and a bundle of long hairs on the free extremity, or elongated cells with the nucleus at the base and the free end swollen out into a disk, which bears short hairs. Probably they act both as tactile and as olfactory organs, the latter function being subserved more especially by the cells on the mantle edge and siphons.

(2) The structures generally regarded as visual organs (fig. 36, Pl. VI.) are found on the summits of the tentacles borne by the outer walls of both siphons. At the free end of each tentacle there is a small depression. The lip of this depression which faces the siphon is gently rounded,

\*Flemming. Untersuch. u.d. Sinnesepithelien der Mollusken. Archiv f. Mikr. Anat. Bd. VI., pp. 439—471, 1870.

and bears a somewhat crescentic patch of pigmented epithelium (*Ep.op.*); the other lip, which is turned away from the wall of the siphon, is sharp, and is raised up to form a screen. The nerve branch entering the tentacle from the posterior pallial plexus runs in the axial part, and at the summit swells out into a nearly globular ganglion (*Ga.op.*) consisting of large, clear, oval cells and a network of fibres. On the siphonal side of the tentacle this ganglion lies close to the wall. It is invested on all sides except towards the tip and the outer wall by a capsule of fibrous tissue, which stains deeply and homogeneously with staining reagents, has no nuclei, and shows little indication of cellular nature. On the tip of the tentacle the hair cells, referred to above, can be traced into the tissue of the ganglion. Nerve fibres from the latter probably spread round the edge of the incomplete fibrous capsule, not through its tissue.

The cells covering the tentacle generally are cubical in form with a continuous cuticle. Towards the tip, however, they become higher and columnar in shape, and the cuticle becomes less evident. On the pigmented spot the outer two-thirds of each of these columnar cells is filled up with brownish pigment, which takes the form of a dense mass of spherical granules lying perfectly free from each other. The nucleus is in contact with the lower layers of this mass of granules, but is usually quite free. The cell body seem to be composed of clear cell substance, in which are embedded the round pigment granules. Beneath the nucleus it is faintly fibrillar, the direction of the fibrillæ being that of the long axis of the cell. A narrow space separates this epithelium from the capsule surrounding the ganglion, and this space is filled by fine fibrous tissue. It is very probable that nerve fibres from the ganglion, passing round the edge of the capsule, form part of this layer, and some at least terminate in or among the cells

on the pigment patch, though the existence of such is difficult to demonstrate.

There can be little doubt that the structure so described functions as a very simple eye, capable only of distinguishing differences in the intensity of the incident light. Thus, if a shadow be rapidly thrown on a cockle lying in a shallow dish, with the siphons fully extended, retraction of the latter generally follows, and it seems reasonable to locate the sensitive parts in the structures on the tips of the tentacles. Very similar organs are found in other species of *Cardium*, and in *C. muticum*, Kishinouye\* has described organs on the tip of the siphonal tentacles which have all the characters of an eye—a multicellular lens composed of flattened cells, beneath which is a retinal layer of elongated cells, and beneath this again a pigment layer. The only other conjecture as to the nature of the structures described in the common cockle has been made by Brock,† who supposes them to be luminous organs; but it does not appear that there are any observations in support of this suggestion.

(3) A pair of otocysts (fig. 34, Pl. VI.) are present in the proximal limb of the visceropedal mass. They are very small—0.07 mm. in longest diameter, and can only be observed in sections taken in the neighbourhood of the pedal ganglion. They are situated a little way above the latter, right and left of the middle line and internal to the cerebro-pedal connectives. They are probably innervated from the latter. They are oval in form, the longest diameters lying parallel to the transverse axis of the foot. A

\*Note on the Eyes of *Cardium muticum*, *Reeve*. Journal Roy. Coll. of Science, Imp. University, Tokyo. Vol. VI., pt. 4, pp. 279—285, Pl. IX., 1894.

† Über die sogenannten Augen von *Tridacna*, &c. Zeitsch. f. wissenschaft. Zool. Bd. LXVI., pp. 270—88, Pl. XXI. (English translation in Ann. Mag. Nat. Hist., 1888, pp. 435—52).

prominent otolith, marked with concentric and radiating lines, exactly spherical in form, and about 0.02 mm. in diameter, is present. The wall of the otocyst is composed of a single, rather irregular, layer of cells; at the extremities of the long diameter are two single, nucleated cells, the cell bodies of which stain deeply, and on either side of each of these are several clear, apparently non-nucleated, spindle cells. The remainder of the wall is composed of irregular cubical cells. Hairs or cilia are not clearly shown. The nerves seem to enter at the internal poles of the organs. Each otocyst is surrounded by a loose investment of fibrous connective tissue, and but for this, lies freely among the transverse muscles of the foot.

#### THE REPRODUCTIVE ORGANS.

The gonad is paired and consists of a branching tubular gland. The external opening (see fig. 3, Pl. I.) is situated on the lateral and posterior body-wall, near the origin of the posterior retractor muscle of the foot. This leads into a very short terminal duct which immediately branches into three main divisions (fig. 3). One of these runs dorsally along the posterior margin of the visceropedal mass, the second downwards along the body-wall, the third duct runs obliquely forwards and downwards towards the bend of the foot. Branches are given off laterally from all these ducts on which are borne botryoidal clusters of secreting alveoli (fig. 37, Pl. VI.). These lateral branches penetrate among the transverse muscle bundles, between the convolutions of the intestine and between the lobes of the digestive gland. They lie principally in the peripheral zone of the proximal limb of the visceropedal mass. There is no extension at any time into the distal limb of the latter, nor into the mantle lobes.

In *Cardium edule* the sexes are separate. In at least

one other species of *Cardium*—*C. serratum* (= *C. norvegicum*), investigated by Lacaze-Duthiers,\* the animal is hermaphrodite; on the same branch duct alveoli are present, some of which are filled with ova, some with spermatozoa; and both genital products may be found even in the same alveolus. In the edible cockle there is little difference between the gonads of different sexes apart from their contents. The male gonad is less voluminous and more opaque.

In the animal taken during the spring or early summer the gonad is nearly filled with ova or spermatozoa, as the case may be. In a transverse section through an alveolus of the male gland (fig. 39, Pl. VI.) there is a peripheral zone of small, dense cells lying close to, and obscuring the wall. Where the latter can be observed it is seen to consist of a single layer of small, rounded cells supported on a delicate basement membrane. Within this is the zone of cells referred to, which results from the proliferation of the germinal epithelium forming the wall. Towards the centre of the alveolus these become smaller and denser as they become transformed into the mature spermatozoa. The elongated head pieces of the latter are arranged in radial streaks converging towards a portion of the wall, which does not consist of germinal epithelium, and where there is generally a slight space. The long tail pieces are directed towards this space and alternate with the rows of heads. In the alveoli this part of the wall, towards which the streaks of spermatozoa converge, is thin and presents no particular structure. In the larger ducts, however, it consists of a strip of ciliated epithelium where the cells are irregular and have clear cell contents. In

\* Recherches sur les organes génitaux des acéphales Lamellibranches. Annales des Sciences Nat. Ser. VI., t. II., Zool., pp. 153—248, Pl. V.—IX., 1854.

the duct, as in the alveolus, this only forms a small strip of the wall, the rest being composed of germinal epithelium.

In the female gonad (fig. 38), at a corresponding stage, the cavities of the ducts and alveoli are filled with eggs in various stages of development. As in the male gland there is a strip of the wall which in the alveolus is thin and membranous, and in the ducts is composed of a ciliated epithelium; the remainder of the duct consists of germinal epithelium which, in some parts, is composed of small, deeply staining cells with conspicuous nuclei. Many of these are enlarged and project out from the wall into the lumen; the largest eggs which are attached have a narrow, short stalk which forms part of the wall. The eggs lying freely in the cavity are flattened against each other by their mutual pressure, and are usually polygonal in section. Their true shape is oval (fig. 35, Pl. VI.). A very thick vitelline membrane (*M.vit.*), secreted apparently from the surface during the later stages of development, surrounds each. The cell contents are coarsely granular. The nucleus is a large, oval body, with a very sharp outline, faintly granular in texture, and with no apparent signs of chromatic material. A single, large, rounded, very distinct nucleolus is always present, the contents of which sometimes show a very regular vacuolation; within the ovary the eggs are frequently adherent together by their membranes.

The eggs and spermatozoa are shed in the early part of the year (March), and spawning apparently lasts till July or August. Fertilisation and development take place at large in the surrounding water, resulting in the formation of a typical veliger larva. After a short free-swimming stage, the velum is absorbed, the shell is formed, and the long vermiform foot is developed. The young cockle, then still less than 1 mm. long, settles down in the sand for the remainder of its existence.



APPENDIX.

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THE ECONOMY OF THE COCKLE WITH SPECIAL REFERENCE  
TO THE LANCASHIRE SEA-FISHERIES DISTRICT.

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THE cockle derives its economic importance from the fact that it is a suitable article of food, and that it is sufficiently abundant, at the same time, on large portions of the coast to give employment to a large number of people in gathering it for the markets. To a less extent, it is economically valuable in that it provides an abundant supply of food to some of the more important flat fishes.

## THE LANCASHIRE COCKLE FISHERIES.

A glance at the map of the Lancashire Sea-Fisheries District, reproduced in this Report, and which has been reduced from Mr. R. A. Dawson's sketch chart of the district, will show the great area covered by the cockle beds. Owing to the nature of the coast, where almost everywhere there are great stretches of clean sandy shore swept twice a day by the tides, there are very few places where the cockle may not be found. It is not, however, the mere occurrence of the animal that is considered in the chart, but its occurrence in sufficient quantities to render an area a sufficiently profitable fishing ground. The red coloured areas on the chart indicate approximately the position and extent of such profitable fishing grounds, and it is evident that these are numerous enough and of sufficient extent to render *Cardium* an animal of some importance to Lancashire fishermen, and to justify the regulation, to some extent, of the fishery.



The cockle beds in the whole district may be conveniently grouped into three principal divisions. At the most northern limit is the estuary of the Duddon, practically the whole of which is occupied by cockle beds. Then comes Morecambe Bay, the whole northern part of which is scattered over with cockle beds. On the western side of the Bay are the important Baicliff and Bardsea beds, and towards the eastward side are the Bolton-le-Sands beds. Between these, and reaching southward as far as Yeoman Wharf is a large stretch of sands over the whole of which cockle beds are found and regularly fished. The chart shows some coloured areas on the southern side of the Bay, but there the cockle fishery is very irregular. The Morecambe Bay and Duddon beds together form the Northern Division.

Between Rossall Point and Blackpool the coast is too exposed to admit of the formation of profitable cockle beds, but from Southshore to Southport is the estuary of the Ribble, containing some very important beds. The most northern of these, the Crusader Bank, is of little value, but the Salthouse and Horse Banks, lying further south, are very valuable, as a glance at Table I. will show. Those banks form the Central Division.

From Southport to below Formby Point is the second barren portion of the coast. Here cockles are to be found, but not in such quantities as to render the beds of any commercial value. South of Formby Point is a narrow strip of from two to three miles in length—Formby Bank—where cockles are very abundant. There are several important beds on the Cheshire Coast. The Formby, Leasowe, Hoylake, and West Hoyle beds are referred to hereafter as forming the Southern Division. There are also a number of areas containing cockle beds in the

estuary of the Dee, but these are not included in the Lancashire Sea-Fisheries district.

I estimate the area covered by cockle beds at 69 square miles in the Northern Division, 19 square miles in the Central Division, and 17 square miles in the Southern Division. Altogether there are not less than 105 square miles of cockle bearing sands in the whole district.

It must not be supposed that each of the coloured areas on the map represents a bank, or portion of a bank, over the whole of which cockles are abundant, and are continually being fished for. At any one time the fishing is practically restricted to one or more comparatively small portions of the bank, and as this becomes exhausted, or as the cockles become so small as to be under the legal size, the fishing shifts to some other part. The whole of a bank may become exhausted temporarily; this was the case in 1899 for the Formby Bank, though in 1897 it was a very profitable cockle fishing ground, as much as 180 cwts. being removed daily during the winter and spring. At present (1899) the cockles on this bank are, as a rule, under legal size; they are, however, exceedingly numerous, and a season similar to that of 1897 may be expected in 1900. Each coloured area on the map represents, in fact, a tract over which cockle beds are distributed. The precise position of the beds is continually shifting to some extent, old beds being exhausted by fishing, or being sanded up with the shifting of the sand banks. New beds are being formed, the position and extent of these being dependent on the deposition of the spat. The newly-hatched cockle leads, for a time, a free-swimming life, and with the acquirement of its shell, settles down for the remainder of its life in the sand. Obviously the conditions which determine the place on which the spat ultimately settles, and the consequent formation of a bed, are complex.

## THE YIELD OF THE COCKLE BEDS.

In seeking for figures on which to base an estimate of the productiveness of the Lancashire cockle fisheries, one turns naturally to the published statistics of the Board of Trade which relate to fisheries. Here, however, there is little available information, for statistics are only collected at the most important ports, and although the collectors discriminate between the various animals landed, crustacea (crabs, lobsters and shrimps), and mollusca (oysters, mussels and cockles) are included in the figures relating to "shell-fish." Owing to this latter cause, comparisons between the amounts of cockles landed at the same port during different years is impossible, and from the fact also that no account is taken of the produce landed at many important cockling centres, even an approximate estimate of the value of the Lancashire cockle beds cannot be made.

In the absence of any published data, an estimate of the value of the fishery has been attempted by finding approximately the number of cocklers employed on the various beds, and the amount gathered daily by each during the time of the year when the fishing is most active. Obviously, only an approximation to the true output of the beds can be made by this method, and it has been regarded as preferable to under-estimate rather than over-estimate the produce of the fishery. The totals given in Table IV. then represent, at the least, the value of the Lancashire cockle fishery. The figures, as to the number of cocklers, &c., have been given for the most part by the officers of the Lancashire Sea-Fisheries Committee. Those for the Northern Division are given by Mr. J. Wright, chief fishery officer at Piel, and the corresponding statement for the Southern Division by Mr. G. Eccles, chief officer at New Brighton. Mr. R. L. Ascroft has

supplied the information relating to the Central Division. This consists of an accurate statement of the amount of cockles landed, month by month, during the year June, 1898—May, 1899, at Lytham. This does not represent all the fishing in the Ribble estuary, and the amount of cockles taken in the Central Division and landed elsewhere than at Lytham is taken as approximately one and a half times the total shown in Mr. Ascroft's table.

TABLE I.—AMOUNT of COCKLES landed at LYTHAM during the year June, 1898—May, 1899:—

	Amount in cWTS.	Relative values. (=R)
June, 1898 ... ..	65	2
July ... ..	114	3·5
August ... ..	151	4·5
September ... ..	1250	37·5
October ... ..	3983	100
November ... ..	3254	100
December ... ..	2586	100
January, 1899... ..	3412	100
February ... ..	2278	69
March ... ..	1547	46·5
April ... ..	1316	40
May ... ..	1165	35
Total amount landed at Lytham ...	21121	
Amount taken in Central Division and landed elsewhere ... ..	30000	
Total amount taken from Central Division... ..	51121	

The figures in the third column show the relative values of the monthly takes expressed as percentages of the average take (3309) for the four months October—January.

In the construction of tables referring to the Northern and Southern Divisions it may be assumed, without serious error, that during the four months, October—January, the yield of the beds is practically constant. For the other

months it is further assumed that the amounts taken vary in a similar manner to those represented in the above table, since causes similar to those operating in the Central Division affect the monthly yield in the Northern and Southern Divisions. If, then, the amount taken in those districts in October be known, it becomes possible to construct a table showing the yearly take. The following table, compiled from information supplied by the fishery officers, shows approximately the amount taken in that month from the beds in the districts referred to.

TABLE II.—Showing the number of COCKLERS and the AMOUNT of COCKLES taken in October, 1899, in the NORTHERN and SOUTHERN DIVISIONS:—

		No. of Cocklers.	Amount gathered by each per day.	Total amount taken during the month of 25 days.
Northern Division.	Duddon ... ..	20	1 $\frac{1}{4}$ cwt.	625 cwt.
	Bailliff and Bardsea	50	1 $\frac{7}{8}$ „	2344 „
	Flookburgh Sands..	100	2 $\frac{1}{2}$ „	6250 „
	Bolton-le-Sands ..	15	2 $\frac{1}{2}$ „	937 „
Total take in October for Northern Division ... ..				10156 cwt. (=M)
Southern Division.	West Hoyle ... ..	20	3 $\frac{3}{4}$ cwts.	1875 cwts.
	Hoylake .. ..	10	2 $\frac{1}{2}$ „	625 „
	Leasowe ... ..	Average daily take=7 $\frac{1}{2}$ cwt.		187 „
Total take for October in Southern Division (except Crosby and Formby) ... ..				2687 cwt. (=M')

No account is taken in the above table of the small amount of fishing which goes on on the southern side of Morecambe Bay. It has been stated above that the cockling here is very irregular. Mr. Ascroft informs me that in 1861 and 1862 as many as twenty carts, with four cocklers to each, from Bolton-le-Sands, fished regularly on

Pilling Sands. At present, however, the fishing there is of little importance.

From this table, showing the extent of the fishing during the best time of the year, and the relative monthly values of the cockles taken, which is exhibited in Table I., an estimate of the amount taken throughout the whole district can now be made. This is given in Table III.; it is there assumed that the fishing is constant during the four months October—January. The values for the other months are calculated; they vary with respect to the value for October—January as the values R in Table I.

TABLE III.—Total YIELD in CWTs. of the beds in the whole DISTRICT during the year June, 1898—May, 1899.

	Northern Division. ( $=\frac{R}{100}M$ )	Central Division.	Southern Division. ( $=\frac{R}{100}M'$ )
June, 1898 ... ..	203	65	53
July ... ..	355	114	94
August ... ..	457	151	120
September ... ..	3808	1250	1007
October ... ..	10156	3983	2687
November ... ..	10156	3254	2687
December ... ..	10156	2586	2687
January, 1899 ... ..	10156	3412	2687
February ... ..	7007	2278	1854
March ... ..	4722	1547	1249
April ... ..	4062	1316	1074
May ... ..	3554	1165	940
Total amount landed at Lytham ... ..		21121	17139
Amount landed in Central Division else- where than at Lytham .. ..		30000	
Total yield of Fomby and Crosby beds during the year ... ..		... ..	650
Totals ... ..	64792	51121	17789

The money value of the cockles taken from the beds will depend on whether the price paid to the fishermen or

the price paid by the consumer is taken as the basis of calculation. Probably 2/- per cwt. represents the average value to the fisherman; this may possibly be too low, since a certain proportion of the cockles landed are hawked in the neighbourhood of the beds by the fishermen themselves. On the other hand, supposing the greater portion to be sent directly by rail to the markets, and adding the cost of freight and intermediate profits, 6/- per cwt. will represent fairly the price paid by the consumer.

TABLE IV.—MONEY VALUE of the COCKLE BEDS in the whole DISTRICT during the year June, 1898—May, 1899.

	Weight of Cockles in TONS.	Money value at £2 per TON.	Money value at £6 per TON.
Northern Division...	3240	£6480	£19440
Central Division ...	2556	5112	15336
Southern Division...	889	1778	5334
The whole District ...	6685	£13370	£40110

The striking variation in the monthly yield of the beds will be noticed. In the table relating to the Central Division the maximum amount is taken in October, and the monthly yield then decreases until, in the June following, only 2 per cent. of the amount taken in the previous October is landed. This variation in the fishing seems to be general in all parts of the district, and is apparently due to the difficulties encountered in sending the cockles to the markets, and in keeping them in the retail shops in a fresh condition during the relatively hot weather of June, July, and August. Other causes operate; in some parts of the district the cocklers leave the fishing for employment in the harvests, or in working pleasure boats at tourist resorts.



## REGULATIONS AND METHODS OF FISHING.

The Bye-laws of the Lancashire Sea-Fisheries Committee are directed towards the regulation of the cockle fishery in accordance with local conditions in various parts of the district, and the methods of fishing vary, to some extent, in the three principal divisions. Over all the district the "craam" may be used, but it is employed chiefly in the Duddon and Morecambe Bay areas. The "craam" is a metal three-pronged fork, fixed on a handle of about 18 inches in length. The prongs are about six inches in length, and about two inches of the extremity of each is bent downwards at a right angle. The cockler pushes a fish basket along the sand in his left hand, and scoops the cockles, one by one, out of the sand into the basket, with the "craam." Often the tuft of Algæ on the shell of the cockle indicates its presence in the sand, but, as a rule, they are so abundant that the "craam" plunged into the sand brings up a cockle. Over the whole district the "Jumbo" may be used, but only from November to February, both months included. Fishing by means of the "Jumbo" is an extension of the method of treading on the sand with heavy boots, in which process the cockles are forced up to the surface and are then gathered. The "Jumbo" is a wooden frame, with a base consisting of a board, the maximum dimensions of which are  $4\frac{1}{2}$  feet in length, 14 inches in width, and 1 inch thick. The frame, with this base-board resting on the sand, is rocked backwards and forwards, with the result that the cockles are forced out of the sand on to the surface, and are then gathered up.

Special regulations apply to the central and southern parts of the district: in the part of the Central Division lying between Formby Point and the Gut Channel in the Ribble, the use of a spade is permitted. The spade is

used to remove the upper layer of sand to the depth of about an inch and half. The cockles occupy this layer and are thus exposed. The use of a spade is not permitted in the other parts of the district. Southward of "Rossall Landmark," near Fleetwood, that is, over the whole of the Central and Southern Divisions, the use of the cockle rake is permissible; the cockle rake does not differ greatly from the ordinary garden rake, but may not exceed 12 inches in length. Thus, in the Northern Division the craam and the limited use of the Jumbo are permitted; in the Central Division the craam, Jumbo, rake, and spade; in the Southern Division the craam, Jumbo, and rake. Practically all the fishing in the Southern Division is done by the rake.

A minimum size, below which a cockle is not legally saleable, is fixed by the Committee's Bye-law, and extends to all parts of the district. This minimum size is that of a cockle which will exactly fit into a rectangular opening in the "gauge" carried by the fishery officer. This opening is two inches in length, and three-quarters of an inch in breadth; the ratio of length to lateral breadth in the cockle is, of course, variable within certain limits, and the smallest legal-sized cockle may be defined as the cockle whose lateral breadth, from valve to valve, when the shell is closed, is just over three-quarters of an inch. This standard of size is, of course, a purely arbitrary one, and has no definite relation to any particular phase in the life-history of the animal: the cockle becomes sexually mature before it has attained this size, and probably has spawned once. It most probably represents the size of the animal which is over two and less than three years of age. But the rate of growth of the cockle certainly differs, probably to a considerable extent, on various parts of the Lancashire and Cheshire coasts. On

the Baicliff and Bardsea beds the average cockle picked out of the fisherman's basket shows, at most, only three of the lines of growth on the shell, which are referred to at the beginning of this Memoir; in the Southern Division, on the Cheshire coast, four or five are generally present in the average specimen. Growth is most rapid in the summer months; on the Baicliff beds, according to the fishermen, the cockles in part of a bed, which are under gauge size in April, may be of legal size in June or July; in that period the shell has increased in girth by as much as half an inch.

The legal size is convenient and most probably eminently useful. On the principle that a marine food animal ought to be allowed the chance of spawning at least once before it is captured for the market, the Bye-law must be regarded as operating for the preservation of the cockle fishery. The present condition of the Crosby and Formby cockle beds is a case in point; here the difference in the output of the beds (180 cwts. daily in the winter of 1897—8, and  $12\frac{1}{2}$  cwts. weekly during the year 1898—9) points to the over-fishing of the beds, which was, of necessity, followed by their temporary exhaustion. But since the cockles then became, on the average, so small as to fall under the gauge size, the fishing of the beds practically stopped for a time. During this period spawning of the remaining cockles went on, the beds being, to a large extent, undisturbed, and it is to be expected, from their present condition, that the fishing will again become abundant.

No close time, as in the case of the common mussel, is enforced. It will be seen from a consideration of the monthly output of the Ribble beds, exhibited in Table I., that natural causes lead to the suspension (to a great extent) of the fishing during the summer months. A certain amount of spawning goes on during May, June,

and July, so that, as in the case of the mussel, the animal is protected for at least a portion of its yearly spawning period.

No recent data exist on which to base an opinion as to whether the supply of cockles from the beds in the whole district is increasing or decreasing; but in 1879 Buckland and Walpole, in the course of an examination into the state of the Sea-Fisheries of England and Wales,\* made a special investigation into the cockle fishery in Morecambe Bay, and obtained data which enable a comparison to be made between the output of the beds at the beginning and end of a period of 21 years.

The Commissioners estimated the value of the produce of the Morecambe Bay cockle beds for the year 1877 at over 3,943 tons in weight, and at £20,000 in money value. Cockles were taken by them as worth £5½ per ton. These figures agree fairly well with those given in this Memoir. For the year 1898—99 the amount landed is estimated at 3,240 tons, and their money value at £19,440. Here, however, £6 per ton is taken as representing the retail price. It is not certain from the Commissioners' Report whether they regarded £5½ per ton as the price received by the fishermen, or as the price paid by the consumer. It was also stated in evidence to the Commissioners that 100 carts, with six or seven people to the cart, were employed cockling in Morecambe Bay. This is far in excess of the number estimated as at present employed in the same area.

A more exact means of forming a comparison is furnished by the return from the Furness Railway Company, which is published in the Report for 1879. I am indebted to the courtesy of Mr. Aslett, the present

\* Report of the Commissioners for Sea Fisheries on the Sea Fisheries of England and Wales. 1879, pp. 21—23.

manager of the Furness Railway Company, for a similar statement for the year 1898, which is here reproduced.

TABLE V.—WEIGHT OF COCKLES, IN TONS, forwarded from ten stations on the FURNESS RAILWAY for the two years 1877 and 1898:—

Stations.	1877.	1898.
Barrow ... ..	10	0
Piel ... ..	70	0
Dalton ... ..	80	0
Askam ... ..	220	72
Millom ... ..	343	0
Ulverston ... ..	290	341
Cark... ..	1160	1696
Kent's Bank ... ..	25	154
Arnside ... ..	5	0
Silverdale ... ..	50	0
Total ... ..	2253	2263

The above Table shews that the amount of cockles forwarded by the Furness Railway Company in 1877 from ten of their stations does not differ by so much as a half per cent. from the amount sent by them in 1898 from the same stations. These figures represent the greater portion of cockles sent from Morecambe Bay and Duddon. To complete the comparison the amount taken from the southern side of the Bay has to be estimated. The Commissioners valued this as worth £5,000, that is, about 940 tons were taken from the Bolton-le-Sands and Pilling Sands beds in 1877. Since these areas are served by the London and North-Western Railway Co., the amount stated does not appear in the Table. From the data obtainable in the course of the present inquiry, it appears that the amount of cockles taken from the same areas does not exceed 300 tons, and the falling off in the produce of these beds accounts for the apparent decrease in the

interval between 1877 and 1899; that is, in 1877 the weight of cockles taken from the whole Bay was approximately 3,940 tons, in the year 1898—99, considered in this Report, it was 3,240, the difference being approximately equal to the decrease in the produce of the beds on the southern side of the Bay. But the irregular nature of the fishing here has been already commented on, and it is fair to conclude that the decrease is only a temporary one.

In this comparison the change in the conditions of the fishery must be borne in mind. In 1877 the fishing was not regulated in any way, and cockles of any size might be sent into the markets, but at the present time, only cockles having the minimum breadth of three-quarter inch are allowed to be landed and consequently sent over rail, so that on the areas compared, cockles must now be more abundant than in 1877.

On the whole, it does not appear that there has been any permanent decrease in the cockle fishery of Morecambe Bay proper. Fluctuations from year to year have been experienced, and it may be gleaned from the Board of Trade Statistical Tables that though there have been some lean years, such as 1895—96, others—such as 1897—have been correspondingly fat, and that, on the whole, the fishing has been, if anything, improving. It has not been possible to investigate the rest of the District to the same extent, but it may be safely assumed that there also, the yield of the beds has been, on the whole, maintained. The Commissioners of 1879, as the result of their inquiries, stated that they had “been unable to trace any decrease in the fishery.” So far as the data obtained in the course of the present investigation go, that statement may be safely repeated.

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## EXPLANATION OF PLATES.

## Reference Letters.

<i>Al.c.1.</i> cesophagus.	<i>Br.I.</i> internal branchia.
<i>Al.c.2.</i> stomach.	<i>Br.E.1.</i> inner lamella, external
<i>Al.c.3.</i> straight division of the intestine.	branchia.
<i>Al.c.3'.</i> sac of crystalline style.	<i>Br.E.2.</i> outer ,, ,, ,,
<i>Al.c.3''.</i> digestive division of the straight intestine.	<i>Br.I.1.</i> ,, ,, internal ,,
<i>Al.c.4.</i> spiral division of the intestine.	<i>Br.I.2.</i> inner ,, ,, ,,
<i>Al.c.5.</i> coiled division of the in- testine.	<i>Br.I.3.</i> ,, ,, ,, ,,
<i>Al.c.6.</i> rectum.	membranous portion.
<i>An.</i> anus.	<i>Br.aff.</i> com. afferent branchial vessel.
<i>Add.a.</i> ant. adductor muscle.	<i>Br.aff.</i> com. efferent branchial vessel.
<i>Add.a'.</i> ant. adductor impres- sion.	<i>Br.aff'.</i> efferent branch. vessel.
<i>Add.p.</i> post. adductor muscle.	<i>Br.aff'.</i> afferent branch. vessel.
<i>Add.p'.</i> post. adductor impres- sion.	<i>Br.j.1.</i> inter-filamentar junct.
<i>Art.pa.</i> anterior pallial artery.	<i>Br.j.2.</i> inter-lamellar junction.
<i>Art.pp.</i> right posterior pallial artery.	<i>By.g.</i> byssus gland.
<i>Art.pp'.</i> left post. pallial artery.	<i>By'.</i> pedal groove.
<i>Art.vp.</i> viscero-pedal artery.	<i>By.</i> byssus thread.
<i>Art.v.</i> visceral artery.	<i>Com.</i> cerebral commissure.
<i>Art.p.</i> pedal artery.	<i>Con.cv.</i> cerebro-visceral con- nective.
<i>A.lab.</i> right and left labial arteries.	<i>Con.cp.</i> cerebro-pedal connec- tive.
<i>Ao.</i> aorta.	<i>Dg.</i> digestive gland.
<i>Aur.</i> auricle.	<i>Ep.I.1.</i> epithelium of wall of crystalline style sac.
<i>Ba.</i> bulbus arteriosus.	<i>Ep.I.2.</i> elongated cells in wall of crystalline style sac.
<i>Br'.</i> base of right ctenidium.	<i>Ep.I.3.</i> epithelium of intestinal div. of straight intest.
<i>Br.E.</i> external branchia.	<i>Ep.op.</i> pigment cells of an eye.
	<i>Ep.p.</i> epidermis of the foot.



- Epic.* epicuticula (periostracum) *N.p.3.* internal pallial nerve.  
*F.tri.* tricuspid body. *N.t.* tentacular nerve.  
*Go.* right gonad. *Pro.* protractor pedis.  
*Ga.c.* right cerebral ganglion. *Pro'.* protractor muscle im-  
*Ga.sp.* parieto-splanchnic gang-  
 lion. *Pa.d.* dorsal labial palp.  
*Ga.p.* pedal ganglion. *Pa.v.* ventral labial palp.  
*Ga.op.* optic ganglion. *Ped.1.* proximal limb of the  
*Lig.* hinge ligament. visceropedal mass.  
*Lith.* otolith. *Ped.2.* distal limb ,, ,,  
*M.* mouth. *Per.* pericardium.  
*Mn.* mantle lobe. *Ret.a.* anterior retractor pedis.  
*Mn'.* cut edge of mantle lobe. *Ret.a'.* scar of attachment of  
*Mn.1.* anterior prolongation of anterior retractor.  
 intersiphonal partition. *Ret.p.* posterior retractor pedis.  
*M.c.1.* anal division of mantle *Ret.p'.* posterior retractor pedis  
 cavity. impression.  
*M.c.2.* cavity of dorsal siphon. *Ret.m.* retractor muscles of the  
*M.c.3.* general mantle cavity. mantle edge.  
*M.c.4.* ventral suprabranchial *Ret.m'.* impression of retrac-  
 cavity. tors of mantle edge.  
*M.c.5.* dorsal suprabranchial *Ret.s.* retractor muscles of the  
 cavity. siphons.  
*M.vit.* vitelline membrane. *Ret.s'.* impression of retractors  
*M.p.i.* straight transverse pedal of the siphons.  
 muscles. *Ren.* renal organ.  
*M.p.c.* circular pedal muscles. *Ren'.* external opening of renal  
*M.p.o.* oblique pedal muscles. organ (ureter).  
*M.p.l.* long. pedal muscles. *Ren.per.* reno-pericardial canal.  
*N.add.* nerve supplying ant. *Si.d.* dorsal or exhalent siphon.  
 adductor. *Si.v.* ventral or inhalent siphon.  
*N.br.* branchial nerve. *Sh.e.* outer shell layer.  
*N.pa.* ant. com. pallial nerve. *Sh.i.* inner shell layer.  
*N.pp.* post. com. pallial nerve. *Sin.p.* posterior pedal sinus.  
*N.p.1.* external pallial nerve. *Sin.ren.* renal sinus.  
*N.p.2.* median pallial nerve. *St.* crystalline style.

<i>Ty.</i> typhlosole.	V ventral.
<i>Ven.</i> ventricle.	E external.
A anterior.	I internal.
P posterior.	R right.
D dorsal.	L left.

## PLATE I.

- Fig. 1. Cockle with the foot and siphons moderately extended, seen from the right side. Nat. size.
- Fig. 2. External anatomy; the left valve and part of the left mantle lobe have been removed. Nat. size.
- Fig. 3. General anatomy; the right valve and mantle lobe have been removed, and the right wall of the visceropedal mass cut away to expose the intestine; the right wall of the pericardium is cut away; the right branchiæ are removed. Magnified  $2\frac{1}{2}$  diameters. The figure is slightly diagrammatic; the convolutions of the intestine are represented as pulled apart, and for clearness, as being less in diameter than the magnification of the figure warrants. Their exact relations are seen in the section represented in fig. 11.

## PLATE II.

- Fig. 4. Section passing through the ureters transversely to the long axis of the shell, and cutting the branchiæ obliquely.  $\times 3$  diam.
- Fig. 5. Transverse section through the bases of the siphons.  $\times 4$  diam.
- Fig. 6. Transverse section through the posterior adductor muscle.  $\times 4$  diam.

- Fig. 7. Section through part of the body passing through the anterior part of the renal organ parallel to the branchial filaments.  $\times 12$  diam.
- Fig. 8. Blood corpuscles from one of the branchial vessels. Zeiss apo. 1.5, compens. oc. 4.
- Fig. 9. Transverse section through a renal tubule.  $\times 500$  diam.
- Fig. 10. The left valve of the shell, seen from the inside. Nat. size.

## PLATE III.

- Fig. 11. Section through the middle part of the proximal limb of the visceropedal mass, transverse to the axis of the latter, and in the horizontal plane of the body.  $\times 7$  diam.
- Fig. 12. Transverse section through the straight portion of the intestine.  $\times$  about 50 diam.
- Fig. 13. Transverse section through the spiral portion of the intestine.  $\times 50$  diam.
- Fig. 14. Transverse section of the rectum near the anus.  $\times 50$ .
- Fig. 15. Section through part of the digestive gland, showing the transition from ciliated to glandular epithelium.  $\times 50$  diam.
- Fig. 16. Transverse section of a secreting alveolus from the digestive gland. Zeiss apo. 1.5, compens. oc. 4.
- Fig. 17. Transverse section of part of a bile duct.  $\times 500$  diam.
- Fig. 18. Vertical section through part of the stomach wall.  $\times 280$  diam.

## PLATE IV.

- Fig. 19. Transverse section of the secreting portion of the byssus gland. The section is cut transversely to the long axis of the foot.  $\times 60$  diam.
- Fig. 20. Longitudinal section through a single alveolus of the byssus gland.  $\times 570$  diam.
- Fig. 21. Vertical section through part of the body-wall of the distal limb of the visceropedal mass, showing a mucous gland cell opening through the epidermis on to the surface of the foot. Zeiss apo. 1.5 mm., compens. oc. 12.
- Fig. 22. An isolated mucous gland from the distal limb of the visceropedal mass. Zeiss apo. 1.5 mm., compens. oc. 12.
- Fig. 23. A radial vertical section of the mantle edge.  $\times 30$  diam.
- Fig. 24. A section through the internal labial palp, passing parallel to the longest border.  $\times 80$  diam.
- Fig. 25. Vertical section through the muscular body-wall of the proximal limb of the visceropedal mass.  $\times 120$  diam.

## PLATE V.

- Fig. 26. Part of a section through a branchia, transverse to the branchial filaments, and including two groups of filaments.  $\times 80$  diam.
- Fig. 27. Transverse section of a single branchial filament. Zeiss apo. 1.5 mm., compens. oc. 4.
- Fig. 28. Transverse section through two adjacent branchial filaments, showing the interfilamentar junction.  $\times$  about 600 diam.

- Fig. 29. Part of a section through the shell, passing vertically to the shell surface and perpendicular to a line of growth.  $\times$  about 25.
- Fig. 30. A schematic representation of the course of the principal blood vessels and channels as seen from the right side.

## PLATE VI.

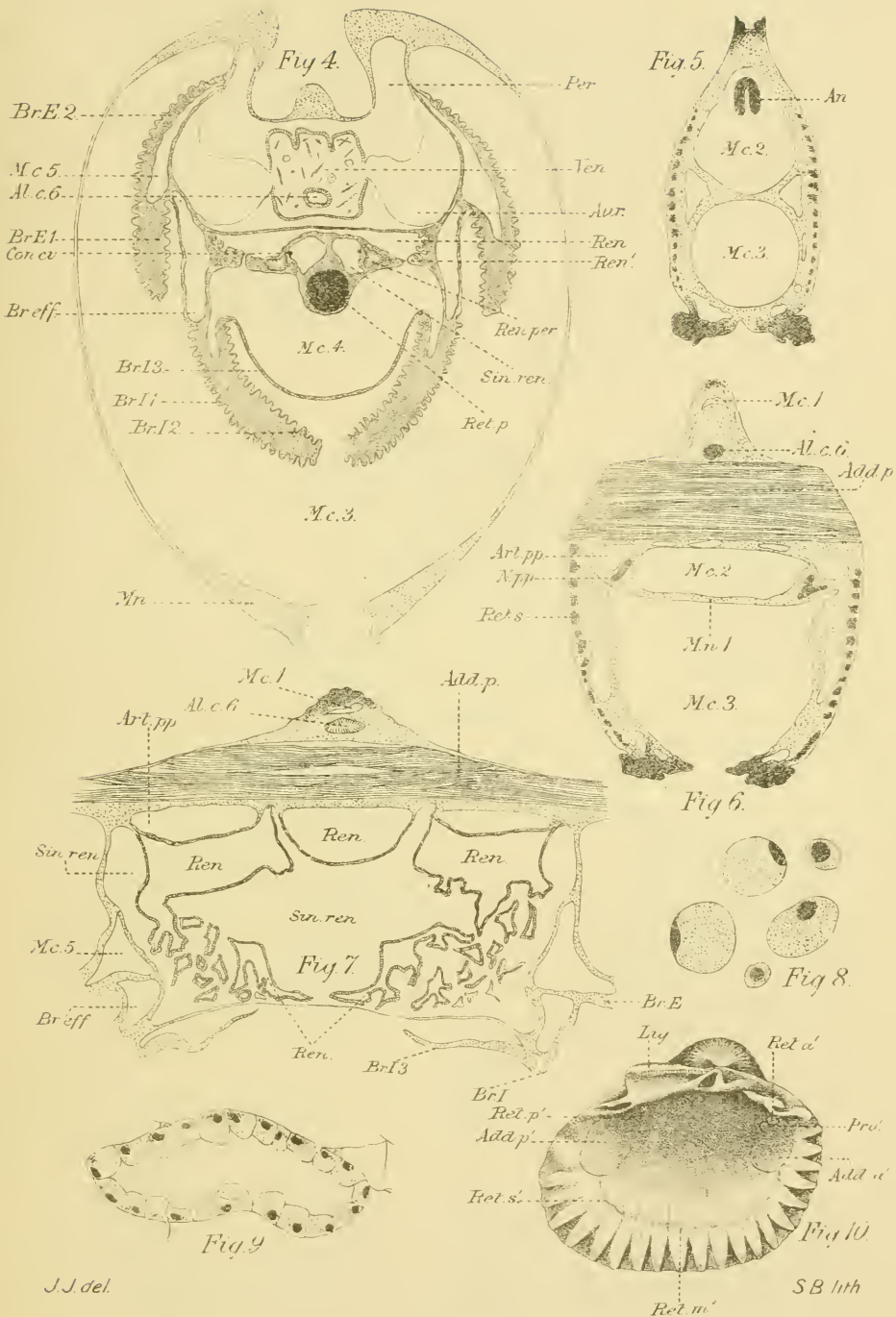
- Fig. 31. Dissection of a cockle from the ventral side, to show the visceral ganglion and nerves. Only the portion of the body behind the visceropedal mass is shown. The fused portion of the inner lamellæ of the two internal branchiæ is cut through in the middle line, and the septum between the siphons and the horizontal shelf continuing this forward are cut likewise.  $\times$  about 2 diam.
- Fig. 32. Dissection to show the right cerebral ganglion and surrounding parts. The extremity of the anterior adductor has been cut away and the muscle separated slightly from the anterior wall of the visceropedal mass. The right labial palps are mostly removed.  $\times$  4 diam.
- Fig. 33. Dissection of the proximal limb of the visceropedal mass from its anterior margin to show the pedal ganglion and nerves. The anterior body-wall and the underlying muscles and genital gland tubules have been removed.  $\times$  3.
- Fig. 34. The otocyst of the right side in longitudinal section. Zeiss apo. 1.5 mm., compens. oc. 4.
- Fig. 35. Section through an ovarian egg.  $\times$  about 200 diam.

- Fig. 36. Transverse section through the tip of a siphonal tentacle passing through an "eye." Zeiss apo. 1.5 mm., compens. oc. 4.
- Fig. 37. A group of secreting alveoli from the nearly ripe ovary.  $\times 25$  diam.
- Fig. 38. Transverse section through two contiguous alveoli from a nearly ripe ovary, showing the germinal epithelium and the eggs lying freely in the lumina of the alveoli.  $\times 90$  diam.
- Fig. 39. Transverse section through three alveoli from a nearly ripe testis.  $\times 90$  diam.









CARDIUM.



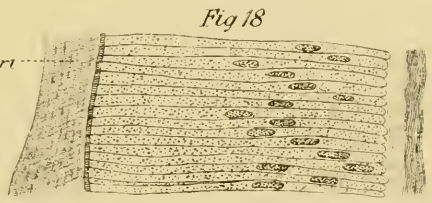
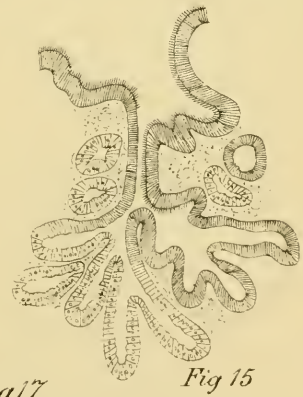
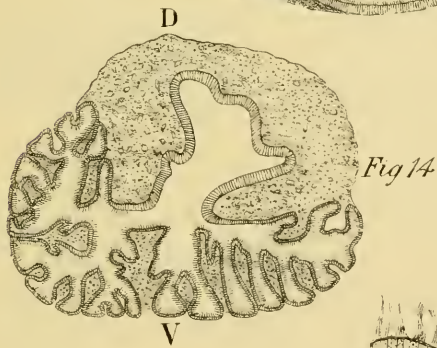
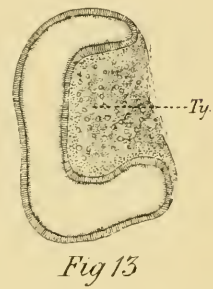
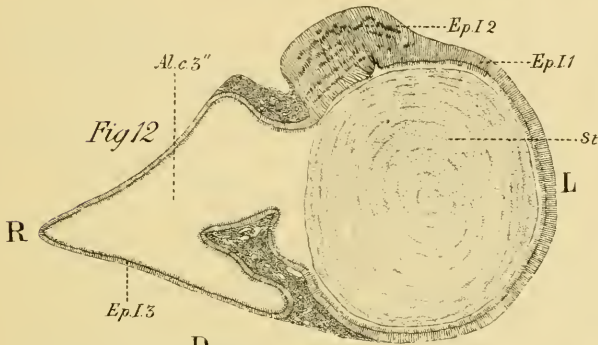
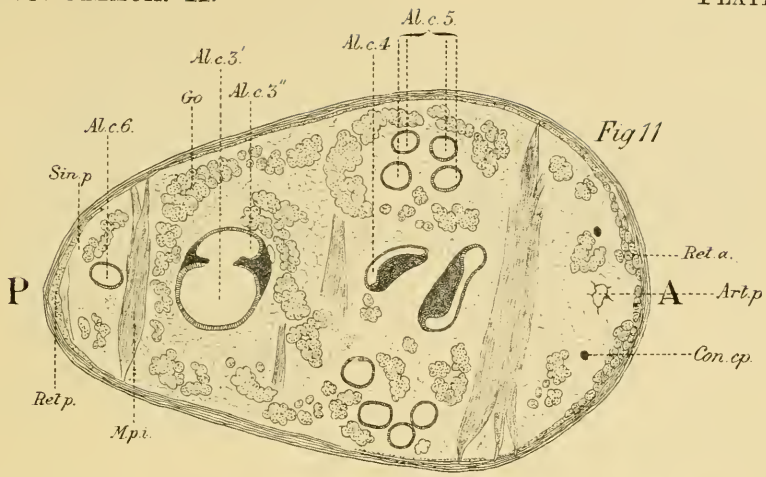






Fig. 19.

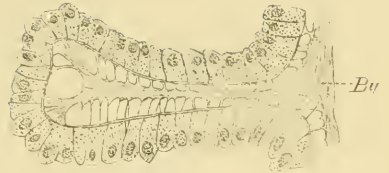


Fig. 20.



Fig. 21.



Fig. 22.

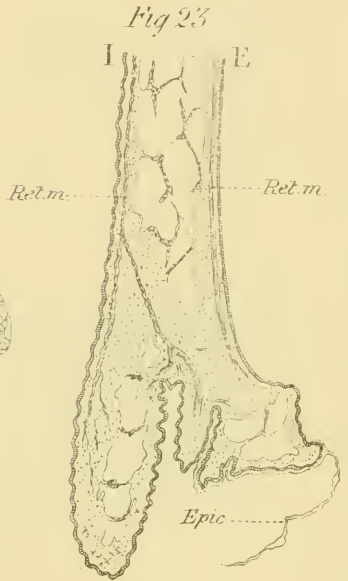


Fig. 23.



Fig. 24.

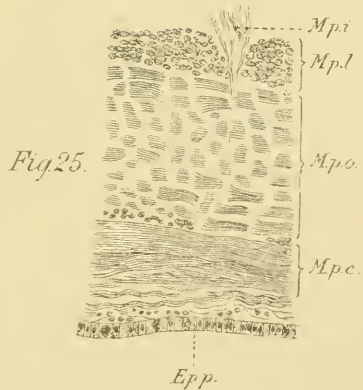


Fig. 25.

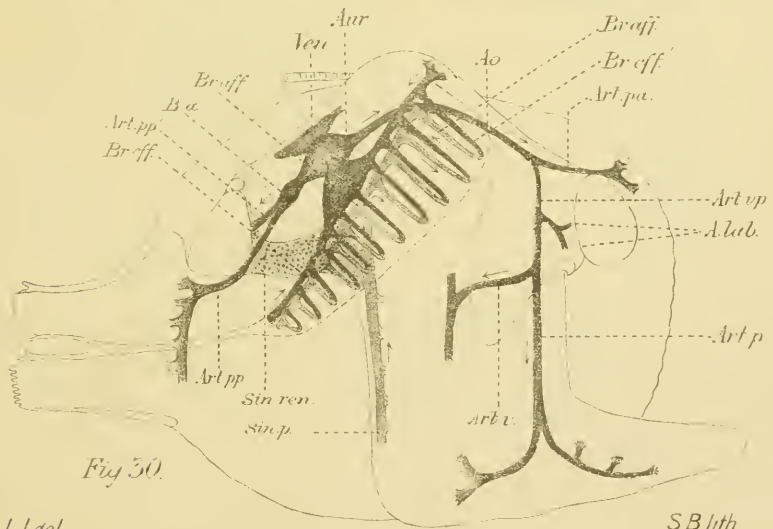
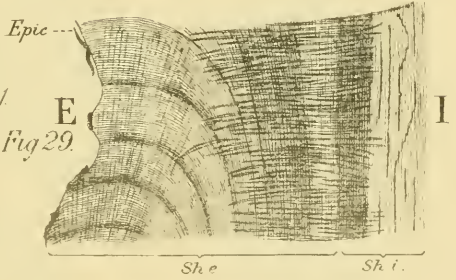
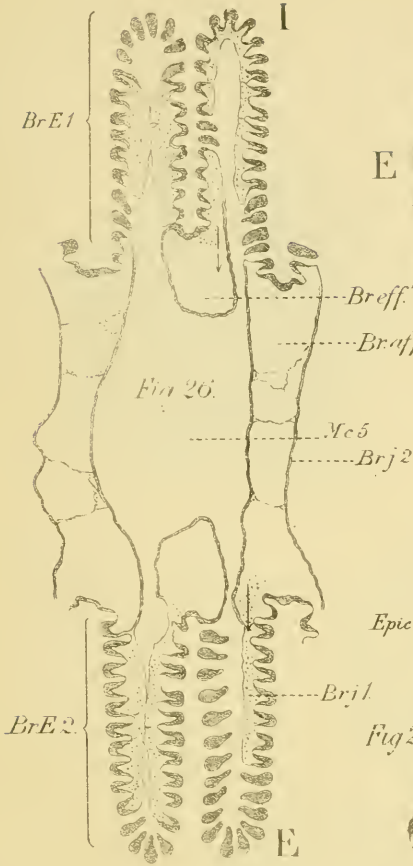
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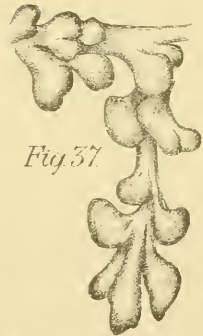
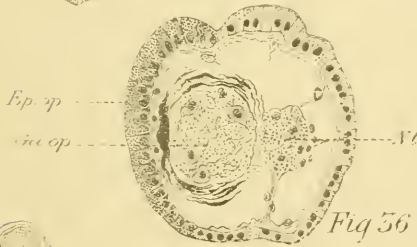
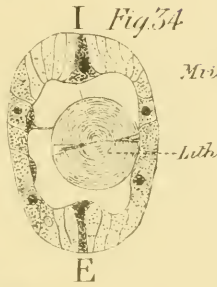
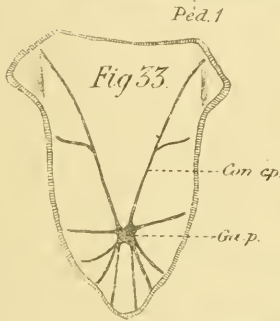
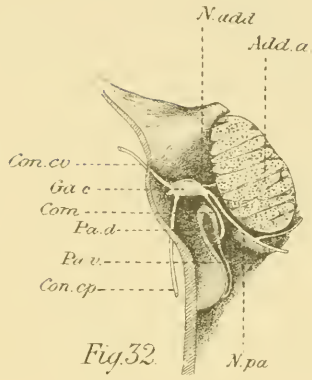
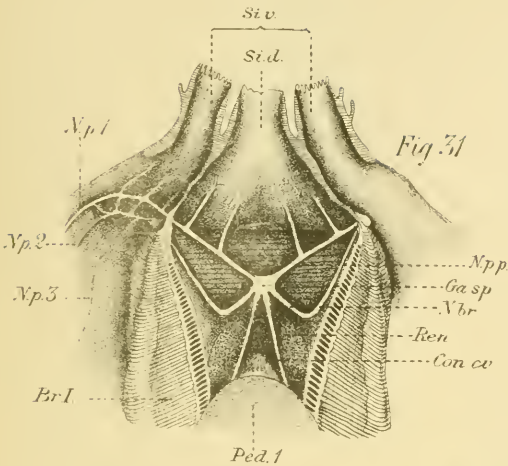


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