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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.

XVII.

PECTEN

BY

W. J. DAKIN, M.Sc.,

1851 Exhibition Scholar in Zoology, University of Liverpool

(With 9 Plates)

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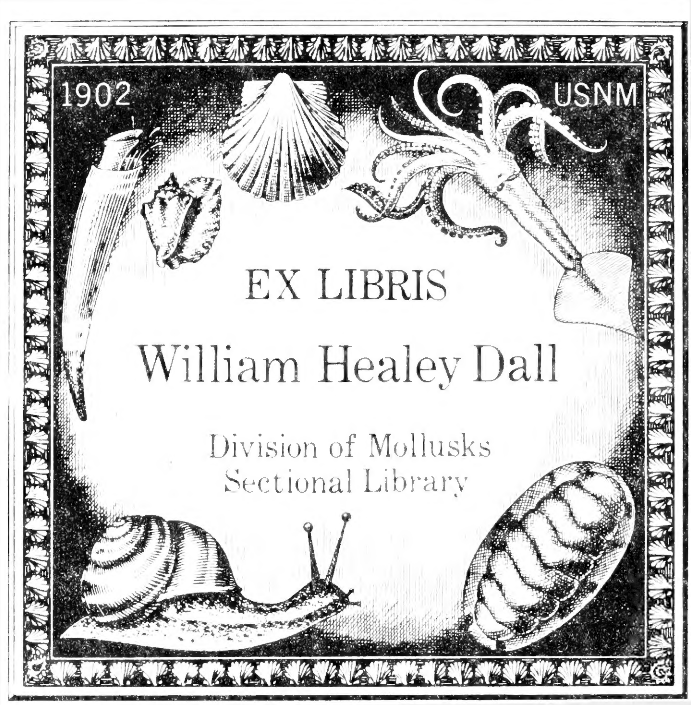
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Liverpool Marine Biology Committee.

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EDITOR'S PREFACE.

The Liverpool Marine Biology Committee was constituted in 1885, 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have been carried on intermittently since that time, and a considerable amount of material, both published and unpublished, has been accumulated. Twenty-one Annual Reports of the Committee and five 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 accessible Station at Port Erin in the centre of the rich collecting grounds of the south end of the Isle of Man. A new and larger Biological Station and Fish Hatchery, on a more convenient site, has since been erected, and was opened for work in July, 1902.

In these twenty-one years' experience of a Biological Station (five years at Puffin Island and sixteen at Port Erin), where College students and young amateurs form a large proportion of the workers, the want has been frequently 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 the Committee and of the workers at the Biological Station were at first chiefly faunistic and speciographic. The work must necessarily be so when opening up a new district. Some of the workers have published papers on morphological points, or on embryology and observations on life-histories and habits; but the majority of the papers in the 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 still further to the records of the Fauna and Flora. But the papers in the present series, started in 1899, are quite distinct from these previous publications in name, in treatment, and in purpose. They are called "L.M.B.C. Memoirs," each treats of one type, and they are 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 laboratories and in Marine Stations, and will be welcomed by many others working privately at Marine Natural History.

The forms selected are, as far as possible, common L.M.B.C. (Irish Sea) animals and plants of which no adequate account already exists in the text-books. 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 list shows those who have either performed or promised.

Memoirs from I. to XVII. have now been published.

Eledone, by Miss A. Isgrove, is completed and will appear at an early date; Doris, by Sir C. Eliot, is far advanced and ought to be out during 1909. It is hoped that Cucumaria, Buccinum, and the Oyster will follow soon.

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HALICHONDRIA and SYCON, A. Dendy.
SABELLARIA, A. T. Watson.

In addition to these, other Memoirs will be arranged for, on suitable types, such as *Pagurus*, *Pontobdella*, a Cestode and a Pycnogonid.

As announced in the preface to ASCIDIA, a donation from the late Mr. F. H. Gossage, of Woolton, met the expense of preparing the plates in illustration of the first few Memoirs, and so enabled the Committee to commence the publication of the series sooner than would otherwise have been possible. Other donations received since from Mrs. Holt, Sir John Brunner, and others, are regarded by the Committee as a welcome encouragement, and have been a great help in carrying on the work.

W. A. HERDMAN.

University of Liverpool,
December, 1908.

L.M.B.C. MEMOIRS

No. XVII. PECTEN.

BY

W. J. DAKIN, M.Sc.,
1851 Exhibition Scholar, University of Liverpool.

INTRODUCTION.

Although the greater part of the following account of this type applies to the anatomy and histology of *Pecten maximus,* the very common smaller species *P. opercularis* has also been investigated. Some details in which the latter differs from *P. maximus* are mentioned in the text, but, on the whole, these differences are but slight, and either species may be dissected and examined while using this Memoir.

The work has been carried out chiefly in the Zoology Department of the University of Liverpool and at the Port Erin Biological Station, Isle of Man. The chemical work was done at Larne, Co. Antrim, and some of the observations on the sense organs at Kiel. My thanks are due to Professor Herdman for his valuable advice, and for aid in obtaining living material by dredging at Port Erin; also to the Larne Aluminium Company for permission to use their chemical laboratory; and finally to Mr. Chadwick, Curator of the Port Erin Biological Station.

TAXONOMY AND DISTRIBUTION.

Pecten maximus and *P. opercularis* are two of the common British species of the genus *Pecten,* and are known in some places as "scallops." Pecten is the most familiar genus of the family Pectinidae, the correct position of which amongst Pelecypoda or Lamellibranchiate Molluscs is not easy to determine. The shells, gills, muscles, mantle, siphons, &c., have all been employed in classifying the Lamellibranchiata, but, so far, without really satisfactory results. The following classification proposed by Pelseneer (**7**), and founded on the structure of the gills, appears to be the most reliable.

Protobranchia—Lamellibranchia possessing gills with flat and non-reflected filaments disposed in two rows on opposite sides of the branchial axis.

Filibranchia—With gills formed of parallel, ventrally directed, and reflected filaments. The successive filaments are joined together by cilia disposed in "ciliated discs."

Eulamellibranchia—In which the gills and branchial filaments are united at regular intervals by vascular junctions.

Septibranchia—Dimyarian Lamellibranchs in which the mantle remains fairly open, the gills have disappeared as respiratory organs and have been transformed into a muscular septum dividing the pallial cavity into two chambers.

Ridewood (**12**) keeps the first of these orders as it stands, but divides the remaining Lamellibranchs into only two orders, as follows:—

Ord. I.—Protobranchia (as above).

Ord. II.—Eleutherorhabda. This is practically the same as the Filibranchia.

Ord. III.—Synaptorhabda. This includes Pelseneer's two orders, Eulamellibranchia and Septibranchia.

Thus according to both these classifications, the older group, Pseudolamellibranchia is done away with. This order included the Pectinacea and the Ostraeacea: the first of these has been removed to the Filibranchia and the second to the Eulamellibranchia.

We see, therefore, that the position of our type is as follows:—

Class: Lamellibranchia. Ord.: Filibranchia. Suborder: Pectinacea. Fam.: Pectinidae. Genus: Pecten.

The American scallop, however, *Pecten tenuicostatus*, has, according to Drew (**1**), the gill filaments united by interfilamental vascular junctions, thus forming one exception to the definition of the Filibranchia, and serving to show how insufficient single characters may be in a scheme of classification.

The genus Pecten is of world-wide distribution, though most of the species are confined to smaller areas, and the habitat extends from the littoral zone down to the 450 fathom line and probably further.

The distribution in time extends from the Cretaceous, and possibly it goes even further back to the Carboniferous period. Jackson (**3**) in his work on the Phylogeny of the Pelecypoda, has shown how this genus is related by the structure of the early nepionic shell to the Aviculidae, and in all probability the fossil Aviculopecten of the Devonian rocks was a connecting link, so that the ancestry of the Pectens can thus be traced back to Silurian times.

In addition to *Pecten maximus* and *P. opercularis*—generally distributed in European seas—the following species are found round the British coast:—*Pecten pusio* (Linné), *Pecten varius* (Linné), var. *purpurea*, Jeffreys, and var. *nivea*, Macgillivray, *P. sulcatus* (Müller), *P. fragilis* (Jeffreys), *P. clavatus*, var. *septemradiatus*, Müller, var. *alba*, Jeffreys, and var. *dumasi*, Payraudeau, *P. tigerinus* (Müller), and var. *costata*, Jeffreys, *P. incomparabilis* (Risso), *P. striatus* (Müller), *P. similis* (Laskey), *P. vitreus* (Chemnitz), *P. grœnlandicus*, Sowerby, and four varieties of *Pecten opercularis*—var. *lineata*, da Costa, var. *tumida*, Jeffreys, var. *elongata*, Jeffreys, and var. *audouini*, Payraudeau.

For systematic descriptions of these species and varieties reference should be made to Forbes and Hanley's "British Mollusca," and Jeffreys' "British Conchology."

Both *P. maximus* and *P. opercularis*, but especially the latter, are gregarious; and in various places round the British Coast beds of scallops exist where *P. opercularis* can be obtained in thousands by dredging. Both species prefer a sand or gravel bottom, but sometimes they occur on mud. The depth of the great bed of *P. opercularis*, situated off Port Erin at the South-west end of the Isle of Man, is about 17-22 fathoms, and all the specimens of both species used in preparing this Memoir came from an average depth of about 20 fathoms.

BIONOMICS.

The animal is found lying free, neither adherent by the shell nor by a byssus. Locomotion, however, is carried on, not by the usual Lamellibranch methods of creeping or leaping, but by spasmodic swimming. This is one of the most interesting peculiarities of the genus, and, moreover, certain features in the anatomy of the mollusc have, in all probability, been modified owing to this habit. *Pecten opercularis* swims much more frequently and for a longer period than *P. maximus*, and if specimens are kept in aquarium tanks, it is quite easy to follow their movements and make out the structures involved in this curious method of progression. It strikes one at once that, contrary to what might be expected, the animal moves with the ventral edges of the shell foremost. The mollusc, which has been lying on one of its valves, causes the shell to open and close in a very rapid manner, and it might be thought that at each sudden clapping of the two valves, the water between them would be forced out ventrally and that the animal in consequence would move with the hinge line foremost. The free or ventral border of the valves is, however, directed forwards in swimming, and the animal seems to take a series of bites at the water.

As will be subsequently described, the valves in both species are not mirror images of each other. *Pecten maximus* has the right valve very much more convex, while the left is quite flat. In *P. opercularis* the two valves are much more alike but the right is slightly less convex than the left. *Pecten maximus* lies on the convex valve or right side, and the flat side is, therefore, superior, and is generally covered with barnacles, serpula, zoophytes, &c. *P. opercularis* also shows by the attached animals being found always on the same side, that it lies on the right valve. If a specimen is turned over on to the other side, it will make efforts to turn back, and usually regains its normal attitude in a few minutes. The two diagrams in text (fig. 1) show that while the two species both lie on the right valve, in one case the more convex side is downwards, and in the other, upwards.

If the undisturbed animal is watched as it opens the valves (which it does very slowly), the tentacles (Plate II., fig. 1, *Tn.*) will first be seen gradually protruded, then the eyes will become obvious, and lastly, when the valves are some distance apart, the two free edges of the mantle (which previously lay against the mantle lobes proper) move outwards until they stand almost at right-angles to the plane of the valves, so as to form one curtain or "velum" (fig. 1, *V.*) hanging from the upper valve and one projecting up to meet this from the lower valve.

In the resting condition the valves of the shell are opened very considerably, but the organs in the pallial cavity cannot be seen owing to the fact that the edges of the upper and lower vela are just in contact. By putting a few grains of carmine in the sea water, an inhalent current can be demonstrated. This enters the pallial cavity by passing between the mantle lobes all round the margin of the shell except for a small distance posteriorly. Here there is a strong exhalent current, and thus, although no morphological siphons are present, there are well-defined areas for the inhalent and exhalent respiratory and nutritive currents.

When the animal is about to swim, the following changes take place: the valves slowly open, that is, they move further apart than in the resting condition, and the visceral mass can be seen between the mantle edges. At the same time the two vela lie slightly turned back against the mantle lobes as if moved inwards by the inflowing water due to the divarication of the valves. Towards the end of this opening motion the tentacles are quite suddenly retracted all round the mantle edge, and immediately the shell shuts with a snap. Just at this moment, however, the two vela take up the vertical position, with their margins touching, and by means of their muscular structure retain this position, acting as a perfect barrier to the water which must escape from the pallial cavity. The result is that the water escapes only where the two vela are not well developed, and where they do not dam back the current, and this is on each side of the dorsal edge of the shell.

There are, therefore, two jets of water shot out dorsally at each sudden closing of the shell, for the process above described is repeated rapidly for several seconds, and consequently the animal moves onward with the ventral margin foremost. An inclination to one side or the other can be effected by partial closure of one of these dorsal openings.

The sudden retraction of the tentacles is always the signal for the closing of the shell.

The animal can, in addition, force the water out at the ventral margin by not bringing the pallial barrier into play. This occurs when it is suddenly stimulated, and then it darts away with the hinge line foremost. It also is interesting to note that when the animal is turned over on to the upper side, it rights itself in a very short time by driving water out sharply between the ventral margins of the shell. This forces the hinge line back against the ground and is then used as a fulcrum on which to turn over. When in the normal position, that is, lying on the convex valve, a slight jet of water sent out ventrally causes that edge of the shell to rise from the bottom, so that the normal movements of swimming can take place without any hindrance from friction with the bottom.

The equilateral character of the shell of Pecten is, perhaps, a modification due to the development of the power of swimming and we may also put down to this, the evolution of a muscular velum, the large single adductor muscle with its adaptations for rapid contraction, and also the large internal cartilage for opening the shell.

It is doubtful whether adult *Pecten maximus* or *P. opercularis* ever employ the foot for purposes of locomotion. This seems to be rudimentary in the adult as far as its use as a locomotive organ is concerned, but as on one occasion I was able to see a *P. maximus* protrude its foot—which is evidently capable of much distension—out of the shell, it may be possible that in its normal habitat it uses the foot more frequently. I have not been able to examine the very young stages of *P. maximus*, but *P. opercularis* and *P. irradians* of the American coast have a period before the free stage is reached, when they attach themselves by means of a byssus.

In a still earlier stage after the free-swimming larva has settled down, the animals are unattached and crawl about actively. The foot is protruded, attached to some object and then contracted, and in this way the animal is pulled along by successive attachments and contractions of the foot. The foot of the adult Pecten is very like a sucker, though in no case have I seen it used in the manner above described.

Following the crawling stage we have the byssus stage, and the foot takes part in the attachment of the threads.

Jackson (**3**), who has watched the American species, describes it as follows:—" Lying on the right valve, the foot is extended on the surface of the dish, the flattened distal portion taking a firm hold as if about to crawl. This position is maintained for a moment or two and then the foot is withdrawn within the body, by the motion of retraction it draws out, or spins, the byssal thread, which the creature had fixed to the surface of the dish while the foot was laid closely against it. Soon the foot is again extended, pressed flatly against the dish and another byssal thread is spun, three is the common number with specimens in confinement."

If disturbed the attached scallop can break or cast off its byssal threads and swim by clapping its shell. The adult *P. opercularis* only occasionally shows any signs of the byssus, but *P. varius*, another common British species, is usually attached.

Pecten feeds largely on vegetable matter, such as diatoms, fragments and spores of algae, together with the smaller micro-crustacea suspended in the inhalent current which is continually passing between the mantle lobes. This current is set up by the cilia on the gills and palps, the water is filtered by means of the gills, and the microscopic matter is entangled in mucus and conducted to the mouth.

The foot is a great mucus-secreting organ, and the labial palps and lips direct the food current to the mouth opening.

When dredging on Pecten grounds, empty shells are frequently dredged up, which are neither old nor have the appearance of having been unoccupied for long. It is probable that starfish, together with the whelk, are accountable for some of these empty shells. A large dog whelk in Port Erin aquarium had killed and partially eaten a *P. maximus* by getting the anterior end of its shell between the separated valves of Pecten, and then attacking the adductor muscle with its proboscis.

Parasites are very scarce, no internal ones having been met with in any of the specimens sectioned. *Lichomolgus maximus* (**8**) is, however, an interesting ectoparasitic copepod which may be obtained by washing in sea water the gills and mantle to which it adheres. It is of an orange colour, very like that of the gills, and, so far, has only been found in *P. maximus*, from which the specific name is taken.

Very often the shells of Pecten are bored through by *Clione celata* (a boring sponge). This ramifies extensively between the outer and inner layers of the shell, and gives off short shoots which pass outwards to the external and internal surfaces of the valves. At the points where these tubes perforate the internal layer of the shell, the mantle secretes calcareous nodules of a dark grey or black colour.

The outer surface of the upper valve forms, as one would expect, a good platform for such sessile animals as Balanus, Zoophytes, Serpula, &c.; and the upper valve, of nearly all the specimens of *P. opercularis* taken off the Isle of Man, and numbering several hundreds, was covered with a Halichondrioid sponge of a rich red colour.

THE SHELL.

Scallop shells are well known at most seaside resorts. They are sold as ornaments, and have been put to various uses by the fishermen. They were used, moreover, in very early times, and it has been supposed that the flat valves were the plates and the hollow ones the drinking cups of Fingal and his heroes. Until recently, in the Isle of Man, primitive lamps were made from the deeper shells.

The majority of Lamellibranchs are equivalve and inequilateral, the right and left valves being mirror images. Pecten, however, shows a departure from this rule as the right and left valves are symmetrical, and in some species, e.g., *P. maximus*, are very unlike each other. The equilateral character is in some species disturbed by the areas near the hinge line being unequal in size. The hinge line is practically straight, and a strong internal cartilaginous ligament is situated in a deep triangular pit, under the beak of each valve (Pl. I., fig. E, *Lg.*). The characteristic shape of the valves is given by the auricular area developed on each side of the beak of the shell (Pl. I., fig. C, *Sh.a.*).

The shell of *P. maximus* is brittle and rather light for the size, which is what one would expect since a heavy shell would be detrimental in swimming. It is very inequivalve, the right valve (Pl. I., fig. C) being very convex, whilst the left (Pl. I., fig. D) is quite flat with a concave area near the umbo. In *P. opercularis* the shell is almost equivalve, both valves being convex, the left, however, is slightly more convex than the right (see Text-fig. 1). Both species have suborbicular valves, and these are marked by plications so that the outer surface has a number of ribs arising near the umbo. The ribs are not present in old specimens of *P. maximus* on the areas immediately adjoining the umbos.

FIG. 1. Diagrammatic sections of *P. opercularis* and *P. maximus* to show shape of valves in natural position.

The number of plications appears to be constant throughout life, no new ones arising by bifurcation or interposition, and there are fewer in *P. maximus* than in *P. opercularis*. The average numbers can be obtained from the following table given by Davenport (**41**) for the shells of *P. opercularis* from three localities:—

Ribs.	Off Eddystone.		Irish Sea.		Firth of Forth.	
14	1	0·2%	0	...	1	0·2%
15	5	0·9%	3	0·5%	8	1·6%
16	77	14·4%	27	4·4%	63	12·4%
17	195	36·4%	152	24·8%	154	30·3%
18	182	34·0%	219	35·7%	164	32·3%
19	66	12·3%	159	25·9%	96	18·9%
20	9	1·7%	45	7·3%	20	3·9%
21	0	...	8	1·3%	2	0·3%
22	1	0·2%	1	0·2%	...	...
	536		614		508	

Davenport has also given the relation of the dorso-ventral diameter to the antero-posterior diameter, for 1,657 shells of *P. opercularis* from these same localities. The results show that the smallest shells are from off the Eddystone lighthouse, the largest from the Firth of Forth, and the intermediate ones from Port Erin in the Irish Sea.

Also that the shells of a given dorso-ventral diameter are longest at the Eddystone and roundest at the Firth of Forth. Davenport concludes from the numbers that the ancestral Pectens had a relatively greater dorso-ventral diameter, and that modern ones are becoming longer, since the measurements indicate that change. The variations recorded with regard to most qualities and the size of shells indicate that the Eddystone and Firth of Forth forms are the extremes in a regular series, the Irish Sea specimens being intermediate. The difference in latitude means a difference in temperature, and probably also in the density of the water.

By means of the ribs and their secondary thickenings on the inner surfaces of the shell, the two valves interlock and shut closely along the ventral margin. The external ribs and grooves are sculptured with well-marked striae, radiating from the umbo. They are due to the presence of minute denticles arranged regularly in rows. There is also a prominent concentric marking as if the shell was made up of a series of lamellae. These are much more pronounced in places forming definite rings which, since they occur very regularly and in the same positions, may be considered as indicating the age of the shell. A *P. maximus* whose dorso-ventral diameter was 7·75 cm. and antero-posterior diameter 8·6 cm. had an indicated age of three and a half years.

The two valves are joined along the hinge line by a narrow external ligament, present in addition to the thick internal ligament for the opening of the shell. The former simply unites the two valves and acts as hinge. The internal ligament is triangular in section, and in appearance like dark brown indiarubber. It fits into, and is attached to, the valves in deep triangular pits. In side view this ligament is also triangular, the apex being nearest the hinge line and the base furthest from it. When the valves are closed the ligament is compressed and the free surface becomes very convex, so that the shell is only kept closed by the adductor muscle overcoming the resistance of the ligament. It will be noticed in both species that when the valves are closed there are two places, one on each side extending from the hinge line to the greatest antero-posterior diameter, where the shell edges do not meet. It is through these two prominent gaps that the water is forcibly ejected in swimming. Owing also to this feature, sea water cannot be retained in the pallial cavity when the animals are removed from their natural habitat, and hence Pecten lives but a short time compared with the Mussel and the Oyster, when exposed to the air.

In *P. maximus* the convex valve overlaps the flat valve by from one-eighth inch to one-quarter inch when they are closed. Jeffreys describes the hinge plate in *P. maximus* as toothless, but mentions certain ridges present on it. There are several tooth-like ridges both on the anterior and posterior sides of the ligamental pit, and these interlock when the valves close, fitting into grooves between similar ridges on the other hinge plate. They are not developed in *P. opercularis*. There are, further, two prominences on the right valve just at the point where the auricular areas meet the main portion of the valve (Pl. I., fig. E, *Sh.p.*). These two tuberosities rest in two depressions on the left valve when the shell is closed.

In both *P. maximus* and *P. opercularis* the auricular areas are almost equal in size, and in the former almost similar in shape, with the anterior and posterior margins inclined slightly, making an obtuse angle with the hinge line. In *P. opercularis* the posterior edges incline, making an obtuse angle as in *P. maximus*, but the anterior margins form acute angles, and that of the right valve is reflected so that the anterior left auricle overlaps it at this point. The valve is also depressed here slightly, so that a groove is formed, known as the **Byssal Notch,** and it is deeper in young forms than in the adult. Since the foot is situated so near the hinge line, it is probable that the groove is due to its presence, because the valves would otherwise have to open much wider for the protrusion of foot and byssus than is the case in the majority of Pelecypods where the foot is protruded ventrally. This would also account for the greater depth in younger forms and absence in the adult *P. maximus.* At the base of the byssal notch are three tooth-like processes, the function of which is unknown. The hinge line is almost level, but in the convex valve it rises slightly on either side of the umbo in such a way that when the shell is closed the most dorsal point is formed by the convex valve which is slightly folded over to join the upper flat valve.

The inner faces of the valves are marked by impressions indicating the attachments of the various muscles.

The Pallial Line is a scar marking the attachment of the numerous retractor muscles of the mantle edge. It is a sinuous line extending without break or indentation (owing to the absence of siphons and their retractor muscles) almost parallel to the shell margin, at a distance of about one and a half inches from it, at the ventral border (Pl. I., fig. E).

The **adductor impression** is larger on the flat upper valve than on the lower convex one. This impression is, moreover, situated nearer the ventral margin of the shell on the left valve than on the right, owing to the oblique track of the muscle fibres. The single retractor of the foot is attached to the left valve, but its impression forms part of the adductor impression.

Microscopic Structure. The observations of Jackson (**3**) on the earliest shell of *Pecten irradians* show that the "prodissoconch" (the completed first-formed shell) has a homogeneous and laminar structure with fine concentric lines of growth, no indications of the byssal notch, and is dimyarian.

The byssal notch arises in the next stage, the "dissoconch," which is sharply separated off both in structure and shape from the early shell, for a thin layer of prismatic cellular tissue was observed in the right valve extending over the whole shell. There are no ears nor plications of the shell at the early dissoconch stage, though they appear very soon after, and this is interesting because the Devonian *Pterinopecten*, an ancestral genus transitional between the Aviculidae and the Pectinidae, also shows but slight development of ears.

It is very difficult to cut sections of the adult shell owing to its brittle nature; but I have been able to examine a transverse section cut along the antero-posterior diameter of *P. opercularis* and a section along one of the ribs, that is, along the dorso-ventral diameter of *P. maximus* (right valve).

The structure of the shell is practically the same in both species, but *P. maximus* is much coarser than *P. opercularis*.

The sections differ considerably in appearance from those of *Anodon*, *Mytilus* and *Cardium*, and one cannot trace the three typical layers—periostracum, prismatic layer and nacreous layer. The first appears to have been worn away in these adult shells, though traces of it may be seen in the hollows. The calcareous structures seen probably represent both the prismatic and nacreous layers, but the crystals are not laid down as prisms, neither can two definite layers be made out. The shell is composed mainly of aragonite, the crystals of which appear to interlace and to be arranged very irregularly (Plate II, fig. 2).

In transverse sections across the ribs (fig. 2), the flattened crystals are laid down so that the structure appears to be lamellar, somewhat like the nacreous layer of other Lamellibranchs. These lamellae run practically parallel to the surface of the shell, and each rib is formed by a great thickening of this lamellate layer, the lamellae being arranged to form two crests as figured. The structure of the shell between two ribs is more irregular, and recalls the geological structure known as false bedding—the laminae lying in various planes.

While the median portion of the thickness of the shell is as described above, the external surface layer is formed of crystals which are arranged in some places perpendicularly, or nearly so, to the surface of the shell, and in this way a kind of pseudo-prismatic layer is built up, but it passes gradually into the coarser and more irregular layer below. The inner surface of the shell is also laminar in structure, the laminae being practically parallel to the surface. If the shell sections be cut through the adductor impression, a thin, delicate layer (Pl. II, fig. 2, *Sh. m.*) will be found situated between the inner lamellar layer and the adductor muscle. This is the limy-looking layer seen in surface view of the muscle impressions, which sometimes adheres to the muscle and can be pulled away with it. It is best seen in sections through a young Pecten, the shell of which has been decalcified. This layer appears to be made up of numerous fine rods placed side by side, vertical to the shell surface. In sections of older shells, the rods are not so distinct, but the layer shows very definite striae perpendicular to its surface. It is by means of this "Durchsichtige

Substanz" of List (**6**) that the adductor muscle is attached to the shell, and it is secreted by the modified mantle epithelium of the muscle area, which in the adult is very difficult to trace.

The formation of lamellibranch shells is not yet completely understood. The Intussusception theory of Méry assumed that the shell was itself a growing body. Réaumur, after Regeneration experiments, laid the foundation of the Secretion theory, according to which the shell is a secretion product of the animal. This is the theory now generally accepted. The periostracum can be traced to the actual secreting cells in the periostracal groove of the mantle edge, but difficulties have arisen in connection with the other layers, and there is no doubt that the Intussusception theory originated through the difficulty of understanding the formation of a complex shell structure from a solution or secretion partly organic and partly inorganic. In those Lamellibranchs where an outer, prismatic, layer is present, this is secreted and grows only at the mantle edge. The inner nacreous layer, or that part of the lamellar layer of the Pecten shell corresponding to it, is unlimited in growth, and is formed by the outer surface cells of the mantle.

The colour of the shell varies considerably. In *Pecten maximus* the upper valve is very generally reddish brown, the lower having a somewhat lighter yellow tint; both valves may be mottled with bands or streaks of burnt umber or yellow. *P. opercularis* varies still more, and may be almost any shade of red, pink, orange, yellow, purple or brown, with streaks and blotches. Both species are sometimes quite white, with a slight orange tint at the umbos. The inner surfaces of the valves are smooth and porcelain-like in appearance, with very frequently in *P. maximus* a broad band of a dark chocolate or burnt sienna colour between the pallial line and the margin of the shell (Pl. I., fig. F). This, however, is absent in some specimens, and does not occur in *P. opercularis*.

GENERAL ORGANISATION AND MANTLE.

It is difficult to kill and preserve the specimens without a considerable amount of contraction and distortion taking place. Crystals of menthol dropped into the sea water in a small dish containing a specimen of *P. opercularis* produce the best results with the least retraction of the tentacles and mantle. For *P. maximus*, the mixture of Lo Bianco, spirit glycerine and sea water, floated gradually over the water in the vessel containing the specimens, gives very good results. When narcotised sufficiently in this way, the animal should be placed in 5 per cent. formalin, and may remain in this until required, the muscle, however, becoming somewhat hard.

The animal should be removed entirely from the shell by separating the mantle lobes carefully with the handle of a scalpel and cutting the attached portions of the adductor muscle, and can then be pinned down and examined under water.

For serial sections, the smallest specimens obtainable should be dropped into Perenyi's fluid or Pikrosulphuric, and fixed according to the usual directions. These fluids dissolve also the calcareous part of the valves so that the specimens are ready for embedding after dehydration.

When removed from the shell it will be seen that the viscera and body proper are hidden between two folds of the body wall, the mantle or pallial lobes, which are almost of the same shape and size as the valves of the shell to which they were attached by muscles (Pl. II., fig. 1, *Mn.*). These lobes enclose the pallial cavity, in which lie the gills (fig. 1, *Br. d.*, *Br. a.*) and the lower part of the visceral mass.

The Mantle consists of two thin lobes, folds of the tegumentary layer of the body, with epithelium covering both external and internal surfaces (fig. 4, *E. Mn.*), and but little connective tissue and muscle fibres except at the free margin which is much thickened and muscular. The mantle epithelium is the outermost layer of the body, the shell being a secretion on its surface. The outer layer which lines the shell extends from the hinge line (where it becomes continuous with the same layer on the other side) to the ventral edge of the mantle, as a continuous sheet. It is to be found, though modified, between the adductor muscle and the shell, lying between the muscle fibres proper and the peculiar calcified layer (fig. 2, *Sh. m.*) which is found on the internal surface of the shell at the muscle impressions.

The inner layer is reflected inwards at several points to be continued over the visceral mass. For example, it passes over the adductor muscle and on to the gonad; dorso-posteriorly it runs across from one mantle fold to the other just above the pericardium (fig. 1, *Per.*), partly forming its roof and supporting the posterior pallial artery (fig. 14, *A. p. p.*) which can be easily seen running up towards the hinge line. The two layers of the mantle do not pass over the sides of the digestive gland (fig. 1, *Dg.*). The inner one becomes closely apposed to it, anteriorly and posteriorly, forming the body wall here, whilst the outer epithelial layer alone clothes the sides of the gland.

Dorsally the right and left mantle folds are continuous along the full length of the hinge line, as has already been pointed out, but the level of this is broken about the middle of its length where there is a rectangular depression of the mantle (fig. 1, *Lg. P.*). Into this depression the ligament dips, lying transversely across it. There are no fusions of the mantle edge to form separate inhalent and exhalent apertures, and consequently there are no siphons. The inhalent and exhalent currents are, however, confined to special regions, so that physiologically the fusions are not needed for the separation of the currents. By scattering some carmine into water in which a Pecten is living, the particles of colour can be seen entering all round the shell between the two folds of the mantle, except for an area extending from the posterior end of the hinge line for a short distance forward. Here there is a very definite exhalent current sometimes accelerated by the animal closing the shell suddenly and forcing the water out at this point only, to eject the faeces.

The free margin of the mantle lobes is much thickened and presents three typical folds (fig. 4). The outer one, the shell fold (fig. 4. *Sh. F.*), is small and bears long tentacles. The median one, the Ophthalmic fold (fig. 4, *Op. F.*), is not so distinct and also bears tentacles and the eyes which form conspicuous objects when the animal is alive. The most internal fold is much the largest and is turned inwards to form a flap, known as the "**velum**" (figs. 1 and 4, *V.*). It is usually pigmented either continuously or at regular intervals. List (**6**) has shown that the storage of pigment in the mantle cells is directly influenced by light, and that removal of a piece of the shell causes a deepening in colour of the tissue exposed, due to formation of pigment. This curtain-like velum becomes reduced in size as it approaches the base of the angle forming the ears, and it is this inner portion of the mantle on both sides that fuses as mentioned above. The outer folds remain free, with their eyes and tentacles, until the dorsal margin is reached. The tentacles (fig. 1, *Tn.*) are long, very extensible and active on the outer fold, while those arising from the velum (fig. 1, *Tn. v.*) are short and move but little. When fixed they appear papillose, but this is due probably to the great difficulty in fixing them without contraction and folding of the surface tissue.

The outer tentacles are roughly separable into two groups, a series of short tentacles, mainly one row deep, lying next to the shell, and longer ones capable of much extension and contraction inserted in one or two irregular rows. The former are unpigmented in both valves, and lie, when the shell is opened, curved back over the shell. The others of the upper or left valve have a streak of pigment on their upper sides, and a similar, but less intense, streak is present to the same side of these tentacles on the lower valve.

Further details in regard to the eyes will be given in the chapter on those organs.

When the valves of the shell are separated the two vela hang at right angles to the plane of the valves, just touching, like two curtains. The small tentacles lie across one another, and form a rude grating. The velum, as we have seen above, is of great importance in connection with locomotion. It has been pointed out in considering the muscle impressions on the shell that the fibres of the adductor cross the body obliquely (figs. 46, 47, *A. s.*), the result is that the right mantle lobe has a free portion of much greater area than the left.

Histological Structure of the Mantle.—Over the whole surface of the mantle there is a single layer of cubical or columnar epithelial cells, forming the epidermis. These cells become much more distinctly columnar towards the free edge of the mantle, and are in many places crowded with pigment granules of a dark brown colour, particularly on the velum. A very delicate cuticle is also present. In the young Pecten the epidermal cells near the margin of the mantle and on its outer surface are very long compared with those of the epidermis elsewhere, and are evidently active secreting cells of the shell substance. In adult specimens this great difference is not seen. The columnar cells on the free margin of the mantle lobes, especially on the eye stalks (fig. 35), have a very peculiar appearance, due either to delicate connecting bridges like the "prickle cells" or to the walls having processes which interlock; most probably the former. Lying amongst these epithelial cells are numerous sense cells ("pinselzellen"), to be described later in the chapter on the sense organs.

Underlying the epidermis, there is at the margin of the mantle lobes (fig. 4) a substantial connective tissue, consisting of delicate fibres with few scattered nuclei. There are numerous blood spaces in this layer, and the circumpallial artery (fig. 4, *A. c.*) and the circumpallial nerve (fig. 4, *N. c.*) pass through it, in close proximity, the blood vessel being situated on the shell side of the nerve. Passing inwards, away from the margins, the mantle lobes become extremely thin, the structure being more and more trabeculated until, after passing the line of attachment of the pallial muscles, there is practically nothing between the epidermal layer of cells but bridges of fibrous tissue, large spaces being left in which are to be seen numerous blood corpuscles with large nuclei.

Ramifying in the connective tissue before mentioned, at the margin of the mantle lobes, are the pallial muscles (figs. 1, 3, 4, *P. M. r.*, *V. M. c.*, *V. M.*).

The pallial musculature of Pecten is both important and complex, and the edges of the mantle are very well supplied, owing to the energetic part played by the velum in the act of swimming and the necessity of withdrawal and protrusion of the edge with its numerous sensory structures. It has both radial (fig. 3, *P. M. r.*) and what may be termed concentric muscles; the latter extend round the margin of the mantle parallel to its free edge, and are well developed in the velum (fig. 4, *V. M. c.*), which has a very compact muscular structure.

The radial muscles are the most obvious when examining the mantle, for it is these which attach the mantle edges to the shell and retract them when the valves close.

The line of attachment on the shell has been previously seen to be a continuous line extending almost parallel to the shell margin and at some distance from it, furthest at the ventral edge and approaching it anteriorly and posteriorly. These pallial muscles proper arise, where attached to the shell, as slightly separated bundles of fibres, as if, in fact, a bundle had the end frayed out slightly. These separated fibres almost immediately come together again to form a conspicuous large fibre which radiates out to the margin and breaks up into very numerous finer bundles, which interlace and become crowded together as they reach their termination at the base of the velum.

Between the outer pallial fold bearing the tentacles and the median one bearing tentacles and the eyes, there is a deep groove, known as the Periostracal groove (figs. 4, 6, *P. gr.*), and in sections the periostracum can be seen arising from the base of the groove through the coalescence of several short fibres from the secreting cells. From here it is continued out, and passes over the edge of the shell to its outer surface.

At the bottom of the groove lying along each side there is a ridge formed by much elongated epidermal cells, together with a fold of this layer with a slight support of the underlying connective tissue (fig. 6, *P. gr.*). The periostracum (fig. 6, *P.*) emerges from between the two ridges, the cells of which differ from those of the surrounding area. They are glandular, and have deeply staining contents.

The cells lining the side of the groove nearest to the eye bear long cilia, and resemble very closely the sense cells which will be described later. Very short cilia are present on the epidermal cells of the outer margin of the shell fold. The cilia are much better developed on the tip of the ophthalmic fold, which bounds the periostracal groove on the inner side. The epithelium of the inner surface of the mantle lobes is also ciliated.

Insinuated between the ordinary epidermal cells on the outer surface of the mantle, near the margin are to be seen peculiar cells (fig. 5, *Eos.*) which contain numerous large rounded granules that stain bright red with eosin or a compound stain containing eosin, such as Mann's methyl blue-eosin. In some places these cells seem to be forcing their way to the surface, and in one or two cases the actual dehiscence of the cell and its contents is observed. They are similar to the cells described as eosinophilous cells by Herdman and Boyce in the Oyster (**42**), and in all probability are wandering cells exercising an excretory function. The tentacles of the shell and ophthalmic folds have a similar layer of columnar epithelial cells to those found on the margin of the mantle, but sense cells are particularly numerous at their tips. The connective tissue of the tentacles (containing muscle fibres running longitudinally from the base to the tip) is divided into segments by transverse muscle fibres, which radiate out from the core of the tentacles to the periphery. A branch from the circumpallial nerve innervates each tentacle, passing up the centre and giving off branches to the sense cells.

If the mantle lobe of one side, preferably the right (where the adductor muscle is attached much nearer to the hinge line), be removed, the general topography of the viscera can be easily made out. The various organs thus exposed are shown in Pl. II, fig. 1. The single adductor muscle occupies a fairly central position (fig. 1, *A. u.*, *A. s.*), and serves as the support for the greater part of the animal which surrounds it. Against the hinge line is the deeply pigmented, green-black looking gland, the so-called liver, which will be referred to as the digestive gland (fig. 1, *Dg.*). The gills (*Br. a.*, *Br. d.*) are very conspicuous structures, lying between the visceral mass and the mantle and attached to the latter on the right side, so that if the mantle were cut away close to the adductor the gills on this side would also be removed. They consist of a long series of orange coloured filaments suspended from a basal lamina.

The body proper may be divided into:—(1) Viscero-pedal mass, (2) the pericardium and rectum, and (3) the renal organs.

The viscero-pedal mass consists of (*a*) the Digestive Gland which is situated at the posterior and dorsal extremity and encloses the stomach, and (*b*) a long, flattened, tongue-shaped reproductive portion, of a brown colour over the whole area, or if the gonads are ripe—white for part of its length (the testis), and pink or brilliant scarlet for the rest (the ovary). There is no distinct division between the digestive gland and this latter portion of the viscera, but just where they are contiguous the rudimentary foot (fig. 1, *F.*) is situated. It is roughly cylindrical in shape; the distal portion, however is sucker-like, with a deep cavity. The foot, it will be seen, appears as an appendage quite distinct from the rest of the visceral mass, and contains no extensions of the reproductive organs.

The pericardium (fig. 1, *Per.*) is situated posterior to the digestive gland. The rectum (fig. *Al. c. 5*) passes through the ventricle of the heart, which is enclosed by the pericardium, and is continued over the adductor muscle, to which it is attached, bending to one side of the median line and eventually terminating in a lipped anus.

The aperture of the mouth is placed not far above the foot on the anterior surface of the digestive gland between the two very conspicuous dendritic lips, pigmented with an orange colour (fig. 1, *L. p.*).

At each side where the gills terminate dorsally are two flaps, also pigmented with a yellowish brown colour. These are the Labial Palps (fig. 1, *L. p. e.*); they become continuous dorsally with the lips.

The renal organs (fig. 1, *R. o.*) are situated on each side of the reproductive portion of the viscera between it and the gills, and the external opening at their ventral end serves both as renal and reproductive aperture (fig. 1, *Ro. rp.*).

The positions of these various organs in relation to the shell are not the same as those in the Dimyaria. Thus the pericardium is posterior, the digestive gland (" liver ") is dorsal and the foot and visceral mass are situated anteriorly, the hinge line being considered as dorsal.

Owing to this, some authors have regarded the hinge line as dorso-anterior, and the antero-posterior diameter as represented by a line drawn from the front corner of the hinge line to the point where the rectum ends. The position of the organs is regarded as due to an increase in size of the posterior adductor after the disappearance of the anterior adductor, together with a movement of the muscle to a more central position. A shortening of the length of the body with a closer attachment of the viscera to the muscle (which plays a prominent part as a support, and rotates slightly), would bring about the conditions observed. Throughout this Memoir, however, the hinge-line has been taken as marking the dorsal edge of the body.

THE MUSCULATURE.

Pecten belongs to the Monomyaria, since it possesses only a single adductor muscle. The possession of one adductor muscle by certain lamellibranchs does not indicate genetic relationship, and species which are Isomyarian, Anisomyarian and Monomyarian may all be found in a single family. In addition to the adductor there are present, the orbicular retractor muscle of the mantle (pallial muscles), a single retractor muscle of the foot on the left side, the intrinsic muscles of the foot and visceral mass, and the heart or cardiac muscles.

The Adductor Muscle of the Shell (fig. 1, *A. s.* and *A. u.* and fig. 47) is the posterior one of those forms with two adductors present. In the early stages, after the free swimming larva, we have first a protomonomyarian stage when the anterior adductor is formed and is alone present. The next is a dimyarian stage when the posterior adductor is present in addition to the anterior. These two stages are quickly passed through, the anterior adductor disappears and the posterior increases in size and takes up a more central position. This may be called the deutomonomyarian stage. The muscle stretches obliquely across the body from one valve to the other. The attachment to the shell is more dorsal on the right valve, and, owing to the fact that the fibres cross obliquely, the various organs of the body that surround the muscle are also asymmetrical, and the right mantle lobe is of much larger extent below the adductor than the left.

There is an obvious separation of the single adductor into two parts (fig. 1, *A. u.*, *A. s.*) one of which is of different structure from the other. In the fresh or living animal these two regions are easily distinguished by their different appearance, but they are quite distinct even in preserved specimens.

The greater part of the muscle (*Add. s.*) has a colourless, semi-translucent appearance, and this part is cylindrical in section near the right valve, but elongates and increases in area as it approaches the left valve, where the muscle impression is slightly larger. Lying against the posterior surface of this main portion, but clothed by the same connective tissue sheath that passes round the two parts and binds them together, is a narrow bundle (*Add. u.*), crescent shape in section and made up of white, more opaque looking fibres. Coutance (**13**) and Thoring showed that the larger part serves only for the *rapid* spasmodic closing of the shell, while the small portion serves for slower but more forcible and sustained activity. If one valve is taken away, which means that the attachments of the adductor are cut through, the small white portion falls into a state of permanent contraction ("tonus") and thus in fixed preparations this portion of the muscle is generally much more strongly contracted, and, therefore, shorter than the larger part of the muscle.

The other part contracts and relaxes rapidly if stimulated. It is obvious that this development is correlated with the function of swimming, and that the clapping of the valves of the shell is due to the large translucent portion of the adductor, whereas the more permanent closing of the shell is due to the much smaller part. *P.*

maximus can resist a considerable pull for a short time, 4,000 grams are not sufficient to pull the valves apart unless acting for some time, when, as is the case with other lamellibranchs, a much less weight suffices to open them, in fact, as has been shown, starfishes are able to open oysters by a sustained pull. Corresponding to these differences in appearance and function there are differences in the histology of the two regions. The fibres of the large, rapidly contracting part, when seen in sections, show a very obvious striation, the smaller portion of the muscle consists of smooth fibres. This relation between the cross striation of muscle fibres and rapidity of movement is of general occurrence (**13** & **15**). The striated fibres are very much flattened so that they can be seen either in surface or in edge view (fig. 30, *b.* and *a.*).

If small portions are fixed in osmic or Flemming and stained with iron haematoxylin it is quite obvious that the striping consists of distinct transverse bands; there is no possibility of its being only an appearance due to fibrillae being thrown into spirals when in a contracted state.

The dark bands are three or four times as long as the light, almost unstained, portions. Moreover, the fibres have a series of constrictions which correspond in position with the light stripe; this can be seen extremely well if a fibre is observed in edge view, so that the dark portions correspond to the swellings and the light stripes to constrictions.

The difference in intensity of the stain taken up by the two parts, however, is so great that it would be difficult to affirm that the dark stripes are due to a greater thickness of stained protoplasm, though it is possible that this may be the case (see **14**).

The nuclei of the fibres are not frequent in occurrence, and are pushed rather to one side of the fibre and elongated.

The muscle is well supplied with blood brought by the adductor artery, and the whole substance of the muscle is permeated with lacunar spaces in which blood corpuscles can be seen. The adductor contains also a very large quantity of glycogen, which can be easily extracted with water and the characteristic tests applied to the solution. The means of attachment of the adductor muscles to the valves can be best observed in complete sections through a very small Pecten, the shell of which has been decalcified. The union of the muscle fibres with the shell is carried out by a special attachment epithelium, the cells of which fuse with the muscle fibres so that their original epithelial nature is difficult to trace; and this tissue element appears to secrete the specialised layer of shell at the adductor impressions (fig. 2, *Sh. m.*).

The Radial Pallial Muscles (figs. 1, 3 and 4, *Pall. M. r.*) are confined to the edges of the mantle lobes, and their attachments and course as seen in surface view, have been described above. At the point where they are attached to the shell, the epithelial cells can be seen extending between them and the shell, but slightly modified. From this point, where the fibres are inserted very obliquely, they pass outwards, towards the margin of the mantle lobes, drawing gradually nearer to the inner surface of the mantle, until most of them terminate at the base of the velum. In certain sections taken through the mantle of *P. opercularis*, some of these fibres appear to be striated, the stripes being apparently transverse. The striping, however, is not nearly so obvious nor so regular as that of the adductor muscle, and, moreover, it cannot be seen in all sections, even those cut very near to each other and treated with the same fixative and stains. The question arises, therefore, whether this cross striation seen in some of the radial pallial muscles is not due to the fibrils being thrown into folds by contraction, producing an apparent striation only. Transverse striation has also been observed in *Pecten opercularis*, on the ctenidial muscles (fig. 45, *Br. m.*), the appearance here being exactly as in the mantle. Both cases are probably due to contraction.

The Circular Muscles run parallel to the margin of the mantle and are very well developed in the Velum (fig. 4, *V. M. c.*), which is made up almost wholly of these muscle fibres. When Pecten closes its valves rapidly, whilst swimming, the water between the valves must endeavour to escape at the ventral margin by forcing the two vela apart. One can see, then, the use of this development of circular muscles, because if the vela are kept in a rigid condition by their action, the water will be compelled to pass out at each side dorsally, near the hinge line, as previously described. These circular muscles are inserted into the shell in conspicuous bundles anteriorly and posteriorly (fig. 3, *V. M. a.*) at the same level as the fusion of the mantle lobes.

The Retractor Muscle of the foot is the posterior retractor of the left side, and is the sole representative of the four retractor muscles which attach the foot and contained viscera to the shell in the majority of lamellibranchs. In monomyarian forms, the two anterior retractors are usually absent, but Pecten has gone further, and, moreover, the single retractor which is obvious in *P. opercularis* has become even more vestigial in *P. maximus.*

In both species the attachment to the shell is in the same position, along the dorsal margin of the adductor muscle, near the junction of its two parts, and the retractor impression on the shell cannot be distinguished from that of the adductor.

The fibres are inserted at a considerable angle, and from the shell, they pass first as a flat band and then, becoming circular in section, across the dorsal surface of the adductor, directly towards the base of the foot. This brings the Retractor under the pericardium and the digestive gland until it reaches the visceral mass, through which it plunges, just at the junction of the digestive gland and reproductive organ, lying enclosed in a fairly definite blood space. Transverse sections through the muscle close to the base of the foot show (fig. 47, *B. g.*) that the muscle has taken a tube-like form, enclosing the byssus gland. The muscle fibres pass around the gland, which has the form of compressed pouches separated by lamellae of connective tissue, and ultimately they become lost in the tissue of the foot.

The Intrinsic Muscles of the foot make up the bulk of the tissue in this part of the body (fig. 8). They run chiefly in two directions. There is a definite layer of circular muscle fibres underlying the surface and extending all round the foot, more internal still is a series of longitudinal muscles running along the axis of the foot. In addition there are many fibres diverging radially from the centre, and also scattered fibres passing in various directions.

Other intrinsic muscles are to be found in the visceral mass in the reproductive region. There is a layer of transverse muscles passing round in the connective tissue sheath which encloses the visceral mass, and connected with this sheath are scattered muscle bundles running across from one side to the other and serving to strengthen and form a support for the alveoli of the gonad.

The Ctenidial Muscles (fig. 45, *Br. m.*, *Br. m.'*, *Br. m.''*) are arranged as follows:—There is first a layer of muscle fibres (fig. 45, *Br. m.'*) underlying the epithelium but separated from it by connective tissue; these run, like the gill filaments, at right angles to the axis. More remote from the surface there is a somewhat scattered layer of fibres running in the direction of the gill axis. Internal to these again and separated from them by more connective tissue is another layer of fibres running in the same direction as the first described (fig. 45, *Br. m.''*).

In addition to the above there are two very important compact bundles (fig. 45, *Br. m.*) which run longitudinally along the gill axis. They are situated at the sides of the axis just above the point at which the various filaments separate from one another (*Br. m.*). In certain sections of *P. opercularis* these muscles have shown a very similar striation to that of the pallial muscles. These last muscles serve for contraction of the gills.

The Cardiac Muscles.—The auricles and still more the ventricle are well supplied with muscle fibres. They extend around the heart, lying just internal to the wall and passing in various directions from the walls across the cavity dividing it up, so that it has almost the appearance of a sponge. These muscles are described with the heart. It is interesting to note here, however, that in the specimens fixed and sectioned, no traces of definite striation were found on these fibres, except in one case, resembling that of the radial, pallial and ctenidial muscles.

FOOT.

The Foot is a very small organ situated high up on the anterior surface of the visceral mass (fig. 1, *F.*), arising from the surface of the gonad close to the mouth. In shape, it is roughly cylindrical with a sucker-like termination (fig. 7, *F. s.*). This free end of the foot which is almost bifid has a very deep cavity, the dorsal boundary wall of which extends further distally than the ventral, which is notched.

Two sides of the foot can be distinguished, the dorsal and the ventral, the latter has a groove running longitudinally along its surface for about half of its length (fig. 7, *P. b.*). This is the byssal groove and communicates with the byssal gland.

The deep cavity of the end of the foot is continued down the centre until it almost reaches, if it does not communicate with, the cavity of the byssal gland and groove. The foot is very contractile, and in fixed specimens is usually much contracted and wrinkled; it does not contain any extensions of the viscera, and the greater part of its bulk is composed of muscle fibres running in various directions in a groundwork of connective tissue. It is bounded by the usual epidermal layer of epithelial cells, which are columnar, the depth being about three times the width. These cells are ciliated over the whole outer surface, and even extend into the deep cavity of the end of the foot. These ciliated cells are very fine objects for showing the striated cell margin seen in ciliated epithelium.

The epidermis lining the cavity of the foot differs, however, from that on the outer surfaces in that the epithelial cells are compressed in the middle part of their length, so that they are somewhat hour-glass shaped and have interposed between them many mucous glands (fig. 10, *Mu. g.*). In these, nuclei are indistinguishable, but from the size and shape it is extremely probable that these glands are unicellular. In places, in sections, the mucus can be seen emerging from between the epithelial cells, and if the foot of living specimens is examined the cavity will be almost always found full of mucus. In addition to these there is another layer of mucous glands (fig. 10, *Mu. g. c.*) situated more internally but not far from the epidermal layer above described. These appear to be similar to the mucus-secreting glands described by Johnstone (**4**) as occurring on the foot of Cardium. The glands consist of groups of cells aggregated together; sometimes where a group is more distinct it can be seen to consist of about 5-8 cells forming a kind of bulb. From this clump of cells a long stalk arises which passes to the surface and insinuates itself between the epithelial cells; it may divide into two or more branches just below the epidermal layer. The stalk is non-tubular, and the contours of the cells composing it cannot be distinguished. The ground substance of the cells is finely granular, and stains a peculiar grey-blue tint with methyl-blue-eosin.

Under the epidermis there is a layer of connective tissue comparatively free from muscle fibres, and the rest of the foot is made up, as previously mentioned, of connective tissue and muscles. Large blood spaces are to be found scattered through the connective tissue and connected at the base of the foot with the pedal artery which enters it on the dorsal side; the blood lacunae are connected with others which pass over the visceral mass to the dorsal extremity of the renal organ.

There is also a very abundant nerve supply; the pedal ganglia, as will be seen later, are not situated in the foot. Two pedal nerves pass from these, and after entering the foot break up into smaller bundles (fig. 8, *N. p.*), which ramify amidst the connective tissue and innervate the muscles.

The Byssal groove which is seen on the ventral surface of the foot, is a deep groove lined by ciliated cells, and extending almost half way across the diameter of the foot. In *Pecten opercularis* the foot is twisted so that the surface with the byssal groove faces the right valve, and it will be remembered that it is the right valve of the shell that has the indentation known as the byssal notch. Though there are no traces of the byssus in the adult *P. maximus,* the byssus gland is very well developed. It is situated very deeply in the tissue, in fact practically outside the foot, in the midst of the retractor muscle. If a series of transverse sections is followed from the byssus groove region of the foot to the retractor muscle, the following sequence will be observed:—The byssal groove is rather wider at the bottom, and this cavity runs in towards the byssus gland. In sections taken below the byssus groove the sides of the groove have coalesced and the cavity alone is present. As we pass further in, the dorsal wall of the cavity becomes ridged by longitudinal projections, which gradually meet the ventral wall, so that ultimately the original cavity is divided up into compartments by parallel partitions running across from the dorsal to the ventral wall (fig. 47, *B. g.*, and fig. 9). These compartments are deep and wide, but very narrow. Sections showing this structure pass through the retractor muscle alone, and are therefore posterior to the actual foot itself.

The partitions are composed of connective tissue in which are to be found many muscle fibres, and are bounded by a layer of epithelial cells almost cubical in shape, and of course continuous with those of the byssal gland. They are well provided with cilia. The compartments terminate blindly, and at the same time become reduced in width; but at their blind ends, the cells (fig. 9 *B. g. c.*) are rather larger than the other epithelial cel's and contain practically no contents. A structureless body, presumably the nucleus, is present in each, but it stains differently from the other nuclei and is probably in some exceptional condition. In addition to these features the cells have long cilia-like processes which are almost as long as the cells themselves, and these meet in the centre of the space. In the Pearl Oyster (*Margaritifera vulgaris*) (**2**). where there is a well-developed byssus, the same threads are present in connection with the secreting cells of the byssus, and they pass into the horny mass which appears to have been secreted round them. No byssus is present in *P. maximus*, but these cells are presumably the gland cells, and the peculiar cilia-like processes are identical with those forming the root of the byssus in the Pearl Oyster.

With regard to the functions of the foot, which seems so rudimentary in the adult, we have already seen that in the early life history it functions as a locomotive organ, while later on it becomes an organ for attaching the byssus threads to a foreign body. In the adult it seems from observations to perform neither of these functions, though in the case of *P. opercularis*, the time during which byssal threads are formed is probably long, and in *P. varius* the byssus is spun and fixed even in the adult stages.

That the foot can be moved about and extended is easily seen when watching the living animal, and in one case it was observed that this extension brought the apex of the foot outside the valves altogether. It probably is of use, therefore, for freeing the palps and gills of foreign particles, as the foot of the pearl oyster has been observed to do. The cavity at the apex always contains a quantity of mucus, and we have already seen how well the foot is provided with glands. This mucus may be secreted for the purpose of entangling the food particles that are wafted to the mouth, by the gills and palps.

THE GILLS.

The Gills or Ctenidia (Pl. II., fig. 1) are conspicuous in the pallial cavity when the valves are opened, and extend like orange tinted curtains on each side of the visceral mass, with their free edges reaching from the labial palps to a point opposite the end of the Rectum. At first sight there appear to be two gills on each side of the body, but the morphological identity of the lamellibranch gills with the ctenidia of other mollusca is now fully established, and there is but one ctenidium on each side. These two apparent gills are two plates (double for the greater part of their area), formed by a series of filaments loosely attached to one another. The two opposite and innermost lamellae meet, fuse, and become continuous with a supporting ridge at their proximal edges, but their lower or distal edges are reflected so that in section each gill has the appearance of a **W**, the two outside limbs being the reflected portions, and only two-thirds the height of the middle ones by which the ctenidium is attached to the body. The transverse section is diagrammatically represented in fig. 20. Each of these double plates is known as a demibranch so that there are two demibranchs on each side, an inner and an outer, which together make up a ctenidium.

Each Ctenidium consists of a supporting axis or ridge (fig. 20, *Br. ax.*) from which depend two regular series of long delicate filaments. These two series form the two direct or descending lamellae, this part of the filaments being known as the descending filament (fig. 20, *Br. d.*). The lower ends of the filaments are reflected as previously seen (fig. 20), on the outer side of the external demibranch and the inner side of the internal demibranch, and the ascending or reflected portions of the filaments make up the reflected or ascending lamellae, corresponding to the outer limbs of the **W** in the diagram.

The direct and reflected lamellae of one demibranch are quite continuous, and the reflection is simply a device for increasing the area of the gills without occupying an awkwardly large space. The reflected lamella (fig. 20, *Br. a.*) does not reach the axis of the ctenidium, neither is it connected by cilia or other means with the mantle or with the ctenidium of the opposite side. Nor is there any connection between the two demibranchs of one side except at the axis from which they arise.

The **Ctenidial Axis** (fig. 20 and 45, *Br. ax.*) is a plate-like ridge of connective tissue of considerable depth, depending from the body wall. On the right side where the adductor is inserted nearer to the hinge line than on the left, the axis arises not far from the labial palps and is attached to the adductor muscle. It continues ventrally, gradually increasing in depth, until it passes the point where the afferent branchial vessel from the renal organ enters it, and just where the pallial nerves from the visceral ganglion enter the mantle. Here its course is diverted and the ctenidial axis leaves the adductor and is suspended from the mantle lobe. It terminates at a point almost level with the end of the rectum, but its posterior extremity does not diminish in depth, the filament-bearing margin continues almost parallel to the attached edge, and the posterior extremity has a slightly bifurcated appearance as shown in fig. 1. On the left side the ctenidial axis is attached to the adductor muscle along its whole length, and does not extend quite so far back as that of the right side.

The axis is made up almost entirely of connective tissue, with a good supply of muscle fibres (fig. 45). It is bounded by the usual epidermis formed of a single layer of epithelial cells, amongst which sense cells occur frequently on the sides.

Under the epithelium the connective tissue is more compact and dense than elsewhere with the series of muscle fibres (fig. 45, *Br. m.'*, *Br. m.''*) which have been already described. Vascular spaces are of frequent occurrence in the connective tissue.

Near the margin to which the gill filaments are attached, and running in the same direction as the ctenidial axis, are the branchial nerve (fig. 45, *N. Br.*) the afferent branchial vessel and the efferent branchial vessel occurring in the order named (fig. 45, *Br. aff.*, *Br. eff.*), the nerve being nearest to the body and the efferent branchial vessel to the gill filaments. The two blood vessels are very close together, and are only separated by a narrow bridge of connective tissue. From the two corners of the afferent branchial vessel nearest to the gill filaments (it is almost rectangular in section) branches are given off which pass between the wall of the efferent vessel and the surface, and open into expansions on certain of the filaments.

The filaments which make up the lamellae are hollow outgrowths from the axis, and arise as simple, straight processes, becoming reflected later. Jackson found in *P. irradians* that the young forms examined had comparatively a much shorter reflected portion than the adults.

The gills of Pecten are amongst the best examples known of the *plicate type*, that is, the filaments, instead of being arranged in a flat uniform series, are so placed that the lamellae are thrown into a series of vertical folds or plicae (fig. 22, and Text-fig. 2). This plication is most obvious near the ctenidial axis where the folds are so deep that their surfaces are situated at right angles to the plane of the axis. The plication is least near the free ventral edge of the lamellae. Further, the filaments are not uniform in size or structure, those occupying the bottom of the furrows between two successive plicae being larger and known as *Principal filaments* (figs. 21, 22, *Fil. p.*). Owing to the presence of two forms of filaments the gills are known as *Heterorhabdic gills.* Principal filaments are only developed in plicate gills, and always in connection with interlamellar septa, which are organic sheets of membrane connecting the ascending and descending portions of these filaments (fig. 22, *Br. g. l.*). In very young specimens the principal filaments and interlamellar septa are not developed, both being secondary differentiations.

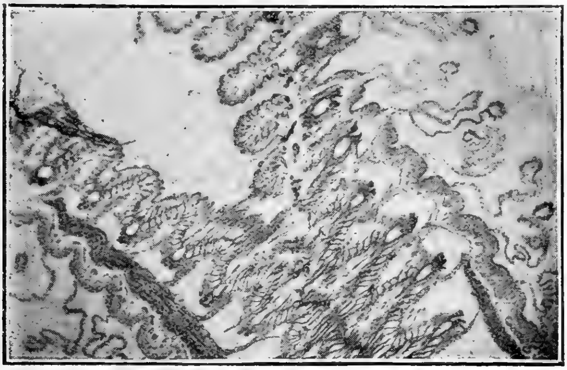

FIG. 2. Section through base of gill filaments. × 50.

The adjacent ordinary and principal filaments are connected in *P. maximus* and *P. opercularis* by stiff cilia only, arranged in patches known as ciliated discs. The cilia of two opposite discs interlock just as two brushes can be made to do. There are no organic interfilamentar junctions, and so the various filaments can be separated easily in the living animal. Organic interfilamentar junctions occur in *P. tenuicostatus* (**1**), which makes with *Avicula argentea* and *Margaritifera vulgaris* (**9**) a third exceptional member of the Eleutherorhabda.

The histology of the gills has been worked out from serial sections cut chiefly parallel to the ctenidial axis, that is transversely through the filaments, but in addition sections have been cut parallel to the filaments in two directions.

Perennyi, or Mann's Fluid, can be used for fixing the gills, and then Methyl-blue-eosin differentiates the chitinous framework well, staining it blue, the cytoplasm purple and the cilia bright red. The principal filaments should be dissected out, stained, cleared and mounted in Canada Balsam in order to make out the various parts.

The filaments are tubes bounded by a very delicate epithelial wall, the cells of which differ in shape and size at various points.

The ordinary filaments (fig. 23, *Fil. o.*) have deeper cells round the margin further away from the interlamellar space, and these cells are deepest in three places forming longitudinal ridges, the cells of which bear cilia. Thus in transverse sections of the filaments there will be seen three sets of cilia on the filament, one down the frontal surface—the frontal cilia (fig. 23, *C. fr.*)—and one on each side of the filament—the lateral cilia (fig. 23, *C. l.*), a narrow space separates the frontal from the lateral cilia. This disposition of cilia is characteristic of most of the Lamellibranchiata. These cilia, unlike those of the ciliated discs, are, in life, in constant action producing the currents of water on which the animal depends for its food supply and oxygen.

The ciliated discs are patches of elongated cells situated on the sides of the filaments near the interlamellar margin, forming little cushions, and these are found at regular intervals down each filament, those of adjacent filaments being, as a rule at the same level. The walls of the filaments are thus brought much closer together, and the narrow space is occupied by the stiff interlocking cilia which these cells bear.

The upper ends of the ascending portions of the filaments (fig. 21, *Br. a.'*) are almost entirely large, ciliated discs, for they have no organic connection, but are held somewhat firmly in position by the great development of interlocking cilia.

Each of the filaments, ordinary and principal, is strengthened by a skeletal support formed of chitin. Thus the skeleton of the gill can be prepared by acting on the soft tissue with warm caustic potash.

In the ordinary filaments this skeleton is a simple tube lining the inner surface of the epithelium (fig 23), the chitin is thinnest on the margins facing the pallial and interlamellar cavities respectively, and thickest on the sides. At one place on each side, nearer the interlamellar margin than the frontal margin, the chitin tube is much thicker, and a septum arises here and crosses the filament dividing the tube into two parts.

This septum, known as the Intrafilamentar Septum (fig. 23, *Fil. sep.*), is generally spoken of as being chitinous. In most of my sections where it is seen distinctly, it appears to stain quite differently from the chitinous skeleton, appearing almost as if it were cellular, and nuclei have been seen in it which were not adhering blood corpuscles.

There has been much discussion regarding the presence of a continuous layer of endothelial cells lining the tube of the filaments on the inner side of the chitinous skeleton, and the point does not seem to be easily settled. Ridewood (**12**) was not able to obtain any conclusive evidence, and Pelseneer (**7**) and Janssens (**10**) state that the layer does not exist, while Kellogg (**5**), Menegaux (**17**) and Sluiter affirm that it is present. It is interesting to note that Kellogg (**5**) states that in *Pecten irradians* the intrafilamentar septum is endothelium and not chitin, and in many cases in *P. maximus* the same appearance is seen. I should not, however, care to affirm that an endothelial lining exists.

With regard to the function of the intrafilamentar septum, a very plausible suggestion has been made that when the ascending filaments are not in organic connection, the blood circulating in them must come back again to the gill axis, and the septum keeps the two currents distinct, whereas when the filaments are united there is only one current running one way or the other in each filament.

Ridewood (**12**) has shown that the septum occurs, however, both in forms with the ascending filaments in organic connection and in those without.

Further, as will be shown later, the ordinary filaments only communicate with the efferent vessel, and I am inclined to believe, therefore, that what circulation there is in the ordinary filaments is simply a current down the filaments which becomes slower, stops, and then returns by the same channel as observed by Kellogg in *Arca*. It is much more likely, as Drew suggests, that the septum is a brace to keep the filament from swelling laterally owing to the pressure of the blood, and in this way becoming circular and obstructing the flow of water between the filaments.

At the interlamellar margin of the filaments, and lying between the chitin skeleton and the epithelium, is a delicate nerve (fig. 23, *Fil. n.*) running longitudinally down the filament. It is connected with the branchial nerves to be described later.

The principal filaments differ in shape according to the level at which the transverse sections are cut.

If sectioned at about the level of the terminations of the ascending filaments, they have a **T** shape, owing to the frontal surface being much extended in an antero-posterior direction, the vertical limb of the **T** representing the interlamellar portion (fig. 21, *Fil. p.*).

The principal filaments have no connections other than by ciliated discs with the adjacent ordinary filaments. The ordinary cilia are to be found chiefly on two longitudinal ridges of columnar cells near the anterior and posterior edges of the frontal surface, but very short cilia are borne by all the cells on this surface.

The chitinous skeleton of the principal filaments is much more extensive and complicated than that of the ordinary filament. The most conspicuous and strongest part consists of two bars, somewhat triangular in section, which run longitudinally down the middle of the frontal surface just underneath the epithelium. The two edges of these bars nearest the frontal surface are fused, the chitin has a homogeneous structure and stains very deeply (fig. 23, *Ch. D.*).

From the outer sides of these two thickenings a strip of the same dark staining chitin extends in an interlamellar direction until it eventually reaches the walls of the filament, which it lines for some distance.

Extending from the sides of the two longitudinal bars, near the frontal surface, are two thick lateral expansions of a paler staining kind of chitin which extend, lying against the epithelium, along the whole extent of the frontal surface, and also line the sides, enclosing a space between them and the darkly staining portion. This pale staining variety of chitin has a more fibrous structure than the homogeneous central portion (fig. 23, *Ch. L.*).

The nerve branch passes down one side between the dark staining chitin, where it approaches the wall of the filament, and the epithelial cells, but between the nerve and the latter is a very delicate strand of chitin or connective tissue.

Several strands of tissue cross the filament, and the interlamellar margin is extended to form a membrane, which towards the lower free margins of the principal filaments extends completely across from the descending to the reflected portions.

The interlamellar junctions (fig. 23, *Br. j. l.*) which unite the two lamellae only extend about one-third of the height of the filaments, though the principal filaments develop interlamellar extensions along the greater part of their length.

This interlamellar extension, however, has a different character in two places. It is well developed on the descending portion of the principal filaments above the level of the free upper edge of the reflected lamellae, that is to say, in a position where there are no opposite principal filaments for it to be connected with (fig. 20, *Br. r.*). This expansion, which is found on each principal filament at its end nearest to the ctenidial axis, will be described below. It diminishes until it practically disappears at about the height of the upper ends of the reflected filaments, and then on the same side another expansion develops, which, more ventrally still, extends across to meet and fuse with its fellow on the opposite principal filament and form the interlamellar septum.

The first described expansion (fig. 20, *Br. r.*) may be termed the **respiratory expansion**, for it is probably here that most of the respiration is performed in the gills. It (see figs. 23, 24, 25) is formed of two bounding layers, a single cell thick, of epithelial cells, continuations of the sides of the principal filament. The space between them is bridged across at numerous intervals by one or two cells, serving to keep the two walls a definite distance apart. At the free margin of the expansion the two walls diverge to form a tube, circular in transverse section (fig. 23, 25, *Br. v.*), which is the channel for the blood.

The free margin of the expansion is attached some distance up the side of the ctenidial axis, and the vessel at its edge becomes directly connected with the afferent vessel of the gills (fig. 45, *Br. v. and Br. aff.*).

The structure of this expansion is more peculiar than it appears from transverse sections, and should be examined in surface view, the whole filament being stained and mounted in Canada Balsam. It then has a folded appearance, as if there were a series of pockets on the sides of a plane surface (fig. 23). A section parallel with the plane of the ctenidial axis shows that this appearance of pockets is simply due to an extensive folding having taken place, as if the greater part of the expansion had, through increased growth, doubled and re-doubled on itself whilst the free margin remained straight (fig. 24). Cilia are to be found on the free outer edge of the expansion, that is on the vessel itself, but do not appear elsewhere.

It will be best now to indicate the changes in detail in the various parts of the lamellae, and the mode of attachment of the filaments to the gill axis.

Commencing with sections through the ventral edge of the filaments, where they are reflected, there is a row of ciliated discs extending along the whole length of the lamellae, and serving thus to keep the filaments in position.

From this point the filaments take up their position so as to form the folds or plicae, but these are not very deep near the base of the lamellae (fig. 22). The principal filaments are as described above. Sixteen or seventeen ordinary filaments are, on an average, to be found between them. Both ascending and descending portions of the principal filaments are connected at this level by the interlamellar septum, which is very narrow.

As one passes by serial transverse sections from the ventral margin to the ctenidial axis the plications increase in depth, and the interlamellar septum is of greater extent until above a point one-third of the height of the filaments, the septum dies away in the middle, leaving an interlamellar expansion attached to both the ascending and descending portions of the principal filaments. The general character of the principal filaments still remains the same.

As we reach the level at which the ascending filaments end (fig. 21), the plication of the reflected lamellae decreases, and at the same time the filaments become more closely crowded. The principal filaments lose their **T** shape, and become more triangular in section.

From this point to the upper edge of the lamellae the chitinous skeleton of the principal filaments becomes more and more reduced, and at the same time the width of the filament diminishes, and its diameter from the frontal to the interlamellar surfaces increases. The ordinary filaments become more compressed and elongated as regards the fronto-interlamellar diameter, until the final result is that both the principal and ordinary filaments look exactly the same, and, owing to the increase in diameter, both kinds of filaments become spatulate at their ends. Some of the ordinary filaments become attenuated and do not reach the level attained by most of them, so that the number of filaments is reduced.

These spatulate terminations of the ascending portion of the filaments (figs. 20, 21, *Br. a.'*) are only united by stiff cilia. In one or two cases, however, in a whole series of filaments, two adjacent ones may be organically connected, but this is exceptional, and usually there is no connection between the upper ends for the circulation of the blood from one filament to another. Instead of there being a septum across the filaments at this level, there are numerous delicate strands crossing from one side to the other. Above the level of the reflected lamellae, the branchial interlamellar expansion is developed on the descending principal filaments, but they change their shape somewhat and the plications of the lamellae become deeper.

The main portion of the principal filament is now roughly rectangular, as fig. 23 shows. The chitinous skeleton is much more strongly developed, the two longitudinal bars can still be made out, but the lateral portions have thickened up considerably and have broad transverse connecting bridges. The pale staining chitin is present in the same position as in the sections cut lower down. Cilia are borne by the frontal edge as before, but owing to the increase in the depth of the plicae the adjacent ordinary filaments have their sides parallel to the frontal margin instead of being in the same relative position with their sides parallel to the sides of the principal filament.

The nerve (fig. 23, *Fil. n.*) can be seen embedded in the chitinous skeleton of one side, and there is also more connective tissue and muscle fibres in the filament.

The branchial expansion, which is on the interlamellar side, opens into the true cavity of the principal filament at one edge and into the longitudinal vessel running down the free margin of the expansion at the other. This brings us to the changes at the ctenidial axis, bringing about the attachment of all the filaments (text-fig. 2, p. 41). The lamellae are most plicate at this level, and the filaments closely crowded together. The first change is a permanent fusion of the ordinary filaments at the apex of the plicae, i.e. at the part of the fold most remote from the interlamellar side. This fusion is due to a development of connective tissue on the sides of the filaments near their interlamellar margins, that is, in the position where ciliated discs are found. The epithelium of the interlamellar margins of the filaments thus becomes continuous and cut off from that of the frontal surface. By further fusion of the filaments they eventually all become continuous; the principal filament also takes part in this fusion, so that there results a plicate lamella having the shape of the former plicae, but made up of organically connected filaments, traces of which are still seen owing to the epithelium on the frontal surface dipping into every former interfilamental gap. The epithelial walls of the principal filaments have become separated by a larger interval from the chitinous endoskeleton, that of the frontal surface becomes continuous with the epithelium of the frontal surfaces of the fused ordinary filaments, and that of the other side with the epithelium of their interlamellar surfaces.

The next series of sections, taken still nearer to the ctenidial axis, show that the grooves between the principal filaments, that is, the deep grooves which open to the interlamellar side, become reduced in depth owing to the fact that the development of connective tissue brings the epithelium of the fused interlamellar surfaces of the filaments more in a plane with the ctenidial axis. This means that the outer surface of the lamella tends to become a continuous plane surface, to which are attached the branchial expansions. The cavities of the ordinary filaments remain in their normal positions, and are far removed from the epithelium which once bounded their inner faces. Furthermore the nerves which ran down the inner edges of the ordinary filaments have become displaced with the development of connective tissue and are near the outer edges of the lamellae, they are much larger, and almost touch each other.

The outer margin, as soon as it becomes a plane surface, is continuous with the ctenidial axis. The expansions formerly on the principal filaments are continued over the outer surface of the axis for a little way, gradually diminishing in size until the level of the afferent branchial vessel is reached and the vessel of the expansion communicates with it.

The nerves from the various filaments, forming almost a lamella on each side, pass between the band of muscles which runs along each side of the gill axis (fig. 45, *Br. m.*) and the surface, and become connected with small ganglia or groups of ganglion cells, from which nerves pass up at the sides of the afferent vessel (fig. 45, *Br. aff.*) and connect on to the ctenidial nerve (fig. 45, *N. br.*). The presence of connective tissue and longitudinal muscles cuts off the cavity of the expansion on the principal filaments from the cavities of the principal filaments themselves, and further from all communication with the other filaments.

On the inner side of the plicate gill lamellae the epithelial layer tends to lose its plications and become a plane surface by the development of connective tissue;

but while this is going on as we approach the ctenidial axis, the same structure of the opposite demibranch is drawing very near to it, until both demibranchs fuse by their inner surfaces. The cavities of the ordinary filaments, bounded by their chitinous skeleton, elongate in a direction at right angles to the plane of the axis, until they eventually come in contact with those of the opposite demibranch, and thus we have the chitinous skeleton of both demibranchs and the cavities of the filaments continuous and all opening into the efferent vessel of the gill axis.

This elongation of the cavities of the filaments with their skeleton is probably only due to the sections passing through obliquely owing to the filaments of both sides curving over as the chitinous framework becomes continuous. Thus the blood, which has been forced to the various parts of the body with the exception of the mantle, and has been collected and taken to the renal organs (fig. 16, *Ro.*), passes from these on each side by the afferent branchial vessels (fig. 45 and fig. 16, *Br. aff.*), and then from these laterally into the vessels running down the margins of the branchial expansions of the principal gill filaments. From these vessels it can pass into the expansions themselves, the whole of which act, therefore, as respiratory surfaces. This brings the blood into the principal filaments, from which it passes into the efferent branchial vessel running just below the afferent. Since the ordinary filaments only open into the efferent vessel, the blood that passes through them must be partially aerated, and there will in all probability be no definite current, but a backwards and forwards motion. It seems certain, from the development of vessels in the mantle, that the great function of the gills is to produce currents of water for aeration, nutrition, and the carrying away of waste products, and the only parts of the gills performing any really important duty in respiration are the branchial expansions of the principal filaments.

ALIMENTARY CANAL AND DIGESTIVE GLAND.

The Alimentary Canal of Pecten is comparatively simple, and there are no complicated convolutions in the visceral mass as in Cardium. The total length is about twice that of the longest antero-posterior diameter of the body.

In order to examine the alimentary canal, it is necessary to remove the mantle and gills from the right side, and it will be easier if the specimen has been left for a day or so in 5 per cent. aqueous solution of formol.

The course of the alimentary canal in the visceral mass can be best made out by shaving off slices parallel to the surface. Sections will also best show the shape and position of the stomach.

The mouth (fig. 39, *M.*) is situated between the lips which are conspicuous dorsal to the foot (fig. 39, *Lp. u.*, *Lp. l.*). It is hidden completely by them, and food particles pass into it by being carried forward at each side of the visceral mass and foot between the labial palps.

The Labial Palps (figs. 1 and 39, *L. p. e. and L. p. i.*) consist of an inner and an outer broad flap on each side of the visceral mass at the points where the gill lamellae terminate dorsally. The outer is a continuation of the upper lip, and the inner palp of the lower lip. They are pigmented yellow-brown, but are very thin and somewhat transparent. The inner palp is rectangular in shape, and is attached to the visceral mass along the inner long edge and the short ventral edge. The attachment is, however, confined to these two edges, and the whole area is therefore free. The attachment of the ventral side is situated on a small protuberance on the side of the gonads. The dorsal short side passes into the upper lip. The outer labial palp is rather more triangular; the attachment is by the proximal side, and mainly to the visceral mass at the side of the digestive gland; the lower end, however, is prolonged slightly, and is attached to the mantle.

The attached sides of the palps join one another, so that a palpar gutter is formed, along which food particles are conveyed to the mouth. The two apposed surfaces of the labial palps are grooved (fig. 40); the other two surfaces are plane. The ridges run across the surface almost at right angles to the attached side, that is directly across the direction taken by the food current, and have their crests directed orally so as to facilitate the passage of particles in that direction and prevent their return.

The plane outer surfaces of the palps are bounded by a layer of cubical non-ciliated epithelial cells (fig. 40), which are pigmented and include a few scattered sense cells. The grooved surfaces are bounded by a layer of much elongated ciliated cells. Those on the summits and sides of the ridges are, however, much longer, and bear more cilia than the cells at the bottom of the grooves; scattered sense cells occur. The rest of the palp is composed of loose connective tissue with scattered nuclei, and numerous spaces with blood corpuscles. A few muscle fibres form a somewhat diffuse layer not far from the surface, and there are in addition nerves from the cerebro pleural ganglia.

The Lips are continuous with the labial palps; the upper with the two external palps, and the lower with the internal. They are, in Pecten, very extensive, highly-developed structures, and very characteristic in shape (fig. 39). They consist essentially of two transverse ridges of tissue, very similar, histologically, to the palps, but without the grooves.

These two ridges, however, are produced in certain places into prolongations, which, as well as the free edge of the lips generally, divide and re-divide into very small, short and swollen processes. In this way the lips come to have a dendritic appearance. There are two main prolongations of the upper lip with dendritic margins, situated one at each side near the origins of the labial palps. The lower lip has a very large median prolongation which interlocks with those above, and lesser ones along the sides. It seems, therefore, that this development of the branched margins is for the purpose of closing over the mouth, leaving a channel which communicates at each side with the groove between the two labial palps.

The margins of the lips are deeply pigmented with the same orange-yellow that is found on the palps, and also lining the oesophagus.

The upper surface of the upper lip and the lower surface of the lower lip are bounded by a layer of epithelial cells, which are almost cubical in shape, and are crowded with pigment granules, especially near the surface. This layer is continuous with the somewhat similar layer that covers the outer surfaces of the labial palps. The surfaces of the upper and lower lips, which face one another and are continuous with the grooved surfaces of the labial palps, are bounded by a layer of much elongated columnar cells, which contain no pigment, but bear numerous cilia. The structure between these two layers is loosely packed connective tissue, with numerous spaces containing blood corpuscles. A slightly denser layer immediately underlies the epidermis.

The mouth itself (fig. 39, *M.*) is a transverse slit leading into a rapidly narrowing oral cavity, which contracts into the narrower width of the oesophagus (figs. 1 and 36. *Al. c. 1*). This latter is a tube about $\frac{1}{2}$in. long in *P. maximus*, dorso-ventrally compressed and leading upwards and posteriorly to the stomach. The opening is not at the anterior end of the stomach, but a little further back and on the roof—rather to the right side in *P. opercularis.* Both the oesophagus and stomach are completely enclosed by the digestive gland, the so-called liver (fig. 1, *Dg.*) The oesophagus is lined by a thick epithelial layer, slightly marked by transverse ridges, which has the same yellow-brown colour that occurs so frequently, and which contrasts strongly with the dark green digestive gland surrounding it. The cells forming the epithelium are long, narrow and ciliated. The height of the cells is many times the width, but since there is very little difference between the cells lining the various parts of the alimentary canal, a fuller description will be given later. Outside the epithelium there is a basement layer of compact connective tissue, and, outside this, looser connective tissue with transverse and longitudinal muscle fibres, which is connected with the strands that separate the tubules of the digestive gland.

The stomach (figs. 36 and 38, *Al. c. 2*) lies in the midst of the digestive gland, but usually nearer to the left side than the right. It is of very irregular, roughly oval shape, with the longest diameter antero-posterior, and with irregular folds and depressions breaking up the wall into certain areas. Two of these on the left side and one on the right are more important than the others and occur with greater regularity. On the left side, not far behind the level at which the oesophagus opens, there is a crescentic, anterior, left lateral depression (fig. 38, *Al. c. 2′*), and a little behind this is another almost circular posterior left lateral depression leading into a short caecum (fig. 38, *Al. c. 2″*). Into the first there open four to seven ducts ("bile ducts") from the digestive gland, and into the second there are about three openings. These ducts are situated on the side walls in *P. maximus*, and are very numerous. The number is, however, variable and difficult to make out, as in some cases ducts may join before reaching the stomach. On the left side they all open into the two depressions mentioned. On the right side there is an antero-posterior groove into which as many as ten ducts may open. The stomach is usually found to contain the remains of vegetable matter. The walls are lined by a gelatinous-looking substance, found also in other lamellibranchs and known as the "fleche tricuspide"; this will be considered later along with the crystalline style, of which it is in all probability a part.

The epithelium of the stomach is for the most part a smooth layer, but on the left side the lining of the posterior wall of the anterior depression has a number of delicate ridges separated by grooves, leading from the openings of the ducts into the main cavity of the stomach. It is on the right side, however, that this grooved epithelium is best seen, and it forms quite half of the wall, extending from the whole width of the crescentic depression to the opening of the intestine, towards which the grooves are all directed. The grooves are not separate and parallel along their whole length, but open into one another as the intestinal opening is reached. This epithelium of the stomach rests on a basement membrane of almost structureless connective tissue. Outside this there is a muscular layer made up of fibres running in different directions, but chiefly transversely. External to the muscle layer, and between it and the digestive gland, are numerous large spaces, crowded with blood corpuscles, amongst which are large spindle-shaped connective tissue cells, the ends of which are drawn out into long fibres.

The epithelial cells lining the cavity of the stomach are very long and narrow, the length attained averaging about 0·07 mm They have prominent elongated nuclei situated at about the middle of their length. These, like the epithelial cells throughout the whole length of the alimentary canal, are richly ciliated.

If sections be cut transversely across the grooved epithelium it will be seen that the grooves and ridges are due to the varying height of the epithelial cells; those which lie at the bottom of a groove are only one-quarter of the height of those forming the ridge. The cell contents are the same in the two cases, and the cells at the bottom of the grooves bear just as well developed cilia, so that they apparently function as channels along which the secretion of the digestive gland passes. Some of the cells (but not those of the grooved epithelium) contain large and small green granules, which are sometimes as wide as the cell, and lie in a distinct vacuole.

THE DIGESTIVE GLAND.

This large gland (fig. 1, *Dg.*), which is the only one occurring in connection with the alimentary canal, has at various times been known as the liver, the Hepato-pancreas and the Gastric gland. The only function that entitles it to the name "liver" is that of apparently forming or certainly of storing fat and pigment. After much investigation, it now appears to be a "pancreas" with the additional function of storing pigment, and in some Lamellibranchs (*Ostrea*) large quantities of fat. It is better, however, to term it simply "digestive gland," for it is evident from experiments that it secretes ferments which perform functions that are specialised in separate organs in higher animals. It is conspicuous both from its size and its very dark colour, due to the contained pigment. The gland itself is of a more solid consistency than is usually the case in Molluscs. It lies dorsally to the adductor muscle, against the ligament, which causes a depression on its surface.

The gland completely wraps round the large stomach, and there is no sign of a division into two lobes in its compact mass except that the ducts open in two series laterally into the stomach, as has already been pointed out.

The gland may be fixed for sectioning in Flemming, Mann's Fluid or by McMunn's method, that is by placing pieces of fresh gland in 20-30 per cent. formol for 12-14 hours, and then in 95 per cent. alcohol.

The green pigment can be seen *in situ* whether fixed in formol or by Mann's Fluid, though it is dissolved out readily by spirit, if placed directly into it.

It (fig. 50) is a tubular gland formed by the ducts dividing up into numerous branches, which, ramifying on their way, divide still further to form caeca.

In Pecten this makes up practically the whole of the gland, for there is no great development of vesicular connective tissue as seen in the oyster. Moreover, in the latter the secreting alveoli are to be seen in sections as tubes with a considerable cavity. In Pecten they are very short, and soon become wholly solid in character, so that the first difference which one notes on comparing sections of the two glands is the solidity of the one and the tube-like alveoli of the other. It is difficult to divide the cells lining the ducts into different categories, for one kind seems to be gradually transformed into another, and probably there is only one type of secreting cell present.

The ducts (fig. 50) conveying the secretion to the stomach divide up in the gland into several branches lined with ciliated epithelium. The cells are columnar and granular in appearance, with a prominent nucleus near the base. They are supported by a layer of connective tissue—the *tunica propria* (fig. 50, *Tu. p.*). Outside this, again, is a layer of circular muscle fibres, which pass round the duct forming the *tunica muscularis* (fig. 50, *Tu. m.*) "Macroblasts," or eosinophilous cells, as seen in the oyster, are not present in Pecten, though under the action of the same fixatives and stains they show up strongly in the mantle.

The only type of cell present appears to be the granular cell lining the alveoli (fig. 50, *Al.*), but smaller cells can be observed between some of these, which stain much more intensely than the others. These are probably similar to the cells described by MacMunn (**21**) in the gastric gland of *Patella*, and are young cells which will replace the others, for, in sections through the alveoli, the granular cells can be seen in process of being shed into the lumen, and there are bodies in the course of the ducts, of common occurrence, that are undoubtedly these shed cells on their way to the intestine. In this way the digestive gland appears to have an excretory function in addition to its storing and pancreatic functions. Pigment concretions do not appear in the lumen of any of the alveoli. Cilia are confined to the ducts, and as an alveolus is followed towards its caecal end the cells become fewer and more swollen (fig. 5, *Al.'*) and intensely vacuolated, the nuclei lying against the connective tissue membrane supporting the cells. Eventually the lumen of the alveolus disappears altogether, and the cells meet in the centre (fig. 50, *Al.''*); their protoplasm has practically disappeared, there are just a few strands left crossing the cells which contain the green pigment granules clustered together in little groups. The connective tissue membrane bounding the alveolus has here become very thin, and the circular muscles have practically disappeared. MacMunn (**21**) has termed the green pigment enterochlorophyll, and finds that the spectrum given by the spectrophotometer is almost exactly that of plant chlorophyll modified by the addition of a little acetic acid acting for several hours. He considers, therefore, the pigment to be modified chlorophyll. Miss Newbigin considers the resemblance of this pigment to chlorophyll to be only superficial, and places it in the same category as Chaetopterin and Bonellin.

It is, however, almost certain that the colour of the digestive gland at any time is dependent on the colour of the food, and several observers, including List and Dastre and Floresco (**6** and **19**), have shown that if Lamellibranchs are fed with colouring matter this appears in the form of small granules in the cells of the digestive gland, and even after two hours can be traced there. List shows, further, that it is a direct absorption, and not a function of the wandering cells.

In order to determine the action of the secretion of the digestive gland, the following bio-chemical experiments were undertaken. They confirm those of Roaf (**22**) on the glands in other molluscs.

The glands were taken from several Pecten, the whole mass weighed and then minced up in a definite volume of distilled water to which a little HCN (or toluol when testing for sugar) was added as a preservative. This was allowed to stand for twenty-four hours and then strained through muslin and a series of solutions made up, each containing a definite amount of the extract, together with the substance to be acted upon. The "liver" extract was neutral, perhaps, if anything, slightly acid in reaction to litmus. The following were the various experiments made:—

(1) 5cc. $\frac{N}{10}$ HCl + 4cc. dist. H_2O + 3cc. extr. + ·5gr. fibrin.

(2) 5cc. $\frac{N}{10}$ Na_2CO_3 + 4cc. dist. H_2O + 3cc. extr. + ·5gr. fibrin.

(3) 9cc. dist. H_2O + 3cc. extract + ·5gr. fibrin.

(4) 5cc. $\frac{N}{10}$ Na_2CO_3 + 4cc. dist. H_2O + 3cc. extr., allowed to stand three hours, and made acid.

(5) 5cc. $\frac{N}{10}$ HCl + 4cc. 2 % peptone + 4 cc. extract.

(6) 5cc $\frac{N}{10}$ Na_2CO_3 + 4cc. 2 % peptone + 4cc. extract.

(7) 5cc. $\frac{N}{10}$ H_2O + 4cc. 2% peptone + 4cc. extract.

(8) 5cc. 1% Methyl Acetate Sol. + 2cc. extract.

(9) 5cc. 1% Methyl Acetate Sol. + dist. H_2O (as control).

To each of these two drops of HCN were added as a preservative.

(10) Extract + Starch Solution; toluol as preservative.

After allowing the various mixtures to stand for forty-eight hours, the following tests were made:—

The residues from 1, 2, 3, 4 and 7 were divided into three parts respectively, and the following products of digestion sought for—peptone or albumoses, tyrosin, and tryptophane.

The Biuret test consists in the addition of one drop of $CuSO_4$ sol. and then KHO—a rose coloration indicates albumoses, a violet colour indicates unchanged protein.

Tyrosin is tested for by adding Millon's reagent to a portion and filtering off the precipitated proteid; the filtrate becomes red on boiling, if tyrosin is present.

Tryptophane gives a reddish violet colour with bromine or chlorine water.

The results were as follows:—The fibrin was all digested in the acid solutions (1) and (4); about three-fifths on the average was left in the alkaline mixture (2), and a little less in the neutral (3). The biuret reaction was very good in (1), medium in (2) and (3). Tyrosin reaction was good in (1), medium in (2), and fair in (3).

There was practically no tryptophane in any of them. It will be noticed, therefore, that digestion proceeds best in acid media, the reverse of the process in the Crustacea. With the peptone solutions (5), (6) and (7), though the same tests were made, it was a diminution of the biuret tint that was looked for, since digestion would convert the peptone into more simple products. The results were almost negative; the residues all gave a strong biuret reaction and no tryptophane; the tyrosin reaction was good, but it was found later that the peptone itself gave this reaction. If there are therefore any ereptic ferments present, they are in small quantities only.

Experiments (8) and (9) were for the purpose of testing for fat digestion; the methyl acetate was broken up into acetic acid, which was estimated by titration with decinormal sodium hydrate in presence of phenol phthalëin.

No. (9) was a control, and required 1·3 c.c. $\frac{N}{10}$ NaHO to neutralise it, whereas No. (8) required 10·6 c.c. $\frac{N}{10}$ NaHO to neutralise it and smelt strongly of acetic acid.

No. (10), after standing 48 hours, gave NO blue colour with Iodine, the starch had all been hydrolysed.

The secretion of the digestive gland is capable, therefore, of acting upon proteids, starch and fats, or, in other words, it contains proteolytic, amylolytic and lipolytic ferments, like the pancreatic juice of vertebrates. The action of these ferments is to convert colloid materials like starch and proteid into the diffusible materials, sugar and peptone, which are eventually absorbed; and the intestine must be considered as the place where this absorption is going on, the descending limb from the stomach being probably the main portion concerned.

The intestine may be divided into three sections, which are of practically the same length: (1) the descending portion (fig. 36, *Al. c. 3*); (2) the ascending portion (*Al. c. 4*); and (3) the rectum (*Al. c. 5*).

(1) The descending limb of the intestine arises from the stomach, not posteriorly, but ventrally, at almost the middle of its length, and passes anteriorly and downwards from the stomach through the digestive gland to the reproductive region of the visceral mass (fig. 1). At the level of the foot this portion of the intestine lies amidst the tubules of the gonad, in the median line, very near to the surface of the visceral mass lying against the adductor muscle. From this point it curves forwards towards the free margin of the visceral mass, and in *P. maximus* extends down to the extreme end of the latter, where it bends suddenly and returns as the (2) ascending limb. This lies close to the adductor surface all the way and at first in the median line, but when the point is reached where the descending portion comes near to the adductor, the ascending portion is displaced and lies to the right of it, so that it eventually plunges into the digestive gland on the right side, and lies near the surface on the right side close to the adductor muscle. It passes up to the dorsal surface of the gland, where it lies in the

median line exactly under the anterior aorta. It now enters the pericardium and passes through the ventricle of the heart.

The course of the alimentary canal in *P. opercularis* is somewhat different, but only in the visceral mass. Instead of the descending limb passing down to the end of the reproductive region, it stops short at about the junction of the seminal portion with the ovarian, and forming a loop at this point returns to the digestive gland as the ascending limb, without passing through the ovarian region at all.

The descending portion of the intestine in transverse section (fig. 37) is almost circular, but owing to differences in the cells lining the cavity, there is a trace of division into two compartments. The larger part of the cavity is lined by epithelium cells, which are elongated and many times their width in length (fig. 42). Most conspicuous, however, are the cilia which they bear. These are strong looking, of considerable length, and present in great numbers. These cells have finely granular contents, and often contain large granules of a green colour. Separating this region from another to be presently described are two ridges situated opposite one another (fig. 37), and formed of epithelial cells about twice as long as those previously described, but their cilia are not so numerous nor as strong, and the cells do not contain the round green granules. The cells lining the smaller cavity (fig. 37, *Al. c. 3′*) are much shorter than any of the others, being only about a quarter as long as those of the ridges. Like those cells, they bear much shorter and weaker cilia. The division between these two parts of the intestine is but slight, and the differences are due to the character of the cells. Projecting into the larger compartment of the intestine (fig. 37, *Cris.*) from the stomach is a gelatinous rod, the Crystalline Style (fig. 36). In dissections it seems to fill the whole lumen of the alimentary canal at this point, though belonging, as pointed out, to the one compartment, for microscopic sections are necessary to see the separating ridges. Pecten shows a primitive condition in that the style lies in the intestine, but other forms are known connecting this with the complete separation of a crystalline style sac, appended to the stomach. There has been a great amount of discussion with regard to the origin and function of the crystalline style, almost every writer formulating a new theory, one or two of which will be considered here. The style has been regarded:—(1) As playing a part in the act of generation (von Heide, Cailliaud); (2) as a rudiment of the radular sac of the Glossophora (Balfour); (3) as acting mechanically upon the food under the action of the digestive fluids (Milne Edwards), or serving to bring the food particles between the style and the dense cilia of the epithelium (Sabatier); (4) as preventing the food from passing too quickly through the alimentary canal before it has time to digest (Kellogg); (5) as a reserve food material (Hazay, Haseloff; (**24** and **25**); (6) as an excretion (Claus); (7) as lubricating the undigested food particles passing through the intestine (Barrois) (**23**); (8) as an active digestive ferment (Mitra) (**26**).

In *Pecten maximus* the style is large, sometimes attaining a length of three inches. It is circular in transverse section, and widest near the stomach into which it protrudes. From here it tapers to a point near the end of the descending limb of the intestine. The upper end is sometimes rounded and enlarged, forming a knob; at other times it is connected with the gelatinous lining of the stomach, and it seems certain that this "fleche tricuspide" and the crystalline style are continuous and have the same structure and function. The fresh styles are flexible, and very elastic. The colour is a translucent brownish-yellow. In some cases the style, when removed from the intestine, came out quite clean. On other occasions there was a beautiful spiral of green substance (like the matter found in the stomach and rectum) encircling it, as shown in fig. 36. It might also have a dark axial portion. In cross section (fig. 46, *a.*) under the microscope, the substance of the style is seen to be perfectly homogeneous, with no organised structure and generally with but little difference between the substance forming the axis and that of the periphery. There is, however, a very distinct laminated appearance, as if the style were formed of concentric layers of a colloid substance, and this gives it a striated appearance in longitudinal section. The dark axis that occurred in one specimen was due to a thick dark ring which was apparently formed of a similar substance to that found encircling the outer surface of some of the styles and, like it, arranged in a spiral manner. The concentric dark rings seen in transverse section are also probably due to the same green food matter from the stomach. Barrois, in a detailed account of the structure and physiology of the style (**23**), gives descriptions of the chemical composition and reactions; and these are borne out by the later work of Mitra, whose analyses show that there is about 88 per cent. of water in the style, about 12 per cent. of proteid, and about 1 per cent. of salts. The style is slowly soluble in water, and the solution is neutral. The tests made on the style of *Pecten* agree with those of Mitra on *Anodon* (**26**) and Barrois on *Cardium* (**23**).

The presence of proteid was indicated by the xanthoproteic reaction (a white precipitate is given by addition of nitric acid to the solution, which turns yellow on boiling and, after cooling, becomes orange on the addition of ammonia). Millon's reagent, when added to the original solution, gave a white precipitate, turning brick red on boiling. The Biuret test also indicated proteid. The concentrated solution is coagulated on heating. The proteid as shown by Mitra belongs to the Globulin class.

With regard to the physiological properties of the style, the following must be noted. It disappears when the animals are kept in sea water free from nutriment of any kind. This has been shown to be also the case in Anodon. After transit Mitra found that fifty might be opened without showing any trace of the style, whereas if placed in a fresh-water aquarium with plenty of food, it was invariably present after an interval of a few hours. Mitra also states that his mussels were not able to carry on respiration and nutrition actively during the night, owing to a leakage in the tank containing them, with the result that the style was absent when mussels were examined at eight o'clock in the morning, and the digestive function was also in abeyance.

Two or three hours afterwards the style would be present. In the case of Pecten such rapid alterations were not found, but specimens kept in a tank which was simply aerated by an air current, and in water which was practically free from food matter, were always found to be without the styles.

It seems that the presence of the crystalline style is concerned with digestion, and it is interesting therefore to find that it contains a digestive ferment.

To test the action a solution of several styles was made up and allowed to act on a starch solution for some hours, precautions having been taken, as a control, to test first for sugar in the reagents. At the end of the time some of the starch had been hydrolysed, and the solution now reduced Trommer's and Fehling's solutions. The phenyl hydrazine test also indicated the presence of sugar.

Mitra was the first to show that the crystalline style contained a digestive ferment (**26**), which was able to convert starch and glycogen into sugar. He assumed from this that the work of the crystalline style was that of a ferment. Now, though I have found the ferment in the styles of Pecten, the amount of starch which was hydrolysed was small, and it is possible, especially if the style be regarded as a secretion of the digestive gland, that the presence of a ferment is accidental.

With regard to the question of the origin of the style, the tricuspid body and the latter have exactly the same structure, and in some specimens appeared to be continuous. Further, the tricuspid body is in close connection with the lining of the stomach and extends into the pockets and openings of the ducts from the digestive gland. I think it probable, therefore, that the style is secreted by the digestive gland. The cells of the alimentary canal, with their long cilia, have not exactly the appearance of secreting cells.

With regard to the various theories named above, there are serious objections to most of them. The style cannot, moreover, be looked upon as a rudimentary structure, since the compartment of the intestine in which it is lodged, and the special caecum of the other lamellibranchs are lined with better developed cilia than the rest of the alimentary canal. The theory of Barrois (**23**) that diatom frustules, &c., are encased by the substance of the style seems hardly sufficient reason for the development of a special caecum and style, when there is no such organ in ascidians, echinodermata or worms, which have similar food matters.

The nature of the style is decidedly not that of a reserve food material, and it seems difficult to comprehend why, under normal conditions, marine lamellibranchs should require to make provision for times of starvation.

Barrois, who rejects the theory of reserve food material, states that he was never able to detect a diminution in the styles at various seasons nor even after keeping specimens of Cardium in filtered water for some days. Both Mitra's experiments and my own confirm Hazay and Haseloff (**24** and **25**) as far as this is concerned, and the chief objection to the reserve food stuff theory must be the composition of the style itself. The position of the style and its composition tell strongly against the theory of it being an excretion. When the animal is kept under such conditions as described by Mitra, is it absorbed by the animal or simply dissolved away by water passing through the alimentary canal? Possibly it is absorbed and the ferment used for converting the glycogen (which is stored up in large quantities in most lamellibranchs) into sugar.

The development of a caecum certainly points to a storage for some purpose. There is no doubt that in Pecten, where the style seems to occupy the whole area of the intestine, it hinders the food from passing too quickly through the alimentary canal, and provides an additional surface over which its contained amylolytic ferment can act. It must be remembered, however, that the presence of this ferment in the style is not conclusive proof that the style has been evolved as a ferment or method for storing a ferment.

It has been already stated that the last portion of the intestine passes through the pericardium and the ventricle of the heart. Here, as in many other lamellibranchs, we must assume that the ventricle has grown up around the alimentary canal, so that the wall of the heart lies between its cavity and the walls of the alimentary canal. Outside the usual lining epithelium there is a basement membrane of connective tissue with a few circular muscle fibres, and external to that a thick sheath of looser connective tissue. The epithelial cells (fig. 44) resemble in appearance those of the ascending limb of the intestine. They are deep columnar cells, the height being many times the diameter, and the cilia are rather poorly developed. The ends of the cells facing the cavity have a strange appearance, as if either a part or the whole cell were being shed into the lumen of the intestine. These shed cells seem to have no stainable contents and no signs of nucleus, and when cut off completely appear in the intestine as spherical bodies faintly stained but with a very definite wall. Lying scattered amidst the connective tissue surrounding the intestine, especially in that part passing through the pericardium, are conspicuous wandering cells, pear-shaped, with most of the protoplasm and the nucleus at the narrow end, and a very large vacuole taking up practically the whole of the rest of the cell. There is generally a large mass of dark yellowish green material in this vacuole, which renders these cells very obvious. The same cells are found in considerable numbers, and carrying the same pigmented contents, in the connective tissue of the digestive gland. It is impossible, however, to say whether their function is excretory or nutritious, and whether the coloured contents are extruded by the cells lining the alimentary canal or not, but they resemble so closely those of the pericardial gland on the auricles, which are excretory, that they are presumably the same.

The epithelial cells lining the ascending portion of the alimentary canal contain numerous granules like food granules, and the same green tint is present here also. It would seem from this that the pigment of the digestive gland is derived directly from the food taken into the alimentary canal.

The rectum, after passing through the pericardium, continues its course over the adductor muscle under the connective tissue sheath. It does not run in the median line, but crosses towards the left side. At about the level where the circular muscles of the mantle edge are inserted to the shell the rectum leaves the adductor, and for its last centimetre is free. The anus is surrounded by a prominent lip.

BLOOD SYSTEM.

The blood system which has been worked out in *Pecten maximus* is very complete, and, like the vascular system of lamellibranchs in general, is entirely closed, so that water cannot enter the circulation directly. There is, moreover, no communication between the heart and the pericardial cavity, and this does not contain blood. The system comprises true vessels, mainly arteries, which are large and easily followed in injections, but the venous system is much more lacunary in character. The amount of blood is considerable, and when the adductor muscle has been cut, on opening the shell as much as 25 c.c. of blood have been obtained from one specimen. The blood is a colourless fluid slightly thicker than water, with a strong saline taste. As is general for aquatic invertebrates, the osmotic concentration of the blood is practically the same as that of the sea water in which the specimen has been living, and small changes in the concentration of the outer medium are followed by the same changes in the blood. The Δ or lowering of the freezing point for some examples taken at Port Erin was as follows (Beckmann's Freezing Point apparatus used):

Sea water in which Pecten were living	Δ — 1·910
Blood from *P. maximus* - -	Δ — 1·910
,, ,, ,, - -	Δ — 1·905
,, ,, ,, - -	Δ — 1·920

An oyster or cockle placed in fresh water might live for some time without any change taking place in the osmotic concentration of the blood. This, however, is simply due to the animal closing the shell valves and completely shutting out the external medium from any contact with the body. In Pecten, on the contrary, as already pointed out, the two shell valves do not close perfectly, and, moreover, the animal persists in clapping the valves, so that a change in the outer fluid is followed by a change in the blood and immersion in fresh water proves fatal. The electrical conductivity is slightly less than that of sea water. If the blood is allowed to stand, after being drawn, the mass does not become jelly-like by coagulation as does crustacean blood, but a white precipitate forms, often in one large mass. The process can be watched under the microscope, and the precipitate will be seen to consist wholly of leucocytes which have collected together and left the fluid portion of the blood practically free from them. The leucocytes are amoeboid corpuscles which have fine bristle-like pseudopodia, often branched and by means of which they can move slowly (fig. 7, *L.*). Sometimes these narrow bristle-like pseudopodia prove to be the edge-view of flattened lamellae. When the blood is exposed to the air, the corpuscles collect together, becoming entangled by the pseudopodia, and in this way *clumps* are formed (fig. 7, *L. cl.*). The boundaries of those near the margins can be traced, but in the centre of a large clump all trace of a cell outline seems to have disappeared and a plasmodium is formed. This probably has the same function as the clotting in crustacean and mammalian blood, but differs in that there is no development of fibrin in the blood plasma which remains fluid on standing in the air, or even on heating. The same feature appears to be present in the coelomic fluid of some other invertebrates (**16**).

The blood as a whole appears to contain very little nutritive matter. In stained sections the leucocytes in the organs are round or oval, with retracted pseudopodia, and a prominent nucleus containing smaller dark bodies.

The central organ of circulation, the heart, is situated on the dorsal posterior side of the large adductor muscle, posterior to the digestive gland, against which it lies. It is contained in a pericardial cavity (fig. 1, *Per.*), which is bounded above by a fibrous roof connecting the two mantle lobes, while anteriorly it is prolonged, forming two deep pouches which extend above the adductor muscle and between it and the digestive gland.

The pericardium is the representative of the coelom, and communicates with the exterior by a pair of excretory organs, which are coelomoducts. The pericardium is lined by a thin endothelium formed of flat cells.

The heart consists of a ventricle and two auricles (fig. 13, *Ven.* and *Aur.*). The ventricle is a large spongy sac, the cavity being cut up and reduced in size by numerous muscle fibres which cross in all directions. When contracted the size is very small. The shape is roughly that of two triangles, with their bases apposed, except posteriorly, and with the apices, which are rounded, opening into the auricles. The ventricle has grown up round the rectum and encloses it (fig. 13, *Al. c. 5,* and fig. 43), as in the majority of lamellibranchs. The wall of the ventricle is composed of a layer of epithelial cells on the outer side, resting on a delicate basement membrane of connective tissue. Internal to, and lying against this latter, are the muscles, which run across the ventricle in all directions, imbedded in a granular matrix which sheathes the bundles of fibres. There appears to be no striation on these fibres.

The **Auricles** are two large chambers, one on each side of the ventricle, and having a brown tint. Their shape is roughly conical, the base being uppermost and communicating on each side with the ventricle, and opening by their narrower ends into the vein bringing blood from the gills and mantle to the heart. In Anodon and many other lamellibranchs the triangular auricles communicate with the efferent branchial vessel by the whole length of the base, and the narrow end opens into the ventricle. The position in Pecten may indicate the primitive molluscan arrangement, with posterior ctenidia.

The walls of the auricles are not smooth like those of the ventricle, but are raised all over into papillae, representing depressions of the inner surface (fig. 13). This peculiar papillated appearance is best seen when the auricle is distended by blood or injection, and is no doubt a device for increasing the area of the auricular walls for the purpose of excretion by means of the pericardial gland. This is confined to the surface of the auricles in Pecten, and gives the brown colour. It will be described later with the other excretory organs.

The auriculo-ventricular openings are guarded by a series of circular fibres which function as valves and prevent the blood being forced back into the auricles. The auricles are also connected with each other by a broad transverse branch ventrally resting upon the floor of the pericardium (fig. 13, *Aur. C.*). The heart beat is slow, an average of about twenty-five to thirty contractions per minute. It is necessary to inject the blood system to follow its course, and owing to the fact that the digestive gland is of a very dark colour, whilst the visceral mass is, on the other hand, of a light tint, injections must be made with both light and dark colours, in order to determine the course of the blood vessels in all parts of the body.

A great part of the vascular system can be made out by using an injection mass formed of a mixture of lard, linseed oil, and yellow oil paint (chrome yellow, as sold in collapsible tubes, will do very well), in such a consistency that it will run fairly easy (a little less viscous than glycerine). Care must be taken not to have any solid particles left in the coloured mass. It is necessary to prepare the specimens, for it is useless attempting to inject the living animal since the contraction of the muscles closes up the vessels. The necessary state of muscular relaxation can be produced by placing the animals in a bucket of sea water and adding slowly, at intervals, to the surface some of the following mixture:—100 c.c. 75 per cent. alcohol, 100 c.c. glycerine, and 200 c.c. sea water. In about eighteen to twenty-four hours, the specimens were narcotised and could be transferred to formalin (5 per cent. solution) for about half an hour without further contraction; they were then ready for injection. For the arterial system, the best point of attack was found to be the efferent branchial vessel (fig. 16, *Br. eff.*), in the ctenidial axis, with the point of the syringe directed towards the heart. This will inject the anterior and posterior aortae, the adductor artery, and in fact the whole of the arterial system, together with the mantle or pallial vein.

In order to inject the venous system the syringe can be put into the afferent branchial vessel (fig. 16, *Br. aff.*). Care must be taken that the tissue separating the two branchial vessels is not perforated. Further, when injecting the venous system, the valves must not be removed, but the convex valve should be broken away carefully, piece by piece, with bone forceps, right up to the attachment of the adductor muscle to the shell. The muscle must not be separated from the valves, for a large sinus will be otherwise broken into. If the oil mixture is used for both these injections the course of many of the main vessels can be followed, but it is not permanent and will not allow of the dissection of arteries and veins in the visceral mass and other deep-lying parts of the body. For this latter purpose, ordinary table jelly coloured with carmine, and melted with just a little water, proved quite satisfactory. It is necessary, previous to injecting with the hot jelly, to place the specimen in warm water for about half an hour.

ARTERIAL SYSTEM (fig. 14).

The blood leaves the ventricle by two main vessels, the anterior and posterior aortae.

The Anterior Aorta (figs. 14 and 19, *Ao. ant.*) is a large artery which arises from the ventricle at the middle of its dorso-anterior edge above the alimentary canal, and passes forwards directly over the latter to the digestive gland. There is an aortic dilation just after leaving the ventricle, inside the pericardium, and this can be seen to expand after each contraction of the ventricle.

On reaching the posterior end of the digestive gland the aorta passes dorsally along its middle line, giving off a small vessel on each side (figs. 14 and 19, *a.*) which pass over the surface of the gland along its posterior lateral margins, providing numerous branches, and eventually plunging below the surface into the substance of the gland. Other small branches are given off, on each side, from the aorta, and pass through the gland to supply the stomach.

Approaching the pit wherein the ligament rests, the aorta curves to the right of the median line so as to bend round the pit, and on reaching its anterior edge plunges down into the midst of the digestive gland, bending slightly to the right, so as to pass the oesophagus on that side. It gives off two vessels, which arise close together on the left side. Both of these leave the gland and pass into the mantle, one curving back to supply the region of the ligamental pit; whilst the other, the anterior pallial artery (fig. 14, *A. p. a.*), which is larger, passes forwards to the anterior dorsal corner of the mantle, where it bifurcates to form the circumpallial arteries running round the margin of the mantle lobes. It also gives off smaller vessels before dividing, which supply this area of the mantle on both sides.

The main branch of the aorta passes, as we have seen, into the midst of the digestive gland (fig. 14), and gives off very close to the two vessels above described a small branch which, passing through the gland, reaches the surface again on the left side and passes into the mantle. This will be easily seen (in injections with lard) on the left side of the gland.

At about the level of the upper lip, a small vessel is given off, passes to the anterior surface, and breaks up to supply the external labial palps and the upper lip (fig. 17, *A. l.*). The capillaries, or very small vessels, can be followed out on the palps if the injection is successfully carried out.

The main branch continues downward, still situated slightly nearer the right side of the animal, to enter the visceral mass, and branches are given off to the digestive gland. On the right side of the aorta a vessel arises which reaches the surface in the median line above the base of the foot, along the upper side of which it passes just beneath the epidermis, to supply the foot with blood (fig. 17, *A. p.*). This vessel gives off branches to the lower lip and inner palps, as indicated in the figure.

Returning to the main branch, this is continued by a smaller vessel which lies on the right side of the alimentary canal, and follows it in its course through the visceral mass, giving off small vessels to the ascending loop of the intestine and to the reproductive organs. There is another vessel of almost the same size which arises from the above, at about the level of the foot, and passing deeper into the visceral mass, bifurcates into two branches which pass along the left side of the descending loop of the intestine (fig. 14, *A. v.*).

The Posterior Aorta (fig. 14, *Ao. p.*) is a large vessel which leaves the ventricle below the intestine and on its right side. It runs for a short distance along the right ventro-lateral side of the rectum, and then gives rise to three vessels, the Rectal Artery (fig. 14, *A. r.*), which runs alongside the rectum, supplying it to the end, and two much larger vessels. One is the Posterior Pallial Artery (fig. 14, *A. p. p.*), the most important artery to the mantle, which turns upwards at an acute angle and runs in the roof of the pericardium towards the hinge line; it then passes to the posterior angle of the hinge and bifurcates, forming right and left Circumpallial (fig. 14, *A. c.*) arteries, which pass round the extreme margin of the mantle lobes and communicate eventually with the much smaller anterior pallial arteries.

The other large vessel arising from the posterior aorta is the Adductor Artery (fig. 14, *A. add.*). This leaves the aorta at a right angle, and plunges into the adductor muscle immediately in front of the deep cleft dividing the striped muscle from the unstriped. On entering the muscle, small vessels are given off from its posterior side, which pass out of the main bundle of striped muscle and, crossing the cleft, enter and supply the unstriped portion. The main artery, however, passes down towards the middle of the adductor, where it divides, sending branches in all directions. The figure shows the course taken in one of the specimens where the injection mass went very successfully, but probably here, as in other places, there is great variation in the smaller branches.

The VENOUS SYSTEM (fig. 18) consists largely of sinuses, and contrasts thereby with the fine arterial vessels. There are three main sinuses situated between the adductor muscle and its connective tissue sheath, which account for the large outflow of blood when the muscle is cut from a valve.

A large Dorsal Sinus (fig. 18, *S. D.*) is situated under the pericardium and digestive gland; anteriorly, this communicates on both sides with the renal organs. On the ventral side of the adductor, there are two sinuses, which extend from the cleft dividing the striped and unstriped portions of the muscle up to the renal organs. They are continued under these and the visceral mass, and communicate with one another. The main opening of these sinuses to the renal organ is at the dorsal end, and by slitting up the outer surface, the renal veins may be seen branching and becoming much smaller as they pass from the pericardial end towards the reno-genital opening (fig. 12, *Ro. r.*).

A large Hepatic vein (fig. 18, *V. h.*) on each side of the digestive gland, lying immediately under the epithelium, passes ventrally and slightly forwards to the anterior end of the renal organ, where it enters the dorsal sinus. Branches join it from the digestive gland and stomach.

A sinus-like plexus of vessels between the muscle and the visceral mass passes blood from the gonads and intestine to the sinuses communicating with the renal organs. The blood from the adductor passes along ill-defined paths in that muscle to enter these sinuses, thus completing the circuit.

The greater part of the blood from the visceral mass and alimentary canal passes by very conspicuous veins on the surface of the gonads (fig. 18, *V. v.*) to the sides of the renal organ, where they communicate with the numerous small vessels of the latter.

Thus all the blood is brought to the renal organs, with the exception of that which proceeds by the pallial arteries to the mantle. This will be considered later.

The blood returning to the heart leaves the renal organ by a series of fine vessels in the outer wall which open into a wide passage, the entrance to the afferent branchial vessel (fig. 16, *Br. aff.*). This soon contracts in size, and the vessel runs along the ctenidial axis proximal to the accompanying efferent vessel. It communicates with a vessel or cavity on each of the respiratory expansions of the principal filaments, but no connections with any of the other gill filaments can be seen.

The blood is brought from the gills, after aeration, to the heart, by means of the efferent branchial vessels, which, coming from the ctenidial axes, pass between the digestive gland and the adductor, and open into the narrow ends of the auricles, after receiving, at about the level of the dorsal extremity of the glandular part of the renal organ, the pallial vein (fig. 11, *V. pall.*), which brings back to the heart, directly, the blood from the mantle lobes.

The mantle lobes have an extremely large system of vessels (fig. 11), which are usually injected along with the arterial system. The Pallial Vein can be first traced at a point just within the circle of attachment of the pallial muscles, posteriorly (fig. 11). From this point it proceeds anteriorly, gradually approaching the adductor muscle on its way, until finally it reaches and opens into the efferent branchial vessels. On both sides, but principally on the ventral, it gives off a series of branches which divide and re-divide, ramifying in the thickness of the mantle and forming a complete network which abuts on the circle of pallial muscles, and is connected by a series of fine passages between these to the circumpallial arteries (fig. 11, *A. c.*) already described. The mantle lobes are thin, and comparatively little metabolism goes on there, especially when one considers the great area of blood spaces, and it must be assumed that the mantle lobes play the most important part in the respiration of the animal. The blood from the mantle reaches the heart without having passed through the renal organ, so that the heart contains mixed blood—completely aerated blood from the mantle, and probably incompletely aerated blood from the gills. This mixed blood will pass both to the pallial respiratory surface and to the body generally, from whence it is collected and taken to the renal organs, then to the gills, and so back to the heart.

NERVOUS SYSTEM.

The nervous system of Pecten is of the typical Lamellibranch type. The usual three pairs of ganglia—cerebral, pedal and visceral—are present, though much modified in shape and position. In addition to these, there are collections of nerve cells along certain nerves, in particular the circumpallial nerve (fig. 26, *N. c.*), which renders the latter almost a fourth ganglion, both structurally and functionally.

Cerebral ganglia.—The pair of ganglia known as the cerebral, or better—the cerebro-pleural, representing the fused cerebral and pleural ganglia occurring in Nucula and Solenomya, are found best by pulling the lower lip dorsally and moving the labial palps aside, so as to lay bare the area between the lower lip and the foot. The ganglia will then be seen faintly through the overlying tissue, which must be removed carefully or they will be pulled away with it. They are situated a considerable distance below the mouth and oesophagus, and very close to the pedal ganglia. Each ganglion (fig. 27, *G. cb.*) shows indications of being bilobed, and this is further borne out by sections which show a distinct, though not a deep, division into two lobes. From the upper corner arises the cerebral commissure (figs. 26 and 27, *Com.*). This connects the two ganglia and passes dorsally over the oesophagus, but owing to the position of the cerebro-pedal ganglia it is a larger loop than is usually the case. From the outer sides of the ganglia, just below the depression dividing them, arise the anterior pallial nerves (figs. 27 and 26, *N. pa.*), and a smaller nerve which gives branches to the labial palps (fig. 27, *N. l.*).

The Anterior Pallial Nerve lies close to the cerebral commissure, and passes with it to the side of the oesophagus, embedded in the digestive gland. It rises to the surface and enters the mantle just dorsal to the upper lip where this joins the outer labial palp on each side, then, dividing into two branches, it passes to the margin of the mantle and joins the circumpallial nerve (fig. 26, *N. c.*) by several branches.

From the inner sides of the cerebro-pleural ganglia two delicate nerves (fig. 27, *N. ot.*) arise which pass deeper into the tissue and innervate two small bodies, which have a white appearance in dissections.

These are the otocysts (fig. 27, *Ot.*), and the Otocystic nerves in Pecten can thus be traced directly from the Cerebro-pleural ganglia. The lower ends of the cerebro-pleural ganglia gradually pass into the cerebro-visceral connectives (fig. 26, *Con. cv.*).

The Cerebro-pedal Connectives are very short nerves (fig. 27, *Con. cp.*), which arise about the middle of the inner sides of the cerebro-pleural ganglia and run towards each other and slightly towards the surface. They each bear a ganglionic swelling just before arriving at the pedal ganglia.

The Pedal Ganglia (*G. p.*) lie closely apposed to one another, so that the pedal commissure is so short that it is barely distinguishable. These ganglia are situated outside the foot, and are the nearest to the surface, so that probably they will be the first seen when looking for the cerebro-pleural. Both the cerebral and the pedal ganglia are pigmented yellow, and both have a similar structure, viz., a cortex of ganglion cells with processes passing into a core, made up of nerve fibres.

From the pedal ganglia, two pedal nerves (fig. 27, *N. p.*) pass directly into the foot, where they break up into numerous small branches, supplying the muscles.

The Visceral or Parieto-splanchnic ganglia are completely fused in Pecten to form one large and complicated mass (figs. 26, 28, *G. sp.*). It is the largest ganglion and gives rise to most of the nerves, and this can be accounted for by the fact that, compared with other Lamellibranchs, it is the posterior region of the body that is most developed in Pecten, the anterior with the anterior adductor having been suppressed and the foot reduced. Furthermore, the mantle, with its important muscles and sense organs, is innervated chiefly by the visceral ganglia.

The fused ganglia lie on the ventral surface of the adductor muscle, imbedded in a mass of connective tissue, and can be generally seen without any dissection (by reason of their yellowish brown colour), on the right side about 0·5 cm. from the last point of attachment of the visceral mass; that is, slightly postero-ventral to the opening of the right renal organ.

Its shape is very striking indeed (see fig. 28). There is a large central lobe, which is divided anteriorly by a transverse division into a light yellow posterior part, and an anterior portion which is more deeply pigmented yellow. This anterior darker part is sub-divided into two lobes. Laterally, the central lobe is connected by a depressed region with two crescent-shaped expansions or lateral lobes, practically without pigment. Thus there is a post-central lobe (fig. 28, *G. c. l.*)—unpigmented except in its anterior margin; two anterior lobes—darkly pigmented (*G. ant.*); and two lateral lobes—unpigmented (*G. lat.*).

These compound ganglia are connected with the cerebro-pleural ganglia by the cerebro-visceral connectives (fig. 28, *Con. c. v.*). These arise, as we have already seen, from the lower end of the cerebro-pleural, and at once take a course slightly inward and away from each other. That on the left side passes to the left of the rudimentary retractor muscle of the foot, and then lies along the base of the visceral mass at its sides, between it and the renal organs and closely apposed to the adductor muscle along the greater part of its course. The two connectives on reaching the visceral ganglion enter it just outside the anterior pigmented lobes, viz., by the anterior ends of the lateral lobes. The right visceral connective comes in rather at an angle, the left being nearer the median line.

Lying almost above the right connective, a little before it reaches the ganglion, and on the other side, a little to the left of the connective, are small pigmented bodies (*G. osp.*), which sections show to be ganglia made up of a cortex of ganglion cells with long processes passing into the centre, and with the outer ends drawn out into several fine fibres. From these osphradial ganglia, nerves pass up through the connective tissue to the epithelium directly above. Here they become connected with numerous sense cells, forming the Osphradium.

The nerves connecting these osphradial ganglia with the visceral, pass into the cerebro-visceral connectives and enter the ganglion with these nerves.

Two conspicuous nerves arise from the visceral ganglion close to the entrance of the cerebro-visceral connectives, but slightly posterior to these. They arise, also, at a slightly higher level than most of the nerves which pass to the mantle. These are the branchial nerves (fig. 28, *N. br.*); they pass out almost at right angles to the cerebro-visceral connectives, and just passing below the extremity of the renal organs, take up a position along the outer margins of the latter, where they are easily seen, being rather near the surface. This course is followed until the expanded end of the afferent branchial vessel is reached, when the nerves bend round and enter the ctenidial axis, along which they pass, gradually becoming more attenuated until the end of the lamellae is reached. The nerve lies alongside and above the afferent branchial vessel along its whole length (fig. 45, *N. br.*), sometimes nearer one side of the ctenidial axis than the other.

This nerve is well supplied with ganglion cells, which lie chiefly on the side nearer the gill filaments. The branchial nerve gives off laterally, from its ventral surface, small nerves, at frequent intervals along its whole length. These pass towards the base of the gill filaments at the sides of the afferent branchial vessel, until the two longitudinal ctenidial muscles are reached. They are continued between the muscles and the epidermis to a point about level with the middle of the muscle bundles, where they bear a considerable number of ganglion cells. From the ganglia thus formed, nerves arise, which extend in almost a continuous sheet to the bases of the filaments, down each of which a delicate branch passes. Thus, the gills have a very thorough nerve innervation, and are probably very sensitive, though specially differentiated sense cells have not been seen.

The Pallial System is supplied chiefly by the visceral ganglia. It is the most extensive in the body, and this is to be expected considering the array of sense organs with which the mantle is supplied, together with its important muscular system. It consists of a large nerve which runs parallel with the mantle edge, just interior to the pallial artery. This, the circumpallial nerve (fig. 26, *N. c.*) is physiologically a ganglion. It is well supplied with ganglion cells, and is thickest in the middle of its course. Anteriorly and posteriorly the nerves become very fine, and eventually reaching the hinge line the nerves of both valves become continuous, so that the circumpallial nerve is one continuous cord, which is much attenuated in two places at the hinge line, anterior and posterior, respectively. From the circumpallial nerve branches arise to innervate the eyes and tentacles (fig. 4, *N. c.*); the optic nerves will be described in the chapter on the eye. Each of the long extensible outer tentacles is supplied with a nerve which runs up to the centre and gives branches to the sense cells. The pallial muscles are also innervated by branches from the circumpallial nerve. The circumpallial nerve is connected with both the cerebro-pleural and visceral ganglia; with the former by the anterior pallial nerves (*N. pa.*) already described (figs. 16 and 18, *N. pall.*).

The pallial nerves from the visceral ganglion do not pursue a similar course on the right and left sides of the body. On the right, that is, the side on which the gill is attached to the mantle, the pallial nerves pass out as a large trunk very close to the branchial nerve, and run alongside this until the point is reached where the branchial nerve enters the gill lamellae.

Here they enter the mantle, and at once divide into branches which radiate out to the circumpallial nerve (fig. 3, *N. pall.*). The main branch, however, passes along in the mantle, after bending sharply, exactly in the line of attachment of the basal gill lamellae, and from this the various branches arise.

On the left side the distribution is somewhat different. The pallial nerves are not collected to form a large trunk, but radiate out directly from the ganglion over the surface of the adductor muscle until the mantle is reached; entering the mantle, they pass out, branching on the way, to the circumpallial nerve. In all probability these pallial nerves also innervate the pallial muscles. There are, in addition to the pallial nerves already described, certain nerves which leave the visceral ganglia from the posterior angles of the lateral lobes, and pass directly back over the surface of the adductor until they reach and enter the mantle opposite the terminal point of attachment of the rectum (fig. 28, *N. pp.*).

With regard to the histology of the visceral ganglion, the ganglion cells are, for the most part, grouped over the surface forming the cortex. The anterior central lobes are almost entirely composed of ganglion cells, which also abound on the central part of the dorsal surface (that is, the surface against the adductor muscle). The main part of the ganglion is made up of fibres, amidst which can be seen a very definite transverse series; probably the representative of the visceral commissure.

SENSE ORGANS.

Pecten is unusually well supplied with sensory structures, certain of which, the pallial eyes, attain a high degree of specialisation, and are a remarkable feature of the animal.

The sense organs are of five kinds, the first three, and probably the fourth, of which are common to the Lamellibranchiata, and do not differ to any great extent in the various genera. They are:—(*a*) Sensory cells in the epidermal layer; (*b*) a pair of otocysts; (*c*) a pair of osphradia; (*d*) an abdominal sense organ; (*e*) a series of highly-developed eyes.

(*a*) The Sensory Epithelial Cells.—These, the "Pinselzellen" of Flemming (**30**), are to be found scattered all over the epidermis, but are present in greatest numbers on the long, extensible tentacles of the mantle edge, where they occur between two "Stützzellen," which according to Rawitz have a common membranous covering. They are most abundant near the apices, and render each of these tentacles a most important tactile organ. This view is confirmed when the animal is observed living, and the greatly extended tentacles can be seen moving slowly to and fro in the water. A very slight motion in the water appears to be stimulus enough for a sudden retraction.

These sense cells are also present on the mantle edge proper, in the epithelium covering the adductor muscle in the neighbourhood of the visceral ganglia and osphradia, on the sides of the gill axis and in the outer epithelium of the rectum near the end of the free portion.

In shape, these sensory cells differ but little from the ordinary epithelial cells, which act as supporting cells around them. In many cases, however, they are very narrow, with the nucleus situated about the middle of their length. The narrow cells have the end towards the surface of the epithelium swollen out into a disc, which is just as broad as the ends of the other epithelial cells around. Another feature is that the sense cells stain more intensely when a nerve stain is used. The cells are provided with a bundle of extremely long cilia, as long, or longer, than the cells themselves. These cilia are quite characteristic structures, and much longer than those of ordinary epithelium. The margin of the sense cells shows a distinct striation vertical to the surface, as if the sense hairs or cilia were produced into the cell, and this striation can often be observed, though less distinctly (still deeper in the cell), as a series of lines converging towards the nucleus. The base of the cell is connected with the nerve fibres, ramifying under the epidermal layer and in connection with the deeper lying nerves, one of which runs up the centre of each of the extensible sensory tentacles. These cells are probably olfactory as well as tactile in function.

(*b*) THE OTOCYSTS.—A pair of Otocysts (fig. 27, *ot.*) are present in both *P. maximus* and *P. opercularis*. They are situated quite external to the foot, embedded in the visceral mass amidst the connective tissue of the digestive gland; and lie beneath the cerebral and pedal ganglia and connectives, that is, on the side turned away from the surface of the body, and somewhat between the ganglia.

They can be seen in dissections as two minute delicate white bodies, if the connective tissue above the cerebral and pedal ganglia is carefully removed, and are perfectly spherical in shape, with a diameter of 0·17 mm.

The position of the otocysts outside the foot is interesting, as the pedal ganglia are also completely outside the foot in Pecten. There can, however, be no question here of the nerve innervation, for the nerves can be traced directly out from the cerebral ganglia without any connection with the cerebro-pedal connectives, thus rendering further proof to the theory that the otocysts are always innervated by the cerebral ganglia, even when they are connected with the cerebro-pedal connective and lie in close proximity to the pedal ganglia. The nerves enter the otocysts on the sides facing the cerebral ganglia, and are thus quite short. The otocysts in both *P. opercularis* and *P. maximus* are spherical closed sacs, the internal cavity of which is bounded by a layer of sense cells. In this cavity there is situated an otolith. This appears in *P. opercularis* as a large ball, formed of small crystals of irregular shape, as if a heap of fine detritus had been heaped together. The otolith thus formed fills almost completely the cavity of the otocyst. In *P. maximus*, I have only found some larger and more scattered crystals (otoconia) in the otocyst. In the adults of both species examined, the otocyst has no duct connecting the cavity with the external world.

THE OSPHRADIA.—These paired sensory structures, named by their discoverer, Spengel (**38**), organs of smell, and which are of general occurrence in Mollusca, are not highly developed in Pecten. They cannot be detected without the aid of microscopic sections, and though pigment granules are then seen to be present to a small extent in the cells, they are not frequent enough to give any conspicuous colour, and the organs differ greatly from the very obvious pigmented osphradia of many molluscs. Two small ganglia, the osphradial ganglia, have already been described in the section on the nervous system. They lie in close proximity to the visceral ganglion, and nerves pass upwards from the ganglion cells forming these two spherical ganglia to the surface epithelium, almost directly above, where there is a small prominent area of elongated epithelium forming the osphradium. If a piece of the adductor muscle is removed so that it bears on its surface the visceral ganglia and overlying connective tissue and epithelium, and sections are cut at right angles to the surface, the osphradial ganglia and their connections with the osphradia can be easily followed. The epithelial cells of the osphradium increase in height until they are about three times that of the adjoining ordinary epithelium. The cells forming the organ bear no cilia, though these occur on the ordinary adjacent epithelial cells, but there is a prominent cuticle present. The nucleus is large and almost round, and small pigment granules occur (though in small numbers) in the cytoplasm. Underlying the osphradia are nerve cells connected with the innervating nerves from the ganglia, and from these, numerous fibrils arise and pass through the connective tissue basal membrane, until, branching still further, they pass between the supporting epithelial cells to the surface (text-fig. 3).

The Abdominal Sense Organ was described first by Thiele in a species of *Arca* in 1887 (**39**), and List in 1902 (**6**) described the structure in detail in the Mytilidae. In *Pecten maximus* it is well developed but is unpaired.

The microscopic structure is almost identical with that in Mytilus, and probably this organ occurs generally in the lamellibranchia. It is a slight uncoloured thickening situated on a connective tissue "flap" which passes from the adductor to the right mantle lobe, just above the last point of attachment of the rectum to the muscle. The free edge of this thin flap is directed towards the hinge line.

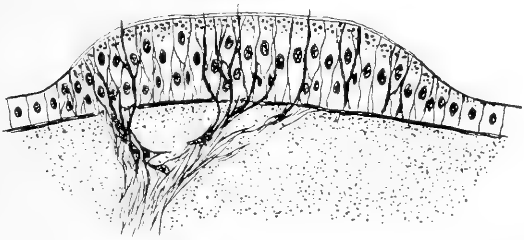

Fig. 3. Section through Osphradium. × 450.

If transverse sections are made through the ridge, the striking microscopic structure of this organ makes it at once obvious. It appears (see fig. 4) as a hillock of sense cells extending on both sides of the edge of the connective tissue flap, and much longer than it is thick. It is rendered very evident because firstly the cells composing it are many times higher than the ordinary epithelium and the junction is very distinct, and secondly because the sense hillock bears a thick covering of extremely long cilia or fibrils, which are themselves several times the length of ordinary epithelial cells and occur nowhere else on the body. The sensory epithelium rests on a basal connective tissue membrane which is pierced by nerves, or rather by nerve fibrils, which proceed from the visceral ganglion and pass directly over the adductor under its connective tissue sheath. In transverse sections stained with haematein the epithelium stains very deeply, and many nuclei are apparent which appear to lie at all levels with the exception of a narrow zone bounding the free surface of the cells.

The nerve fibrils break up into finer processes amongst the cells, and form a very complex network around them. Many of the nuclei appear to belong to the nerve fibres, whilst others much rounder and lighter staining probably belong simply to supporting cells. The nerve fibrils can be traced from their nuclei to the edge of the hillock, where they are continued free as the long cilia, so that these are in reality the terminations of primitive neuro-fibrillae.

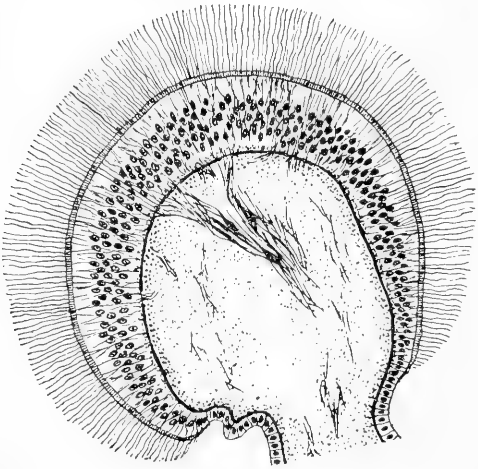

FIG. 4. Section through abdominal sense-organ. × 300.

There is, in addition to the covering of long cilia, another much narrower "seam" lying at the bottom of the cilia, and in fact having the appearance of a very thick cuticle formed of a number of delicate parallel rods. It has rather the appearance of another short layer of stiff cilia. These rods can also be traced for a short distance within the cells.

With regard to the function of this well-developed organ, it is difficult to see that it can be any other than a water-testing, either smell or taste organ, yet this sense is generally ascribed to the osphradia, and it is difficult to understand the presence of two organs doing the same work, situated very close to one another, and yet having a different structure.

The histological structure is remarkably like that of the "Seitenorgane" described by Eisig (**43**) in the Capitellidae, and Thiele himself supposes that the function, like that of these organs and the lateral line of fishes, is the perception of vibrations in the water, though no experimental evidence is put forward.

THE EYES.—No organs of Pecten, nor of the Lamellibranchs in general, have given rise to more discussion with regard to details of structure than the eyes; and as one would expect, these remarkable organs, which are so prominent, glittering like minute diamonds set amidst a forest of tentacles, attracted the attention of early naturalists. They were first described by Poli, as far back as 1795. The first fundamental work was that by Hensen in 1865 (**31**), and since then the most important papers are those by Hickson in 1880 (**33**), Carrière 1885 (**29**), Patten 1886 (**35**), and Rawitz in 1888 (**36**). The structure of the retina was, however, still very uncertain, and this has been the chief feature of the works of Schreiner 1896 (**37**), Hesse 1900 and 1907 (**32**), and Hyde 1903 (**34**), bringing the matter up to date. The difficulty of making satisfactory preparations, and the frequency of artifacts caused by fixation and further treatment, has been the cause of much confusion.

The mantle, as previously described, has a margin bearing the characteristic lamellibranch structures (see fig. 4). There are three folds, on the outer of which are borne tentacles, and on the median and smaller are situated the eyes (fig. 4, *E.*), on short stalks which resemble the basal portions of the ordinary tentacles. Many workers have noticed this similarity, which, together with the course of the nerve fibres, has led them to the conclusion that these are homologous organs modified for different functions. The Pecten eye is an inverted eye like those of Planarians and Vertebrates, and resembles the latter in some respects. It is derived from both ectoderm and mesoderm, the lens being formed from the latter. The number of eyes varies considerably in the different species, and there is further a difference in the number on the two mantle lobes.

In *Pecten maximus* the numbers average about 35 on the left (flat) side and as few as ten, separated by long intervals, on the right (convex) side. In *Pecten opercularis* the numbers are more equal, the following being some series:—right, 37, 35, 41, 51; left, 52, 51, 56, 61; but it will be seen they still are more numerous on the left than on the right, though the left valve of *Pecten maximus* is the flat one, whereas the right valve is the flatter of the two in *Pecten opercularis.*

Patten (**35**) observed that *P. jacobaeus* always lay on its right valve, that is the convex, and if turned over it soon righted itself.

Pecten maximus, which like *P. jacobaeus* has very unequal valves, is always to be found lying on the right convex valve—which suggests that the greater development of eyes is always on the flat upper valve. This is supported by the condition in *P. opercularis*, where little difference can be detected between the valves, and the number of eyes is more alike than in *P. maximus.* One might at first expect that the eyes looking up toward the light would be the better developed, but the eyes on the left upper valve are the more numerous, are larger and situated on longer stalks in *P. maximus.* This may be a result of the asymmetry of the animal, and I have observed that the left mantle lobe is frequently extended so far out that it overlaps the shell edge, and the eyes are directed horizontally out, or even upwards, in place of downwards towards the ground, as has sometimes been stated. The eyes vary in size considerably. There is a group of large eyes anteriorly and posteriorly on each mantle lobe.

In *P. opercularis* there are about five eyes in each such group, and separated by an interval from these we have a series of eyes in the ventral margin. Those nearest the interval are the smallest, and the largest are to be found mid-ventrally. I do not find, however, the regular arrangement of large and small eyes described by Patten (**35**). Neither have I been able to find in *P. opercularis* any eyes "the pupils of which are entirely covered with pigment" (Patten, **35**).

The eye stalk (fig. 29, *E. st.*) which supports the eyes is a short column, and is retractile, but one does not observe the eyes being turned in different directions as is the case with the tentacles. The lower part of this eye stalk is bounded by unpigmented epithelium, but as the eye is approached, the amount of pigment granules in the epithelium cells increases until the whole cell is almost filled. The pigment is of a dark brown or blackish colour. In sections it will be seen that the epithelium is composed of columnar cells, which are lowest at the base but become taller as one approaches the cornea (*Cor.*), which is a continuation of the same layer over the surface of the eye.

The pigment granules are thickest at the bases of the cells, the nuclei of which are generally situated in the upper part. The pigmented cells are not equally distributed, but are most numerous and extend nearest to the base of the eye stalk, on the upper side which is turned towards the light (fig. 29, on left side).

The name **iris** has been given (fig. 29, *I.*) to the zone bounding the cornea where most pigment is present. The cells of the iris become rapidly less tall, the nucleus becomes more central, and then suddenly all pigment is lost, and they pass into the cubical, transparent cells of the cornea (fig. 29, *Cor.*). A thin layer of cuticle covers the epithelial cells of the eye stalk, the iris and the cornea.

The function of the iris seems to be, like that of the pigmented sides of the eye vesicle and stalk, to prevent lateral rays of light penetrating to the retina.

The cells of the cornea were discovered by Patten (**35**) to be pentagonal or hexagonal in surface view, hour-glass shaped in section, quite free from pigment, and to have a curious interlocking or notched appearance on the edges, so as to give the cornea a much firmer and more rigid structure as a membrane. This appearance was described by Schreiner (**37**) as being due to intercellular substance and to fixation alone.

From transverse and longitudinal sections through these cells fixed in Mann's Fluid, Flemming's Reagent and Osmic Acid, I am of opinion that they do possess processes on all sides which probably connect them together, as in the so-called "Prickle Epithelium." This occurs also in the epidermal cells of the eye stalk (fig. 35).

The connective tissue which makes up the rest of the eye stalk is a continuation of the same from the mantle, and is similar in structure. There are numerous lacunae with blood corpuscles, and the rest consists of almost structureless, homogeneous connective tissue with scattered nuclei and a few muscle fibres (fig. 29, *Op. m.*), which later are present in considerable quantity in the layer immediately below the epidermis, and probably cause the slight movements of the eye. I have seen no trace of Patten's long striated muscle cells; but the muscle fibres when contracted may be thrown into a series of short waves, which possibly produced the striated effect.

The connective tissue of the eye stalk is continued up to form the sides of the optic vesicle, and is actually prolonged under the cornea as a structureless layer with a few nuclei—the pseudo-cornea (fig. 29, *Cor. ps.*) of Patten (**35**).

The muscle fibres extend up laterally as far as the edge of the iris, and end quite suddenly with an upward curve, as if attached to the last cells of the pigmented iris. This is the region that Patten has termed the Ciliaris.

Scattered ganglion cells are also occasionally to be seen in the connective tissue of the stalk. They are probably connected by nerve fibrils with the nerves of the eye.

Lying in the optic vesicle, against the pseudo-cornea, is the Lens (fig. 29, *L.*), which Patten has figured and described correctly (**35**). It is biconvex, but the dome-shaped surface towards the retina is very much more convex than the corneal surface. The lens is composed of large cells, irregular in shape, but more or less rectangular in the centre. They have distinct walls, and granular contents which stain somewhat deeply with eosin. The nucleus always lies to one side of the cell, so that in thin sections some of the cells appear to be without a nucleus. Fibrils are of frequent occurrence in these cells, and Hesse (**32**) states that they have a radial arrangement from the centrosomes to the periphery.

The cells are smaller at the circumference of the lens, and the cells bounding the corneal and retinal surfaces, especially the latter, are elongated and flattened. It is probable, owing to the layers of the flattened cells with fibrils and prominent walls that the appearance of a membrane, called by Patten the suspensory ligament, arose. No definite membrane can be seen by Schreiner or myself.

The lens lies suspended in a space which has been termed a blood sinus, as blood corpuscles are occasionally found. This space, which is situated between the retina and the lens, like the chamber in the vertebrate eye containing the "vitreous humour," does not appear to have any connection with the lacunae of the eye stalk. I have found blood corpuscles only present in very few out of a great many sections, and these were probably abnormal occurrences due to fixation only, and the space cannot, therefore, be looked upon as a blood sinus.

The Septum.—The portion of the optic vesicle containing the retina is separated from the lens chamber by a membrane which runs completely across the eye. This is the Septal Membrane (fig. 29, *Sep.*). Commonly the retinal surface of the lens lies against it. Patten, however, considers it a support for the lens to which it is actually attached, and, further, that it plays the part of an elastic cushion elevating the lens when it has been pulled in by contraction of muscle fibres.

Owing to the retina being pulled away from its underlying layers in sections, the septum comes perhaps to touch the lens, but in the natural conditions the lens and septum are not attached, and the latter can thus not act as an elevator. Moreover, the whole appearance of the eye and its reactions to stimuli render it extremely improbable that it possesses any means of accommodation or focussing.

The septum in the adult appears structureless, thickest in the middle, where it is perforated by the outer branch of the optic nerve. At this place the septum has the appearance of being formed of two membranes placed together, and which are here slightly separated. the nerve passes intact over the septum to the middle, where its several fibrils penetrate the membrane, diverging at the same time in all directions to make their connections with the outer layer of retinal cells. The peripheral edge of the septum appears to be a direct continuation of the sclerotica (fig. 29, *Scl.*).

Retina.—The Retina and its two underlying layers have received, at different times, varying names. I have adopted in the main those of Hesse, with some alterations; the chief synonyms will be referred to in the text. In sections the retina appears as a thick band lining the inner wall of the optic vesicle, but separated from it by two other concentric layers—the argentea and the tapetum (fig. 29, *Arg.* and *T.*). The retina further resembles in a remarkable way that of the vertebrate eye, in the fact that the light rays must pass through it to the argentea, and then the nervous reactions aroused pass back again through the various elements to the optic nerves which innervate the retina on its distal surface. This arrangement is only approached outside the vertebrates in the Planaria (Hesse, **32**), and there the structure is much simpler. In most figures a space is shown between the retina and the argentea. This appearance, however, is due to contraction on fixing, and normally retina, argentea and tapetum are in contact. The retina has been the source of all the disagreement with regard to the structure of the Pecten eye, and I have endeavoured to examine the various views held and compare them with the appearances of my own preparations; but a complete elucidation has not yet been arrived at. The retina can be divided into three main layers, viz.:—

(*a*) An outer layer lying against the septum, and made up of the Distal Cell layer (fig. 29, *D. c. l.*) and Outer Interstitial Cells (fig. 30, *In. c. o.*). This is Patten's outer ganglionic layer and the Ganglienzellenschicht of Rawitz (**36**).

(*b*) The layer of Rod Cells (Retinophorae—Stäbchenzellen (fig. 29, *R. C.*).

(*c*) The layer of Rods (Stäbchen) (fig. 29, *R.*).

The cells of the inner ganglionic layer of Patten, corresponding to the Zwischenzellen of Hesse, and what I shall call the inner interstitial cells, are to be found between the rod cells (fig. 30, *I. c. i.*).

Rod Cells.—With regard to the minute histology of these structures much confusion exists. They form the most conspicuous portion of the retina in transverse sections, and are prominent as a layer of columnar cells, the basal proximal ends of which are continued as the rods forming another well-defined layer of the retina.

The rod cell layer is thus the middle layer of the retina, lying between the layer of rods and the distal layer of cells, to be considered below. The rod cells are of considerable length, and decrease gradually in thickness towards the periphery of the retina until, indistinguishable from nerves, they become connected with the fibres of the inner branch of the optic nerve (fig. 29, *Op. n. i.*) which pass down outside the optic vesicle on all sides and unite to form the nerve branch under the eye. In order to study the details of a rod cell, sections must be cut in the plane of the retina and at right angles to the long axis of the eye-stalk. An examination of teased preparations is also necessary in addition to the sections.

The rod cell increases gradually in diameter from a mere thread at the back of the retina to the typical columnar region. At about a fourth of its length is a slight varicosity, and a short distance further and nearer the basal end the nucleus causes a rapid increase in the diameter (fig. 30, *R. C. n.*, and fig. 29, *R. C. n.*). The nuclei of the rod cells are to be found in longitudinal sections through the eye, in a cluster not far from the sides of the retina (fig. 29, *R. C. n.*) and before the point is reached where the cells curve almost at right angles to form the basal portions, which like a series of columns lie with their long axes in a proximal-distal direction.

Another series of nuclei is generally conspicuous (fig. 30, *C. i.*), but, as first shown by Patten (**35**), these do not belong to the rod cells, but belong to cells lying between them (inner interstitial cells). The rod cells all terminate at the same level, or rather pass directly into their continuations—the rods. At the line of junction of these two elements there are traces of a delicate membrane extending across the retina, called by Schreiner (**37**) the outer sieve membrane (fig. 30, *S. m. o.*). This is perforated by the rods, and does not, as Patten stated (terminal membrane), separate the rod cells from the rods, that is, form the actual base of the rod cells. Each rod cell is connected with a rod, the one being a continuation of the other, the line of division being marked by the outer sieve membrane outside the cell, and internally by a difference in cell structure. Like Schreiner, I have seen no vacuole described by Patten as existing at the base of the rod cells.

The Rods (fig. 30, *R.*) are difficult to preserve in good condition, but absolute alcohol sublimate gives good results, and sometimes Flemming, though with large *Pecten maximus* eyes the latter probably does not penetrate quickly enough. They are cone-shaped bodies, longest in the centre of the retina and decreasing slightly in size towards the periphery. The basal portions of the rods are separated from each other by, and rest on, a substance staining rather darkly with Iron-Haematoxylin (fig. 30, *S. m. i.*) which separates them from the underlying argentea. There has been some disagreement as to whether this is a secretion of the argentea or an artifact. It is certainly not the latter, nor have we to do with single rod mantles as stated by Rawitz (**36**). It is simply a homogeneous mass in which the rods are imbedded, and I propose the name Basement Membrane instead of Schreiner's Inner Sieve Membrane, owing to the difference from the outer sieve membrane. Hesse (**32**) has calculated in *Pecten jacobaeus* there were present 24,000—27,500 rods to the sq. mm. That is about 2,400 rods as the average for a medium-sized eye.

The internal structure of these elements, both rods and rod cells, has caused much confusion. The rod cells have rather more compact protoplasm than the rods, which appears in sections to be condensed rather in the middle (fig. 32). In transverse section the rod cells appear rather irregular in shape—some circular, others rectangular or triangular; the appearance, in short, that cylindrical columns might have in consequence of the pressure of adjoining cells. The rods are not so irregular in shape, and the cell contents are not so conspicuous, but running down through the middle is a well-defined axial fibre (fig. 32, *Ax. f.*). This can be seen excellently after fixation in Flemming and staining with Haematoxylin, and is distinct, both in transverse and longitudinal sections. It was, however, best followed after treatment by Apathy's "Nachvergoldung Method" or by the same author's Haematein IA. This fibre can be seen distinctly in all rods extending from the base of the rod cell to the base of the rod (fig. 30, *Ax. f.*) Patten (**35**) described it as dividing at the base into two branches, which became connected with other nerve twigs outside the rod. This is not the case, it passes directly to the base of each rod, where it terminates. Both Patten (**35**) and Rawitz (**36**) have followed this structure through the rod cells. Rawitz stated in addition that there was a fine canal running through the middle of the rod cell, in which lay the fibre. Schreiner (**37**), after making a careful series of preparations, came to the conclusion that there was no axial fibre in the rod cell, and that the appearance of one was due to the contours of adjacent cells, or an optical effect formed owing to the rod cells being slightly angular in transverse section and not perfectly cylindrical. Hesse (**32**) acknowledges that it is often extremely difficult to find the fibre in the rod cells, even when it is perfectly obvious in the rods, but confirms Patten, and states that in *Pecten aratus* the fibre is easily followed in the rod cells.

The eye of *Pecten maximus* is not suited for this histological work, but transverse sections made through the retina (figs. 32 and 33), and cutting both rods and rod cells, show how distinctly the fibre is to be seen in the former whereas it is absent in the latter, and here both rods and rod cells have been subjected to exactly the same conditions of fixation and staining. In the Gold Chloride preparations, however, the fibre was seen in some rod cells to extend very slightly above the base, and not to end abruptly but rather to thin out. Apathy's (**27**) and Bethe's (**28**) work on the nervous system has thrown much light on the structure, and if we regard the nerve cell as simply a cable, the conducting wires of which are the neural fibrillae and the perifibrillar substance the protective and insulating material, we can apply this to the rod cells. The axial fibre in the rods is a nerve fibril lying in its nerve cell. It is so obvious because it is in all probability the product of the fusion or very close apposition of several primitive fibrillae.

Now, it is very difficult to consider this ending abruptly at the base of the rod cell, especially if it be regarded as the conducting element. It is also certain that it is always seen only with great difficulty in the rod cells, and I could not demonstrate its appearance in the eyes of *P. maximus*.

Hesse (**32**) states that in some cases he could see several fibrillae in the rod cell, and in any case the neuro fibril was always thinner there.

Furthermore, the appearance in transverse sections shows that the cell contents which seem equally distributed in the rod cells (fig. 33) are condensed, and with the prominent axial fibril run down the centre of the rods (fig. 32). Bethe (**28**), in his work on the nerve elements of *Carcinus*, states that after using Toluidin and Methylene blue methods the primitive fibrillae appear with different intensity, and says there is in places a more or less stronger apposition of the " Elementar fibrillen " which form the primitive fibrillae, and the darker stained primitive fibrillae are due to the union of more " Elementar fibrillen."

I believe, therefore, that in the rod cells there are a number of very thin primitive fibrillae which at the periphery of the retina become connected with the neuro fibrillae of the optic nerve. These are only with difficulty to be made out, but have been seen on some occasions, and also by Hesse and Schneider (**44**). At the base of the rod cell there is, however, a fusion or an apposition of these neuro fibrillae, and the resultant obvious axial fibre of the rods is produced. I have reproduced this somewhat diagrammatically in fig. 30.

Hyde (**34**) has published an account of the structure of the Pecten eye which differs considerably from all the previous accounts. Unfortunately, no transverse sections are figured, and I have failed to find the structures described in my sections, which agree with those of Hesse. Hyde describes the rod cells as being simply supporting, and not visual sensory cells, and, further, that it is the inner interstitial cells (which lie between the rod cells) that are continuous with the axial fibril of the rods on the one hand and the optic nerve on the other. The rods, however, as above stated, are undoubtedly continuations of the rod cells, and though Methylene blue may be perfect for nerve fibrils, it cannot alter this fact, which has been observed by all observers in teased preparations and sections. Any continuations of the inner interstitial cells penetrating the outer sieve membrane will lie, therefore, between the rods, just as the former themselves lie between the rod cells.

In addition to the normal rod cells with their rods which have been considered above, there is a peripheral region in which rod cells are present which differ slightly in structure from the others and do not bear rods at their bases (fig. 29, *R. C. p.*); these were called Pseudoretinophorae by Patten. They are regarded by Hensen as young rod cells, and Schreiner states that he found them to be more numerous in young specimens than in the adult.

So far we have only considered the rod cells and the rods. In addition to these, the retina is made up of a number of other cells which form a definite band between the rod cells and the septum, and another layer, previously mentioned (inner interstitial cells), which lie between the rod cells. Patten classified all those between the septum and the rod cell layer as belonging to the outer ganglionic layer, and the others to the inner ganglionic layer. Rawitz also classified all these cells together as ganglion cells, and later Schreiner describes the outer ganglionic layer as being four cells deep in its thickest region. Hesse first showed the incorrectness of these statements. In the first place, the cells are of at least two different forms, and cannot all be classified as ganglion cells, and the so-called outer ganglionic layer of Patten and others is really a complex which must be broken up.

There is a distinct distal cell layer (fig. 29, *D. c. l.*), one cell deep only, extending across the retina against the septum. Between these cells and underneath this layer are a number of irregularly placed cells, which agree in many ways with those between the rod cells. Since their function is not known, it is best to drop the term ganglion cells, and to call them all interstitial cells; and so there are the two groups—outer interstitial cells (fig. 30, *In. c. o.*) underlying and partially penetrating the distal cell layer, and inner interstitial cells (*In. c. i.*) between the rod cells.

The Distal Cell Layer is a very regular layer of roughly triangular cells, the base of which is turned towards the septum. The septal surface of these cells is drawn out into numerous fine processes almost like cilia, which reach up to the septum, so that in sections across the retina a cilia-like border appears between the septum and the retinal cells. They appear almost like numerous nerve fibrils in connection with the optic nerve, and make the task of following the real nerve fibrils in this region very difficult. The apex of the cell is drawn out and, according to Schreiner, becomes dendritic, sending delicate fibrils ramifying between the interstitial cells and rod cells. In the gold preparations these nerve fibrils appeared as a very complete network, and their number adds again to the task of examining their connections.

Schreiner stated that the epithelial distal cells were in direct connection with the outer optic nerve by means of one of the cilia-like fibres, which he illustrated as coming from the middle of the septal surfaces.

Hesse, in 1900 (**32**), could not see any connection between the fibres of the optic nerve and the distal cells, but traced the nerve fibres between them to connections with the interstitial cells, which he regarded then as sense cells but not ganglion cells. In a later paper, however (1907), after a study of the very early stages, he shows that the optic nerve is already connected with distal cells before the interstitial cells are in existence. According to him, the nerve fibrils of the outer optic nerve, after boring through the septum, pass between the distal cells and connect to the sides, and not the middle of the septal surface as stated by Schreiner. The attachment of the outer optic nerve to the distal cells is practically certain, but there is still great doubt about the interstitial cells, and though I could trace their processes to the cilia-like border, there could be no certainty of connections in the confusing mass of fibres.

The Interstitial Cells are irregular in shape and drawn out into fine branching processes. The outer interstitial cells bear processes which pass between the distal cells to the retina surface. The inner interstitial cells are very much flattened, and lie in such close proximity, wrapping as it were round the rod cells, that their nuclei were first taken for the nuclei of these. The cells are rather small, very little larger than the prominent nucleus, and, in addition to processes extending amongst the rod cells, one from each cell penetrates the sieve membrane and lies between the rods.

The nuclei of the interstitial cells stain very darkly with Haematein, and quite differently to the nuclei of the rod and distal cells. Hesse, Patten and Schreiner have regarded the interstitial cells as sense cells. Schneider, however, on the ground of structure, the nucleus, and the failure to prove a connection with nerve fibres, considers them to be supporting cells. Until the difficulties of following their fine fibrils are overcome, it will be better to call them interstitial cells, which leaves the question of function open.

Argentea.—Underlying the retina is this layer (fig. 29, *Arg.*, fig. 34), made up of refractive granules. This is the layer which gives the eye the beautiful metallic appearance, aided, of course, by the pigment layer—the tapetum. Patten, by painting several white lines on the base of the objective and focussing down on a large eye removed from the mantle, was able to see the image formed in the eye. The different layers could be followed, and the image was seen to be most distinct just before reaching the tapetum and argentea, so that the lens and argentea together act as a true optic lens and mirror, and form an image just where the rods are placed to receive it.

The argentea (which does not generally stain in sections), is made up of several laminae, and longitudinal sections have the appearance of a series of layers of small iridescent scales. If the argentea be looked at from the surface (fig. 34), it is seen that the layers are formed of numerous very small and almost square plates. These are arranged regularly together in one plane, so that the square face of each plate is in the plane of the argentea, and the edges only are seen in longitudinal sections. The argentea is thickest in the centre, where the laminae are most numerous, and towards the sides it thins out. There are no nuclei in this layer.

Tapetum.—Below the argentea is this red pigment layer (fig. 29, *Tap.*). It is of considerable thickness in the centre, but, like the argentea, decreases towards the periphery, and terminates at the point where the retina comes in connection with the sides of the optic vesicle. The tapetum is composed of large irregular cells arranged rather irregularly in two layers, and in many cases the margins are difficult to define owing to the dense pigment contained in them. The cells contain each a nucleus, often obscured by the pigment, which is present in the form of rather large granules, in shape something like those found in the digestive gland cells, but of quite a different colour—a dark brown-red. The pigment granules are much larger than those found in the cells of the iris.

There only remains to be described the inner wall of the eye vesicle against which the tapetum rests. This is known as the sclerotica (fig. 29, *Scl.*), and is a differentiation of the connective tissue of the stalk, which becomes tough and hyaline and stains rather more deeply than the surrounding tissue. It passes into the septal membrane at the edge of the retina, so that septal membrane and sclerotica together form a closed vesicle in which is situated retina, argentea and tapetum, the whole being known as the ommateal sac.

Optic Nerves.—The eyes are innervated by optic nerves, which arise from the circumpallial nerve and pass through the centre of the eye stalk (fig. 29, *Op. n.*) until the eye vesicle is almost reached. Here the nerve divides into two branches, one of which, the inner nerve (*Op. n. i.*), continues its course until immediately below the sclerotica, where it breaks up into many bundles of nerves, which radiate from this point and ascend on all sides of the eye vesicle to reach the periphery of the retina where they are continuous with the rod cells. The other branch, the outer nerve (fig. 29, *Op. n. o.*), passes distally on the shell side of the eye stalk, and, as already described, passes over the surface of the septal membrane, perforates it, and its fibres unite with the distal cells.

As to the function of the eyes in Pecten, Patten, apparently in order to surmount the difficulty of an animal having more than two eyes of such complexity, has advanced the theory that they are organs for the reception of solar energy, which is then transmitted along the optic nerves to centres where it is used in the building up of protoplasmic compounds, or in metabolism generally. Leaving aside the physiological objections to such an idea, which has been severely criticised by more recent workers, it will be seen that Patten assumes the structures are such as would be evolved for the purpose of receiving solar energy, the rays of which are concentrated by the lens.

A lens, however, cannot increase the solar energy falling upon its surface, it can only cause the rays to fall upon a smaller area of the retina. In a review of Patten's paper in the Q. J. M. S. for 1887, it was pointed out that "a naked epidermic surface of area equal to that of the lens would present a perfect instrument for the absorption of solar energy."

Observations carried out on Pectens living in the tanks at the Port Erin Biological Station have shown that they are very sensitive both to light and to sound waves. If a dark object is moved in front of a Pecten so that the shadow falls over the eyes, a rapid closing of the valves immediately follows. A sudden increase in the illumination apparently produces no effect. The flashing of the light from a bright lantern on the animals, which have the valves open and the tentacles extended in the darkness of the aquarium at night, causes no retraction or closure of the valves.

It is obvious that with a lens forming an image on a retina of such a type as is present here, the several eyes will have but a limited area from which rays can be focussed on the receptive surface. I have never observed the eyes of Pecten being moved in various directions, they can only form an image of some object directly in front of them. This will account for the need of such a number of eyes, if they are to be of real use as visual organs.

EXCRETORY SYSTEM.

The most important renal excretory organs are the paired glands (fig. 1, *R. o.*) lying at the sides of the visceral mass, and sometimes known as nephridia. They were formerly termed the organs of Bojanus, after their discoverer, who first described them in 1819.

Morphologically, they are like nephridia only in as far as they open on the one hand to the exterior and on the other hand into the pericardium—the remains of the coelom. But, since they are out-growths from the coelom, they are true coelomoducts.

In Pecten, they are elongated pouches of a light to dark brown colour. They are attached to the anterior surface of the adductor muscle, on each side of the visceral mass, and lie between the latter and the ctenidia, extending over the muscle for about 90° from the region of the digestive gland to near the last point of attachment of the visceral mass.

They are slightly asymmetrical, the left being the larger of the two, and this difference is correlated with the position of the visceral mass. The organ lies directly on the adductor, the glandular walls being separated from it by connective tissue. The outer wall of the organ of Bojanus is formed by a direct continuation of the epithelium of the visceral mass over it, on its way to form the epidermis over the gill axis. The coelomoducts are flattened sacs, increasing in width from their upper ends and widest at a point where the afferent branchial vessel leaves them. From this point they narrow rapidly to their distal end, which is pointed and lies close to the visceral mass. They are simple hollow sacs with glandular walls, and the organs are not bent on themselves as in Anodon, nor are there two cavities which differ in position and structure. The external openings (fig. 1, *Ro.*, *rp.*) are the renal reproductive apertures by which the excrete matters from the pericardial gland and the coelomoducts, together with the ova and spermatozoa, pass to the exterior. They are prominent vertically-placed slits, the long axis of the opening lying almost in the same direction as that of the organ itself and situated very near the distal end, rather on the free surface of the gland. The slit has prominent lips, which are often white in fresh or spirit specimens, and thus contrast with the brown colour of the organ itself.

The reno-pericardial opening is very difficult to find, and can only be made out with certainty by serial sections. The pericardium cannot be injected from the renal organs, so that the passage of fluids from the coelomoducts to the pericardium is prevented. It has been pointed out that the pericardium is prolonged at each side of the digestive gland, and between it and the adductor, so as to form two somewhat deep pouches, in which lie the distal portions of the two auricles communicating with the efferent branchial vessels. In the pallial cavity, very close to the digestive gland, there is a nook formed by the mantle, visceral mass and digestive gland. Just at this point the efferent branchial vessel and the upper end of the renal organ lie alongside each other, and the former passes into the pericardium; the latter a little distance below its upper extremity gives off a tube which is lined by columnar ciliated cells, differing much in appearance from the glandular cells of the rest of the renal organ. This reno-pericardial canal passes to the dorsal side of the efferent branchial vessel, and opens into the pericardium above it and rather to the outer side. Both renal organs communicate at their upper ends by a transverse branch running under the visceral mass above the adductor muscle. The cells lining this channel have the same appearance as those lining the rest of the cavity, but the walls are not folded and the space between them is but small.

The structure of the renal gland is as follows (figs. 42 and 43):—Lying underneath the outer epithelium (fig. 43, *Ren. ep.*) there is a connective tissue layer which forms a definite sheath and supports the internal glandular layer. Longitudinal and circular muscle fibres occur in this connective tissue sheath. The inner surface of the gland, bounding the cavity, is complicated in its folding. This can be seen by slitting up the side of the renal organ, but better still by cutting transverse sections. The whole cavity is much reduced and divided up by these folds, longitudinal folds predominating (fig. 6), but they are not regular and appear to bifurcate and anastomose. The folds that are seen with the naked eye are really themselves made up of numerous folds, as shown by the sections (fig. 43); and so in this way the glandular area is increased very much, and the cavity broken up and reduced in size. Two layers are concerned in the formation of these folds, the connective tissue (fig. 42, *R. con.*) and the glandular layer (*Ren. c.*). From the prominent connective tissue sheath which surrounds the organ, folds are given off which support the epithelium. Thus, both layers are seen together forming the folds.

There are two series of spaces seen in sections through the gland—the lumen or gland cavity lined by epithelium with all its diverticula, and the blood spaces bounded by the connective tissue in which they lie (figs. 42 and 43, *Ren. v.*) and containing scattered corpuscles, so that the blood is only separated from the glandular epithelium by a thin layer of connective tissue.

The glandular epithelium is composed of cells which are about three times as tall as their width. The cells do not contain much stainable protoplasmic contents, and high magnification shows that they are much vacuolated with the protoplasm situated near to the cell bases, towards which end the nucleus is also to be found. The large vacuole occupying most of the cells is filled by a refractive colourless or slightly brown crystalline body, which is a concretion of excrete matter. The free surfaces of the cells facing the lumen of the gland bear delicate processes almost exactly like cilia, so that in some places it is very difficult to detect any difference. They are irregular in distribution, sometimes quite abundant, and have also a beaded appearance which makes them a little unlike cilia—which, moreover, have not been found on the cells of the renal organ of Lamellibranchs. It is unusual for excretory cells (loaded with excrete matter in many cases) to have cilia, and I am inclined to think, therefore, that this very cilia-like appearance is due to an excretion which takes place in a fibrous manner. There are generally present in the lumen of the organ masses which look as if they contained these cilia-like processes. In the figure (fig. 52) these are too much like cilia, and are rather too regularly disposed. In addition to these processes there are always to be found cells in the act of extrusion, so that by actual dehiscence of the cells the excretion is thrown into the cavity of the duct. The opening to the exterior is lined for a short distance with non-glandular, more compact, normal ciliated epithelium, the lips being formed by a slight development of cushions of connective tissue.

In addition to the organ of Bojanus, excretion is carried on by the pericardial glands. These are confined to the auricles, to which they give a very distinct brown tint. The auricle has the wall thrown into numerous pockets, which increase its surface. It is formed of a single layer of epithelial cells (fig. 49, *Aur.*), somewhat flattened, and with prominent nuclei. Internal to this, there is a considerable amount of loose connective tissue with scattered muscle fibres, and amidst these lie the cells (*Aur. ex.*) which by reason of their contents give the brown colour to the surface. They are large, and very similar in form to those described in the connective tissue sheath of the alimentary canal, except that more protoplasm appears to be present; oval in shape, with the nucleus near one end, and the rest of the cell almost filled by a mass of some refractive structureless substance surrounded by a thin cortex of protoplasm. Usually, the large mass of cell contents shows a granular central portion of an olive green tint, and surrounding this a part which stains, like connective tissue and chitin, a light blue with Methyl-blue-eosin.

The two forms of excretory organs already described seem to perform different work. If indigo carmine solution is injected into the animal, it will be eliminated by the cells of the organs of Bojanus; whilst if ammonium carminate is injected, it is taken up by the pericardial excretory cells.

The latter cells, which have been described as placed chiefly on the auricles, occur also in the mantle, the visceral mass and around the intestine.

The first kind of cells, those lining the coelomoducts, have been found in Lamellibranchs to contain Urea or Uric Acid, whilst in *Pecten maximus* the excretory cells of the auricle have been found to contain Hippuric Acid (**18**). In both cases the contents are extruded, in the former into the cavity of the coelomoduct and in the latter into the pericardium (at least by the cells of the auricles), from whence they pass by the renal-pericardial openings into the coelomoducts, and so outwards.

Finally, there are granular eosinophilous cells, which are found in numbers along the mantle edge. In places they can be seen extruding their contents, and they probably also perform some excretory function, though since none are found in the connective tissue it is not easy to determine their origin.

REPRODUCTIVE ORGANS.

The genus Pecten is interesting because both unisexual and hermaphrodite species exist. *P. tenuicostatus* (Mighels), the giant scallop of America, is unisexual. *P. opercularis* and *P. maximus* are both hermaphrodite. In the two latter species the reproductive organs are posterior and ventral to the rudimentary foot, forming a tongue-like mass attached to and depending from the adductor muscle (fig. 1, *Go. o.* and *Go. s.*). They do not extend into the mantle or encroach upon other organs, even when expanded to their greatest extent in the spawning season.

When the sexual products are nearly ripe the organ is at its largest, and is firm in consistency as if the contents were pressing against their walls. At this time the male portion of the gland (fig. 1, *Go. s.*), which is situated most dorsally and anteriorly, extends to a point about midway between the mouth and the foot and abuts on the liver lobules at this point. It is rather flattened here, but from a point immediately below the foot it contracts considerably from side to side and becomes deeper. The deepest part is where the male abuts against the ovigerous portion, and the organ gradually tapers to a rounded point. Midway between this free end and the parieto-splanchnic ganglion it is attached to the adductor by the connective tissue that covers the under surface of the muscle and the adjacent organs of Bojanus. The whole of this mass is not gonad, for, as described above, part of the alimentary canal courses through it (fig. 1, *Al. c. 3*, *Al. c. 4*), and is thus surrounded by the sexual organs; but the intestine does not penetrate to the ovigerous part in *P. opercularis*, whereas in *P. maximus* it runs almost to the end of the mass.

The ovigerous part occupies the hinder end, and can be easily distinguished from the male part when the products are ripe, for it has a beautiful vermilion-pink colour, becoming deeper as the eggs approach maturity. During the ripening of the products, the male part becomes cream coloured, and the junction of the cream and red is quite sharp though irregular in outline, and there may be islands of ovigerous tissue surrounded completely by the male organ, or the female part may extend a considerable way forwards into the centre of the seminal portion which then lies on the exterior. After discharge of the contents, or when collected before the products have developed, the organ has a shrunken and flabby appearance, and is of a yellowish-brown colour, and the intestine may be seen through it.

The male and female products of the one individual do not appear to be ripe at quite the same time, though there cannot be much difference in this respect. Fullarton found that when the ova were quite ripe the spermatozoa had either been shed or were not quite ripe, some being found with ripe ova and sperms not ripe and others just the converse. The same applies to *P. maximus*, and the difference in the time of maturity of ova and sperms cannot be more than a few days.

Specimens of *P. opercularis* with ripe gonads have been obtained at all times of the year on the scallop beds in the Firth of Forth, the maximum of reproductive activity being, however, in July and August. *Pecten maximus* has been dredged off Port Erin with ripe gonads in December, April, May and throughout the summer, and in the same condition off Belfast Lough in February and March, so that the reproductive activity extends at least over the greater part of the year.

The gonads have one opening on each side into the renal organ, situated near the pericardial end, at the level of the prominence on each side of the visceral mass near the attachment of the lower ends of the inner labial palps. The ducts can be traced in serial sections, and although the opening cannot be made out in dissections, it is possible, by pressing the ripe gonad, to force the products out into the renal organ, though care must be taken not to force them through one of the veins leading from the visceral mass, which may be easily mistaken for the oviducts. The products of the gonads must be poured directly into the sea through the renal organ, and thus fertilisation takes place externally.

The gonad consists of many branched tubuli (fig. 53, *Go. d.*), bearing numerous almost spherical sacs, the alveoli (fig. 53, *Go. al. s.* and *Go. al. o.*). The sexual products, spermatozoa or ova according to the position, arise by the proliferation of the cells forming the germinal epithelium on the walls of the alveoli. As the gonads ripen the alveoli become filled with the products, and thus there is a general expansion of the reproductive mass, and the alveoli near the surface appear to the naked eye as rounded elevations or as small eggs.

In teased preparations of the ripe ovary the alveoli are so numerous that it is difficult to see the connecting tubules, but in sections they are easily traced by their ciliated lining, and may be seen gradually joining up to form the reproductive ducts. These ducts can only be definitely traced by serial sections, but in some specimens of *P. maximus* the duct on the right side, which is by far the largest, can be seen with the naked eye as a thick white thread running parallel with, and very close to, the junction of visceral mass and renal organ until it opens into the latter. If the point of an injecting syringe is inserted near the opening, this duct may sometimes be injected, but unless it is visible through being near the surface, care must be taken not to mistake an injected arterial vessel for it. The duct on the left side is much smaller and only extends a little way, acting as conduit for the male portion on the left side in the neighbourhood of its opening. The rest of the gonad is supplied by branches of the large duct which opens on the right. The main ducts are lined by an epithelial layer of columnar ciliated cells (fig. 54, *Go. d.*), the height of which is about twice the diameter, while the cilia are about as long as the cells. This epithelial layer is supported by somewhat delicate connective tissue which is continuous with the scattered strands that cross in all directions and pass round the alveoli and the ducts, forming a framework for the reproductive organs.

This columnar ciliated epithelium passes into the flattened germinal epithelium (fig. 53, *Ge. ep.*) lining the alveoli, and in the ovarian region ova in various stages of development (fig. 53, *O′*.) can be seen attached to the wall, but gradually projecting more and more as they increase in size until they are set free in the cavity (fig. 53, *O*.).

The ova are large cells about 0·05 mm. in size, and when lying in the alveoli are polyhedral in shape. The nucleus is very large, spherical or oval in shape, and about two-thirds the diameter of the cell. A delicate network is present, extending over the nucleus, and in addition, they are small granules staining with eosin, and a conspicuous nucleolus. This is situated close to the periphery at one side of the nucleus. In some cells more than one nucleolus is present, there being often a large and two smaller ones at its sides.

The cytoplasm is granular and dense, and around the ovum is a prominent vitelline membrane which leaves an opening—the micropyle, at the point where the egg remained last attached to the epithelium of the alveolus.

The spermatozoa (fig. 53, *S*.) are rather small and of the typical shape; in fixed preparations the head is oval in shape and stains very intensely. From the middle of the broad end a long flagellum arises. In the alveolus the tails of the spermatozoa are generally all directed in the same way towards a point in the centre or nearer one end where the duct opens, whilst the heads are directed towards the wall of the alveolus. Both spermatozoa and ova travel along the same gonoducts to the exterior.

EMBRYOLOGY.

I have been unable to obtain enough specimens of *P. maximus* sufficiently ripe at the same time to artificially fertilise the eggs, but hope to continue this work at some future date. It has been already pointed out that the generative organs are not ripe simultaneously, but that a very short interval of time separates them.

The development of *P. opercularis* has been worked out by Fullarton (**40**). He fertilised the eggs by mincing the ovarian and seminal parts into two glass vessels of sea water, which, after straining through muslin, were mixed.

The polyhedral egg cells soon assume a spherical shape, the time varying according to the state of maturity, from a few minutes to half an hour. A vitelline membrane is clearly visible, and a delicate hyaline investment can be sometimes observed outside the bounding wall of the ovum. A considerable quantity of granular deutoplasm is also present, which partially obscures the nucleus. The size of the ovum is 0·068 mm. After fertilisation a polar globule is extruded, which in many cases remains in contact with the oosphere for a considerable time. The next visible change that takes place is that the contents become much clearer at the animal pole. This end is prolonged, so that the oosphere becomes pear shaped, and eventually a constriction appears and the embryo divides into a macromere and a micromere, the latter occupying the animal pole. A second and a third micromere are then budded off from the macromere, and so the four-celled stage is reached. The micromeres now become active, and each sub-divides into two, and they gradually spread over the surface of the macromere until it is almost covered by them. The macromere now begins to segment, two equal cells resulting from the first division, which are the first two cells of the endoderm. These continue to divide, and are completely enclosed by the micromeres, which form the ectoderm and become ciliated; the continuity is broken at one point, however—the blastopore. The next occurrence is the development of a furrow proceeding from a small depression on the surface of the embryo, which is the early shell gland.

A velum is developed as a circular ridge covered with long cilia, and encircling the embryo between the blastopore and the shell gland. The stages following have not been observed in *P. opercularis*, but probably there are one or two long apical cilia developed in the centre of the velum, and the embryo elongates in the direction of the axis of these cilia, though in the stages which Fullarton observed with the shell valves developed, there were neither apical cilia nor flagellum present. A trochospere larva is thus formed, with a velum but no shell. Later the mantle folds are developed and two shell valves, and the veliger stage is entered upon, locomotion still being carried on by the velum, which is extended beyond the margins of the valves and is retracted by two velar muscles. A single adductor, the anterior, is developed, and the alimentary canal formed; the mouth-opening being just posterior to the velum, and the anus close to the mouth.

ECONOMIC IMPORTANCE.

Pecten opercularis occurs in large beds which are found in many localities round the British Isles. In most of these places little use seems to be made of the scallops, though they might be of considerable value both as food and bait. The species occurs in such abundance in the Firth of Forth that an important industry has arisen, which once employed a considerable number of hands, though in recent years the number has diminished. In Scotland, *P. opercularis* is known as the "clam," though it must be remembered that this name has been applied also to other genera of marine Lamellibranchs, both round our own coasts and in America.

The condition most favourable for the formation of a Pecten bed is a shelly bottom, with a little mud. Too much fine mud is detrimental. The most favourable depths are from five to twenty fathoms, though the species occurs sporadically in much deeper water, but not in communities. The animal seems to be readily injured by a low temperature, and in the year 1895 large numbers were killed in the Firth of Forth by the long continued cold weather.

Scallop dredging extends almost throughout the year in the Firth of Forth, but very little goes on during the time of the herring fishing in summer, and this is the time when the shellfish are least valuable, for owing to their gaping shells and their habit of clapping the valves the sea water cannot be enclosed, as in the mussel or oyster, and the animal, consequently, soon dies when removed from the water.

The dredge used for the purpose of clam fishing is an oyster dredge of five to six feet in breadth of mouth. The net attached to the frame is made up, on the lower side, of a series of iron rings laced together with short pieces of wire, so that repairs can be very easily made with additional rings and wire. The upper side of the net is composed of ordinary twine. The clams are mostly used for the baiting of long lines, five hundred clams being required for a line of one thousand hooks.

With regard to the value of clam as bait, experiments have been carried out by the Scottish Fishery Board, from whose reports the figures given have been taken. The lugworm (*Arenicola*) seems to have given the best results, though the mussel (*Mytilus*) and clam (*Pecten*) come close after, and the three are probably about equally successful. The clams are preferred most in winter and least in summer, when they soon die. Since the shell valves do not fit closely, as already pointed out, Pecten cannot stand as much exposure to the air as most of our edible molluscs, and this will always be a difficulty in transporting to the markets.

Pecten have been put to a most interesting use at the large trout hatchery of Howietown, near Stirling. The breeding trout in their fifth year are fed with more mussels and less horse flesh, and in the sixth year clams (Pecten) are substituted for mussels. It is found that the ova from trout of six to eight years of age have a pink colour when the fish are fed on clams. Trout thus fed on clams yield the smallest number, proportionately, of eggs, but these are of the largest size and darkest colour, and these have been found to be the most valuable ova for rearing purposes.

There seems to be no reason why the scallop should not become much more important as a source of food, and it is eaten both raw and cooked by those on the fishing grounds and a few others who are aware of the delicacy of its flavour. It has a peculiarly sweet taste, which is preferred by some to that of the oyster. At Billingsgate, *Pecten maximus* (known in the trade as " Escallops ") are not marketed in summer. The season begins in November and continues until March, and generally the demand appears to exceed the supply. During the winter season of 1907-08 the supplies were the lightest for years, with prices, perhaps, the highest ever reached. Wholesale prices averaged from 25s. to 45s. per bag of twenty dozen. In the Liverpool Fish Market, the season is practically the same as at Billingsgate, viz., from November to May, and December is the heaviest month. The average number of scallops is about five hundred each week, and the price 1s. 3d. per dozen. They are caught by sailing trawlers in the Irish Sea, the greatest quantities being found between Fleetwood and Douglas (Isle of Man). In the Isle of Man, *Pecten maximus* is known locally as "tanrogan," and *P. opercularis* as "queens." When trawled they are occasionally used as food, and a few connoisseurs cure and pot them.

Little or no use seems to be made of the large bed off Port Erin, which might supply the fishermen of that place and Peel with bait for the long lines.

The following are the quantities and values of the "clams" (*P. opercularis*) landed from the Firth of Forth beds for the last twenty years, from 1888:—

1888, 20,674 cwt.	£2,918	1898, 14,013 cwt.	£1,595
1889, 23,811 cwt.	2,563	1899, 12,125 cwt.	1,485
1890, 25,706 cwt.	3,297	1900, 6,372 cwt.	861
1891, 28,512 cwt.	3,347	1901, 6,587 cwt.	802
1892, 20,769 cwt.	2,736	1902, 4,320 cwt.	586
1893, 17,684 cwt.	2,388	1903, 4,606 cwt.	637
1894, 25,583 cwt.	3,317	1904, 6,993 cwt.	944
1895, 19,535 cwt.	2,645	1905, 7,848 cwt.	1,129
1896, 22,353 cwt.	2,915	1906, 7,391 cwt.	1,083
1897, 19,258 cwt.	2,408	1907, 7,197 cwt.	953

It will be seen from the above that a great falling off in the clam industry is recorded, especially beginning with the year 1900. This, together with the slight increase from the years 1904 onwards is to be put down to the decline in line fishing and the slight revival in the last few years recorded, and not to any decrease in the actual number of the Pecten on the beds.

No figures are given in the English Fishery Reports of the value or quantity of scallops landed, but they are recorded as being fished from several places—Scarborough, Brightlingsea, Dover, Newhaven, Weymouth, Portsmouth, &c.—in almost every case the scallop fishing being carried on during the winter months.

Probably unrecorded or occasional scallop fishing is carried on at many other places, not as an independent industry, but to obtain bait for the lines of a few local fishermen. It is certain, moreover, that much could be done to locate, improve and exploit beds of this useful shellfish if a greater demand for it arose in the future, either as human food or as bait for the fishing lines.

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DESCRIPTION OF PLATES.

Reference Letters.

a. = Hepatic artery.
A. add. = Adductor artery.
A. c. = Circumpallial artery.
A. l. = Labial arteries.
A. p. = Pedal artery.
A. p. a. = Ant. pallial artery.
A. p.p. = Post. pallial artery.
A. r. = Rectal artery.
A. s. = Striped part of adductor.
A. u. = Unstriped ditto.
A. v. = Visceral arteries.
Al, Al′. Al″. = Alveolus digest. gland.
Al. c. 1. = Oesophagus.
Al. c. 2. = Stomach.
A. l c. 2′ = Ant. left lat. depression, ditto.
Al. c. 2″ = Post. ditto.
Al. c. 3. = Descend. loop of intestine.
Al. c. 4. = Ascend. loop of intestine.
Al. c. 5. = Rectum.
An. = Anus.
Ao. a. = Anterior aorta.
Ao. p. = Posterior aorta.
Arg. = Argentea.
Aur. = Auricle.
Aur′. = Wall ditto.
Aur. C. = Transv. connect. ditto.
Aur. ex. = Excret. cells ditto.
Aur. m. = Muscles ditto.
Ax. f. = Axial fibril of Rods.
Bl. c. = Blood corpuscles.
B. g. = Byssal Gland.
B. g. c. = Byssus cells.
Br. = Branchia.
Br. a. = Ascending lamella of Branch.
Br. a′. = Termination ditto.
Br. aff. = Affer. branchial vein.
Br. aff′. = Entrance to ditto.
Br. ax. = Ctenidial axis.
Br. d. = Descending lamella.
Br. eff. = Effer. branchial vein.
Br. j. l. = Interlamellar septum.
Br. m. = Long. mus. ctenidium.
Br. r. = Respir. expans'n prin. filam't.
Br. v. = Blood vessel of ditto.
C. fr. = Frontal cilia.
C. l. = Lateral cilia.
Ch. D. = Dark staining chitin.
Ch. L. = Light staining chitin.
Com. = Cerebro-pleural comm.
Con. cp. = Cerebro-pedal conn.
Con. cv. = Cerebro-visceral conn.
Cor. = Cornea.
Cor. ps. = Pseudo cornea.
Cris. = Crystall. style, cav. of intest.
D. c. = Cell of Distal cell layer.
D. c. l. = Distal cell layer.
D. g. = Digest. gland duct.
Dg. = Digestive gland.
E. = Eye.
E. Mn. = Epith. of Mantle.
E. st. = Eye stalk.
Eos. = Eosinophil. cells.
Ex. = Wandering excret. cell.
F. = Foot.
F. s. = Foot sucker.
Fil. n. = Nerve of gill filament.
Fil. o. = Ordinary gill fil.
Fil. p. = Prin. gill fil.
Fil. sep. = Intra-fil. septum.
G. ant. = Ant. lobes of visc. ganglion.
G. cb. = Cerebro-pleural gang.
G. c. l. = Post. centr. lobes, visc. gang.
G. lat. = Lat. lobes, visc. gang.
G. Osp. = Osphradial ganglion.
G. p. = Pedal ganglion.
G. sp. = Visceral gangl.
Ge. ep. = Germinal epith.
Go. al. o. = Ovigerous alveolus.
Go. al. s. = Seminal alveolus.
Go. d. = Gonoduct.
Go. o. = Ovigerous part of gonad.
Go. s. = Seminal part of gonad.
Gr. = Granular cells, digest. gland.
I. = Iris.
In. c. o. = Outer interstit. cell.
In. c. i. = Inner interstit. cell.
L. = Lens.
L. cl. = Leucocytic clumps.
L. p. e. = R. ext. labial palp.
L. p. i. = R. int. ditto.
Lc. = Leucocytes.
Lg. p. = Ligament pit.
Lp. = Lips.
Lp. l. = Lower lip.
Lp. u. = Upper lip.
M. = Mouth.
Mn. = Mantle lobe.
Mu. g. = Mucous glands, foot.
Mu. g. c. = Compound ditto.
N. br. = Ctenidial nerve.
N. c. = Circumpallial nerve.
N. l. = Nerves, labial palps.

N. ot. = Otocyst nerve.
N. p. = Pedal nerves.
N. pa. = Ant. pallial nerve.
N. pall. = Visceral pallial nerve.
N. pp. = Post. pallial nerve.
O. = Ova.
O′ = Young ovum.
Op. F. = Ophthal. pallial fold.
Op. m. = Eye stalk muscles.
Op. n. = Optic nerve.
Op. n. i. = Inner branch ditto.
Op. n. o. = Outer branch ditto.
Ot. = Otocyst.
P. = Periostracum.
P. b. = Byssal groove.
P. gr. = Periostracal groove.
P. M. r. = Radial pall. muscles.
P. s. = Periostracal glands.
Per. = Pericardium.
Pig. = Pigment cells.
R. = Rods of retina.
R. C. = Rod-cells ditto.
R. C. n. = Nuclei, rod cells.
R. C. p. = Pseudo-rod cells.
Ro. = Renal organ.
Ro. c. = Gland. epith. ditto.
Ro. c′. = Ditto, with concretions.
Ro. con. = Connect. tissue, renal org.
Ro. ep. = Epithel., renal org.
Ro. m. = Intrinsic muscles, renal org.
Ro. rp. = Reno-reprod. apert.
Ro. v. = Renal veins.
S. = Spermatozoa.
S. D. = Dors. venous sinus.
S. m. i. = Basement membrane.
S. m. o. = Sieve membrane.
S. V. r. = R. vent. venous sinus
Scl. = Sclerotica.
Sep. = Septum.
Sh. a. = Auricula of shell.
Sh. F. = Shell fold, mantle.
Sh. m. = Calcar. layer of add. impress.
Sh. p. = Artic. surf. of shell.
T. = Tapetum.
Tn. = Tentacle.
Tn. v. = Velar tentacle.
Tu. m. = Tunica muscularis.
Tu. p. = Tunica propria.
V. = Velum.
V. a. = Adductor veins.
V. h. = Hepatic vein.
V. M. = Radial velar muscles.
V. M. a. = Attach. of velar musc.
V. M. c. = Concent. velar musc
V. p. = Pedal vein.
V. pall. = Pallial vein.
V. v. = Visceral veins.
Ven. = Ventricle.

Plate I.

Fig. A. *P. opercularis*, right valve, showing byssal notch. Natural size.

Fig. B. *P. opercularis*, left valve. Natural size.

Fig. C. *P. maximus*, exterior R. valve (young). $\times \frac{2}{3}$.

Fig. D. *P. maximus*, exterior L. valve (young). $\times \frac{2}{3}$.

Fig. E. *P. maximus*, interior of R. valve, showing adductor impression and pallial line (slightly darkened), also ligament and ridges of hinge area. $\times \frac{2}{3}$.

Fig. F. *P. maximus*, interior of L. valve; pigmented specimen showing muscular impressions. $\times \frac{2}{3}$.

PLATE II.

Fig. 1. *P. maximus*, general anatomy, R. valve and mantle lobe and right ctenidium removed.

Fig. 2. Transverse section through rib of shell (*P. opercularis*). × 26.

Fig. 3. R. mantle lobe showing distribution of pallial nerves and muscles. Nat. size.

PLATE III.

Fig. 4. Transv. sect. of mantle edge and velum. × 20.

Fig. 5. Epithelium with eosinophilous cells, from the mantle. × 500.

Fig. 6. Transv. section of periostracal groove. × 350.

Fig. 7. Foot, showing pedal groove, &c.

Fig. 8. Transverse section through foot, along A. B., fig. 7. × 20.

Fig. 9. Section through byssal gland. × 130.

Fig. 10. Mucous glands from foot (*P. maximus*). × 480.

PLATE IV.

Fig. 11. *P. maximus*, blood vessels of R. mantle lobe injected with lard mixture.

Fig. 12. Renal organ, slit open, to show ridges and vessels on inner surface. Natural size.

Fig. 13. Heart, distended with air. × 2.

Fig. 14. Arterial system injected (*P. maximus*). Pallial arteries omitted.

Fig. 15. Leucocytes, and " clump " or pseudo-plasmodia. × 700.

Plate V.

Fig. 16. Diagram of vessels of ctenidium.

Fig. 17. Arteries of lips and labial palps. Nat. size.

Fig. 18. Part of venous system of *P. maximus*, from injections.

Fig. 19. Ventricle and anterior aorta.

Fig. 20. Trans. section (diagram.) of ctenidium through prin. filaments, showing course of blood. × 4.

Fig. 21. Section of ctenidium, transverse to filaments, at level of top of ascending filaments. × 130.

Plate VI.

Fig. 22. Section of ctenidium trans. to filaments, near free margin, showing both demibranchs with interlamellar junctions. × 110.

Fig. 23. Trans. section of principal and four ordinary filaments, near base, showing respiratory expansion. × 480.

Fig. 24. Section of respiratory expansion of prin. filament in same plane as ctenidium. × 10.

Fig. 25. Respir. expansion of a principal filament. × 20.

Fig. 26. General view of nervous system (*P. maximus*).

Fig. 27. Cerebro-pleural and pedal ganglia.

Fig. 28. Visceral ganglia (*P. maximus*), showing osphradial ganglia and chief nerve trunks.

Plate VII.

Fig. 29. Longitudinal section of eye (*P. maximus*). × 150.

Fig. 30. Retinophorae, with rods and ganglionic cell layers (semi-diagram.).

Fig. 31. Cells of outer ganglionic layer. Zeiss apo. 1·5, with comp. oc. 4.

Fig. 32. Trans. section of rods. Zeiss apo. 1·5.

Fig. 33. Trans. section of retinophorae. Zeiss. apo. 1·5.

Fig. 34. Argentea in surface view. Zeiss apo. 1·5.

Fig. 35. Epithelial cells of eye stalk. Trans. sect. Zeiss apo. 1·5.

Plate VIII.

Fig. 36. Alimentary canal of *P. maximus.* Nat. size.

Fig. 37. Trans. sect. through upper part of descending loop of intestine, showing division into two compartments. × 40.

Fig. 38. Left inside of stomach, showing cavities into which ducts open.

Fig. 39. Mouth, lips (separated) and labial palps.

Fig. 40. Section of internal labial palp, across ridges. × 66.

Fig. 41. Crystalline style of *P. maximus,* showing two conditions. Natural size.

Fig. 41*a*. Trans. section through crystalline style. × 7.

Fig. 42. Section of wall of intestine (same plane as fig. 37), showing cells of crystalline style cavity. × 244.

Fig. 43. Section of posterior part of ventricle and rectum. × 25.

Fig. 44. Wall of rectum, same section as fig. 43. × 300.

Fig. 44*a*. Wandering excretory cell (*Ex.*). × 300.

Fig. 45. Trans. section of ctenidial axis and bases of filaments, showing latter opening into afferent branchial vessel. × 16.

Plate IX.

Fig. 46. Dorso-ventral section of small *P. opercularis*, through centre of adductor. × 5.

Fig. 47. Section of small *P. opercularis* (same plane as fig. 46), through digestive gland and anterior end of adductor. × 5.

Fig. 48. Section of small *P. opercularis* (same plane), anterior to adductor muscle through visceral mass. × 5.

Fig. 49. Section of wall of auricle, showing the excretory cells of pericardial gland. Zeiss apo. 1·5.

Fig. 50. Section of digestive gland, showing alveoli with pigment, and digestive ducts. × 170.

Fig. 51. Trans. section through renal organ. × 50.

Fig. 52. Part of previous section more highly magnified. × 400.

Fig. 53. Section through ovigerous and seminal alveoli of gonad (almost ripe). × 200.

Fig. 54. Striped muscle fibres from adductor, in surface (*b*) and edge view (*c*). Zeiss apo. 1·5 mm

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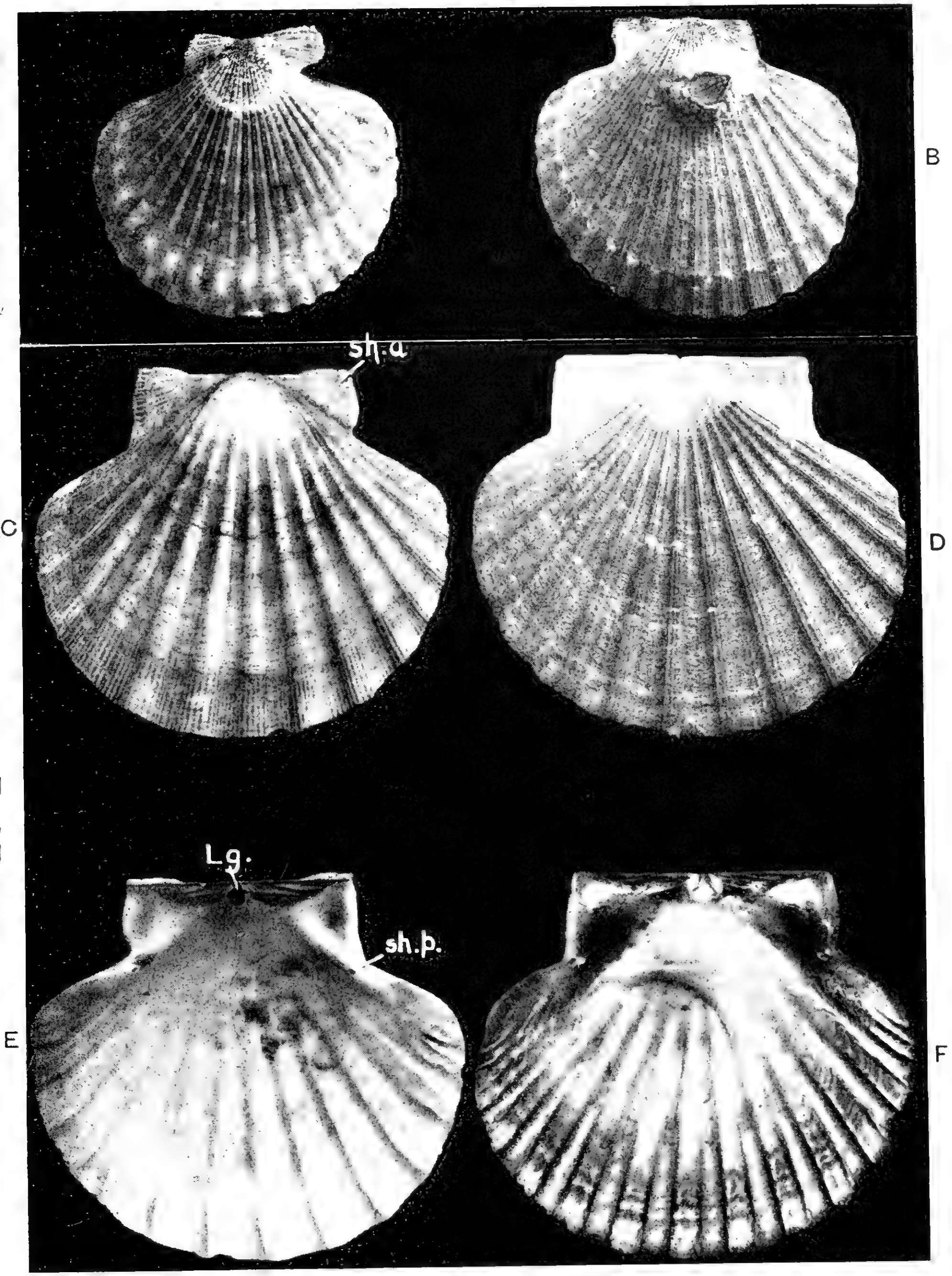

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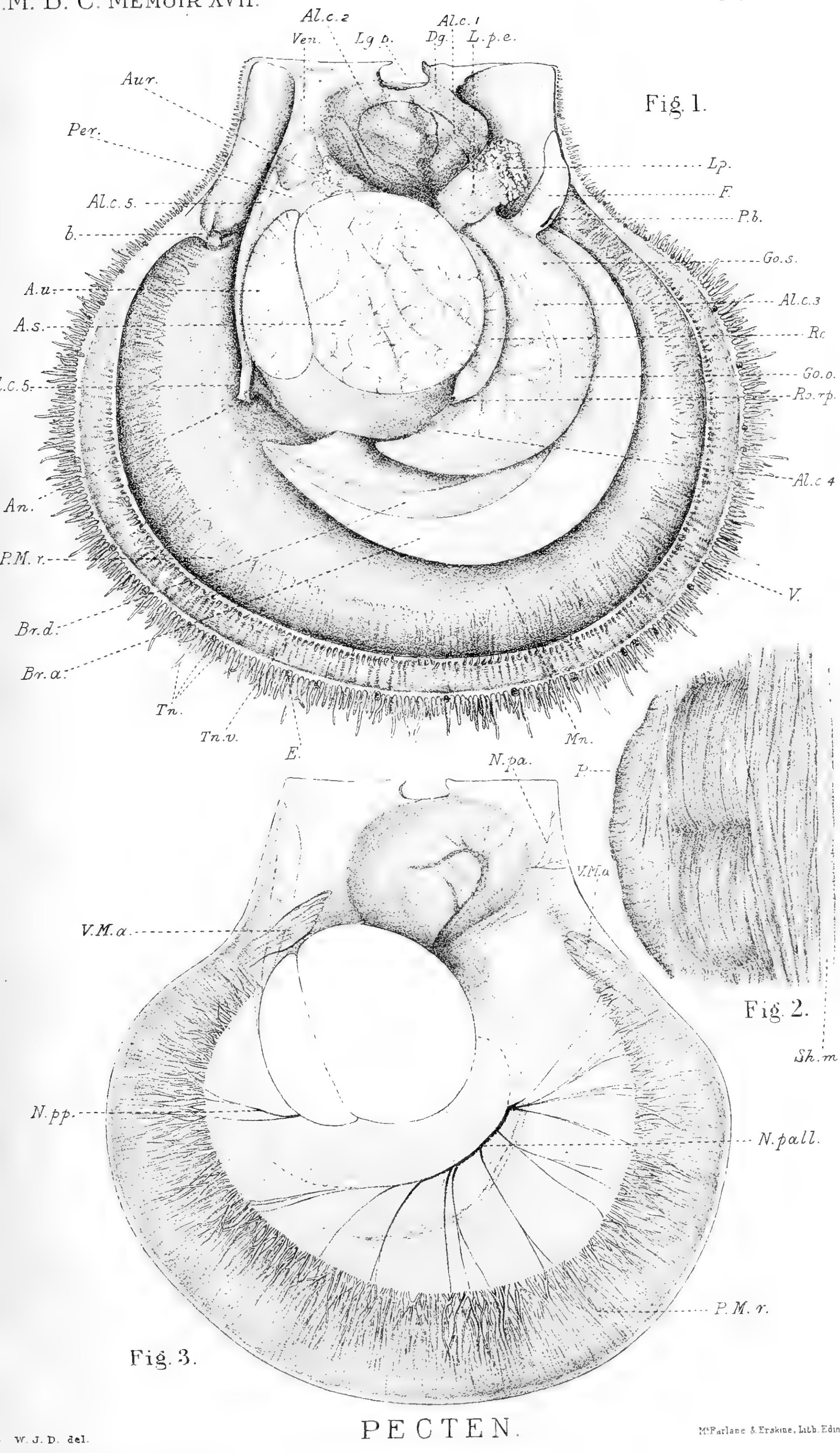

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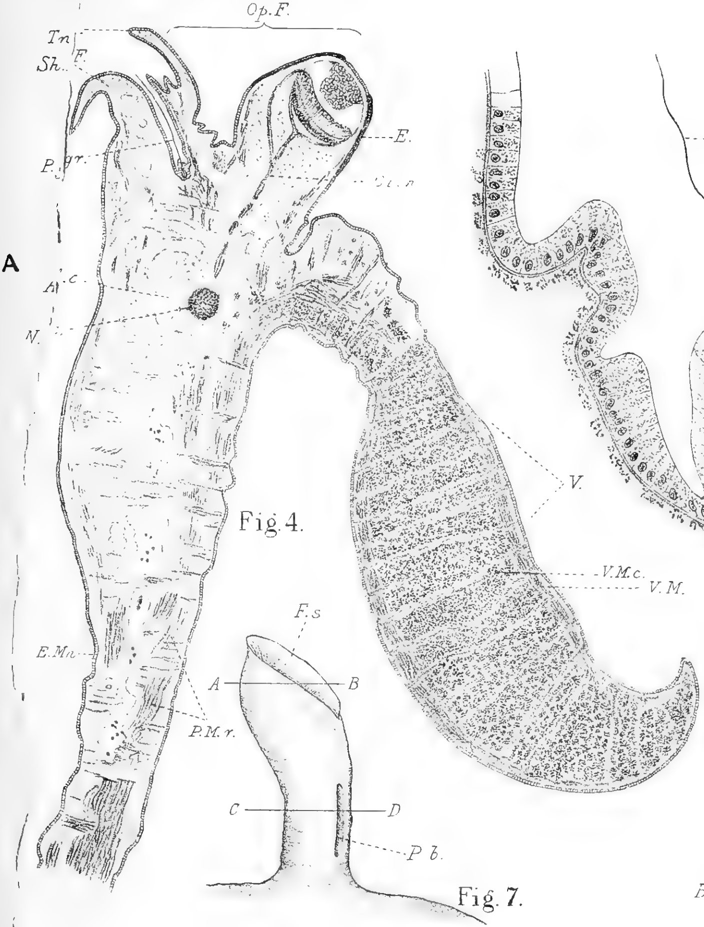
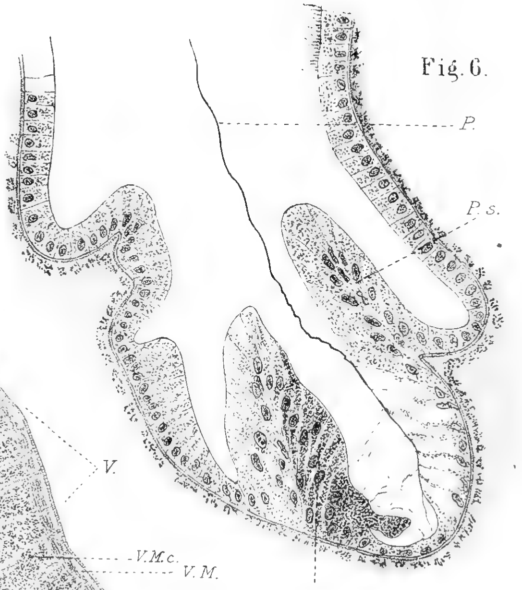


Fig. 4.

Fig. 7.



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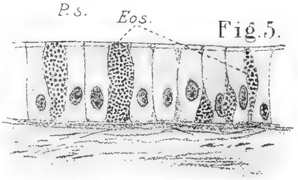

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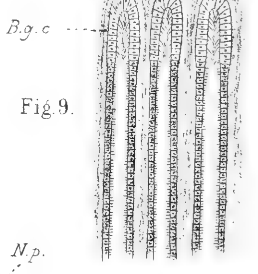

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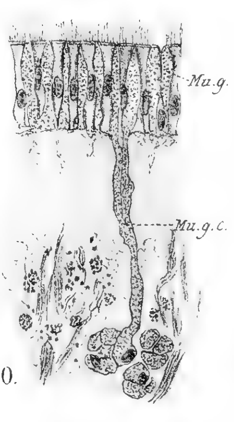

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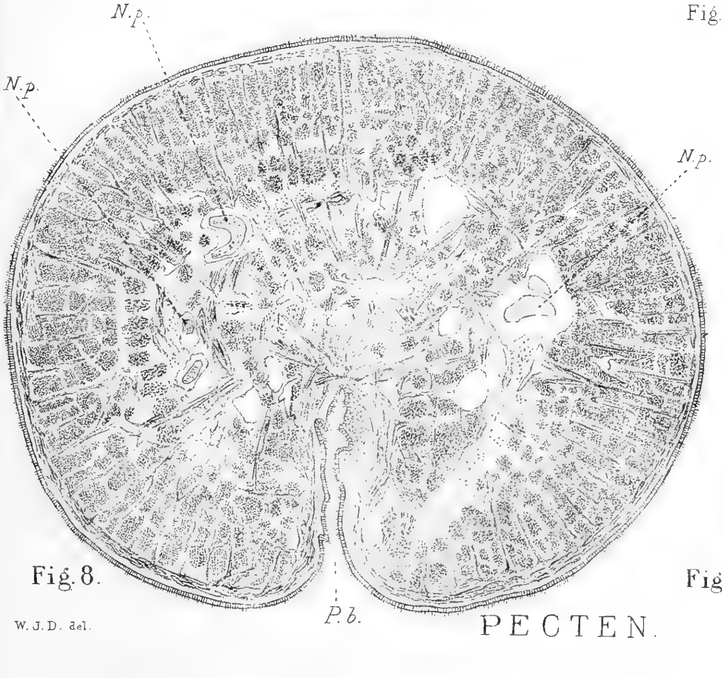

Fig. 8.

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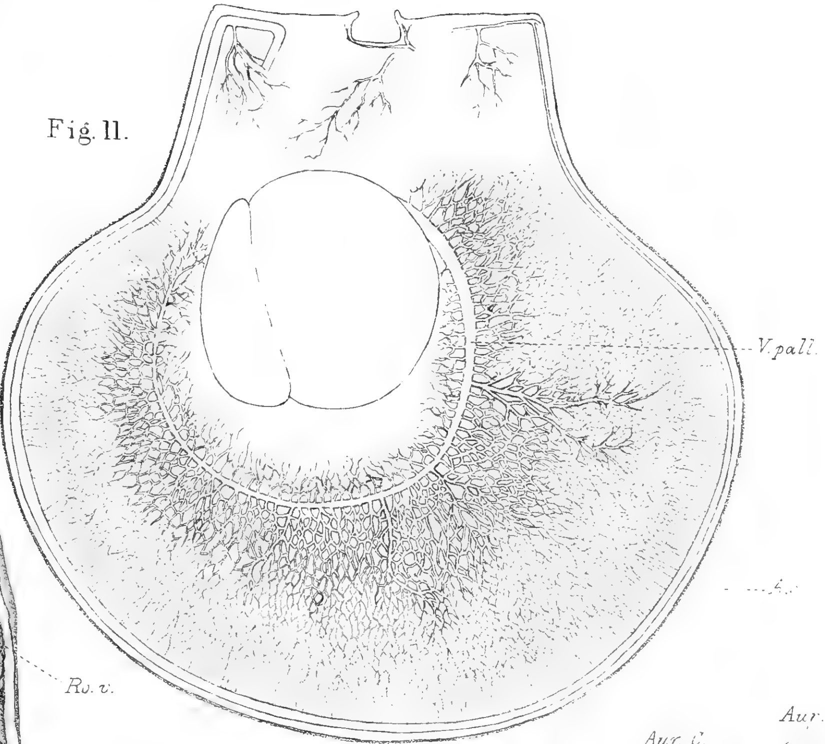

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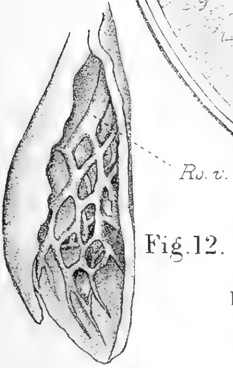

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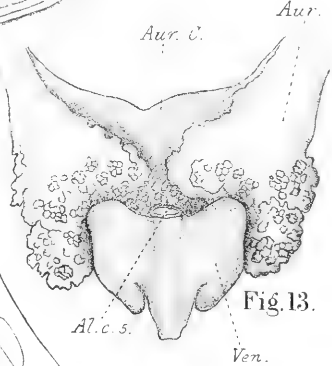
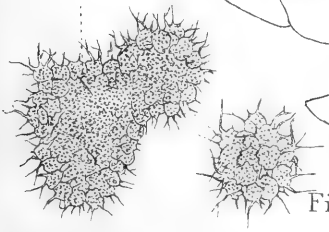


Fig. 13.

Fig. 14.



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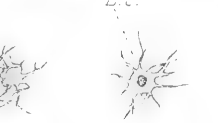

Fig. 15a

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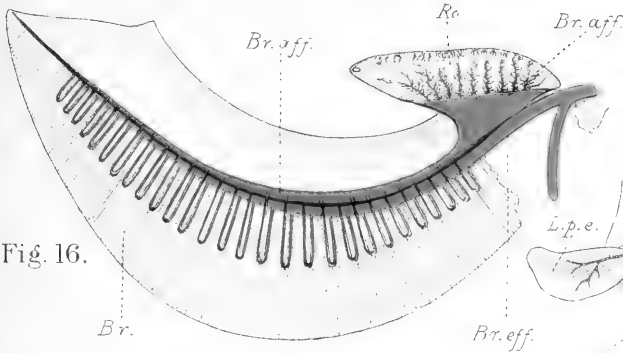

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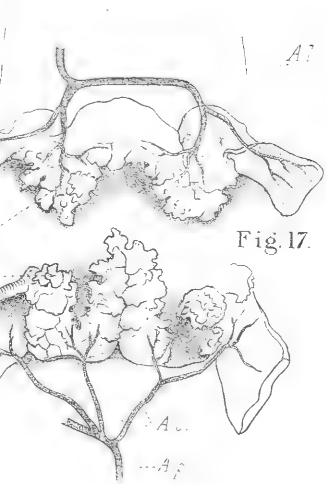

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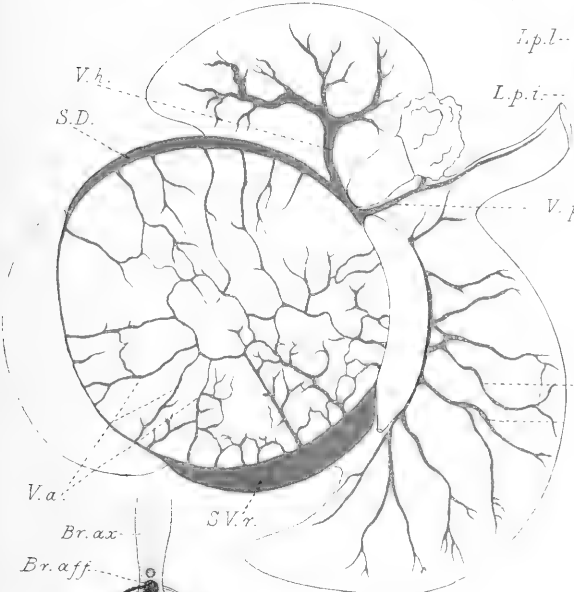

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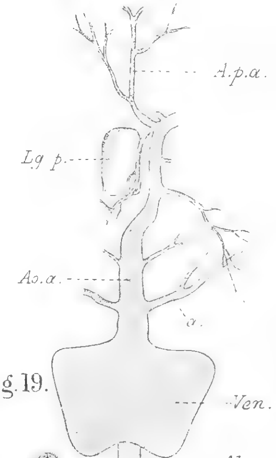

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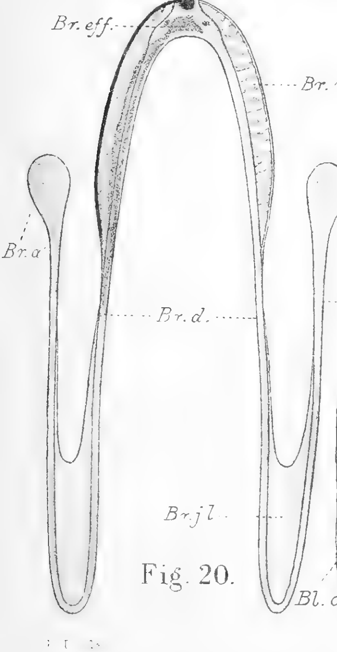

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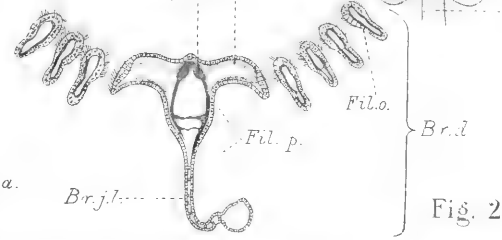

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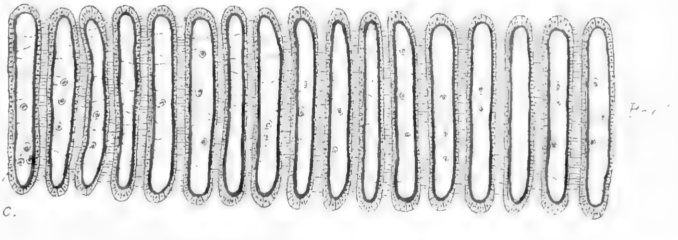

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PLATE VI.

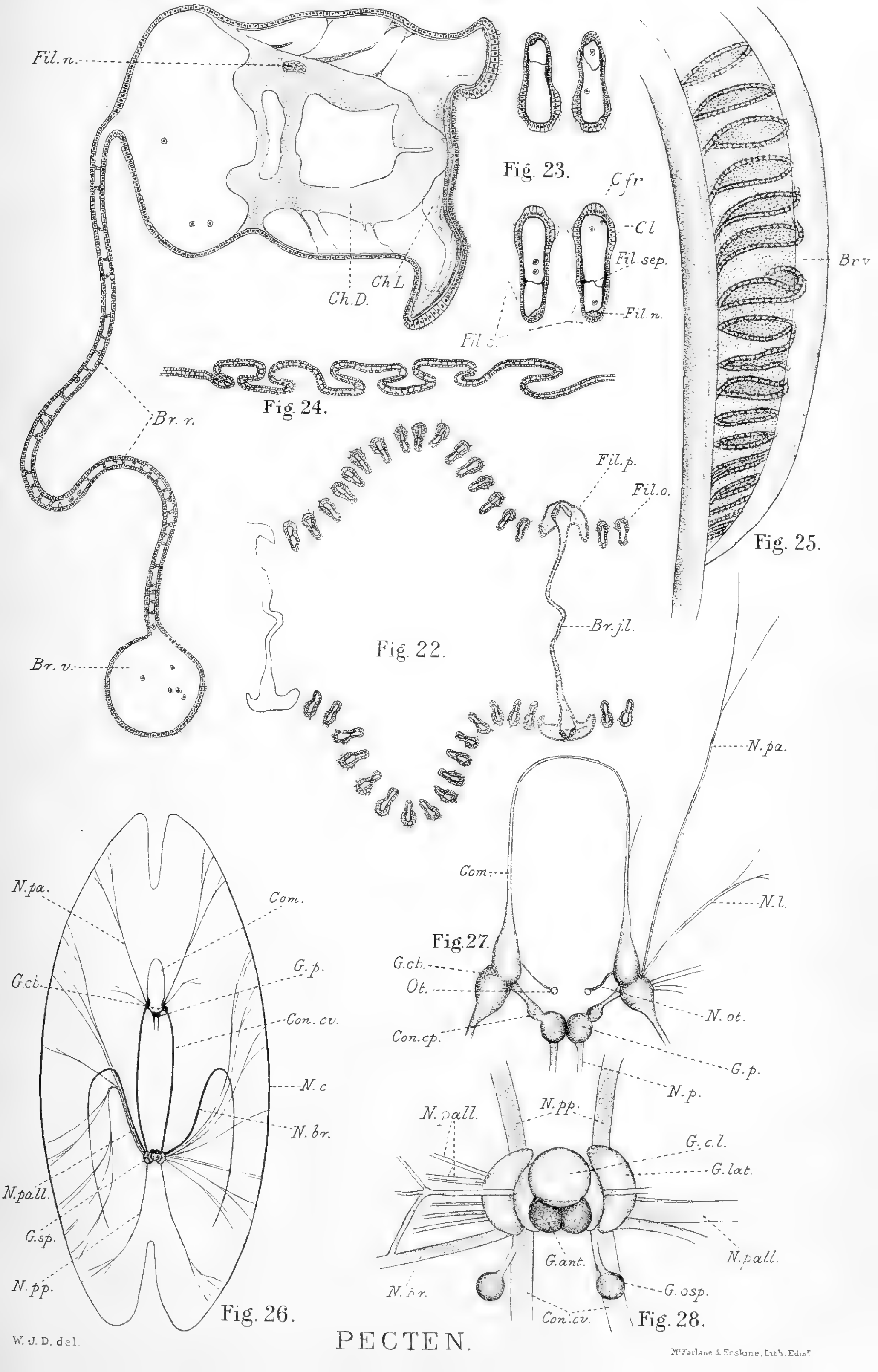

Fig. 22.

Fig. 23.

Fig. 24.

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Fig. 27.

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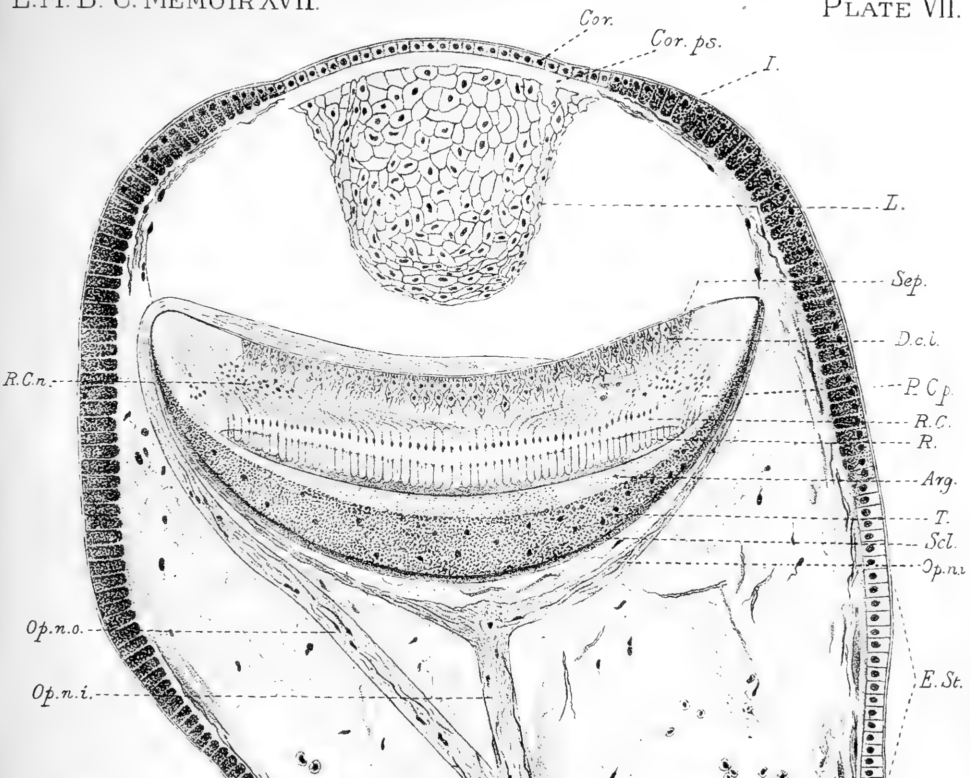

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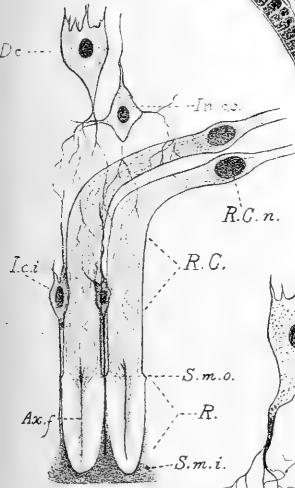
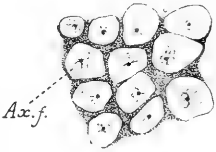


Fig. 30.

Fig. 31.



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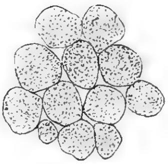

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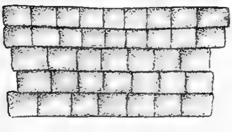

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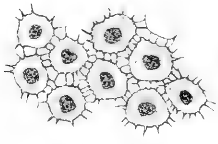

Fig. 35.

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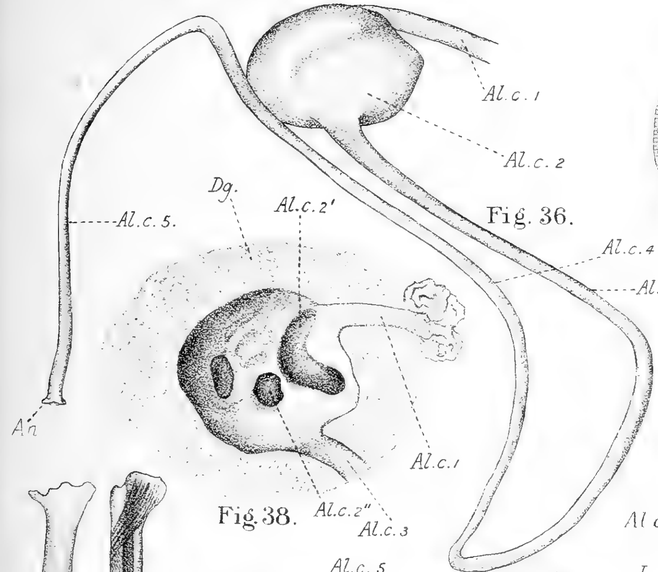
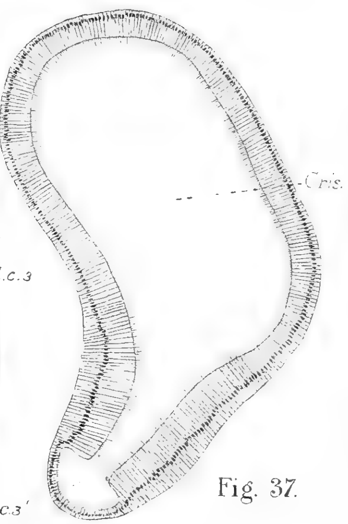


Fig. 36.

Fig. 38.



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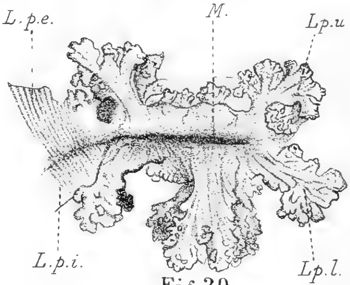


Fig. 39.

Fig. 41.

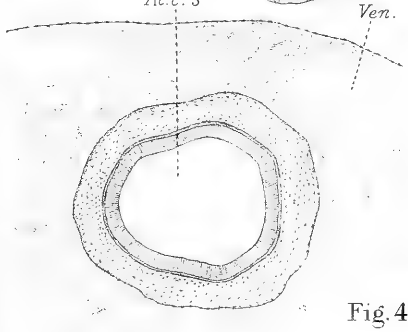
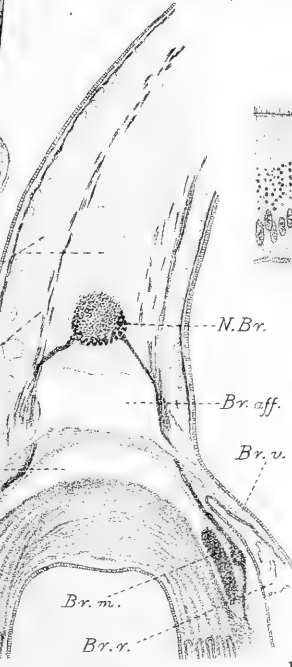


Fig. 43.

Fig. 41*a*.



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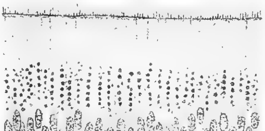

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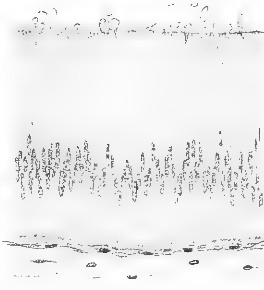

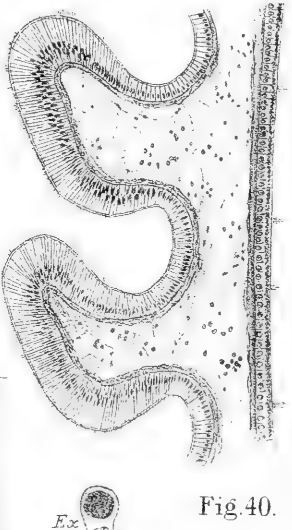

Fig. 44.

Fig. 40.

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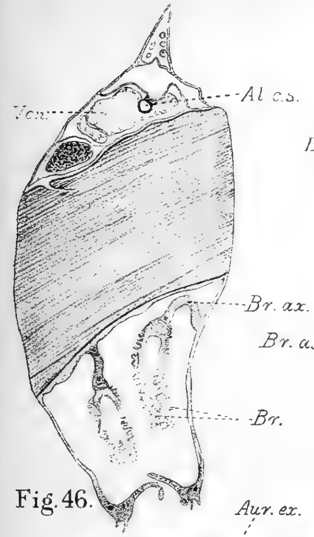

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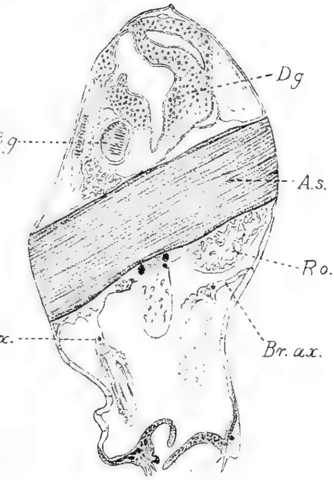

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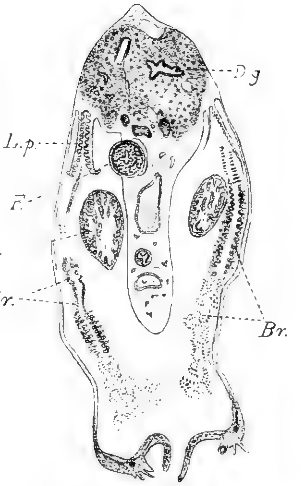

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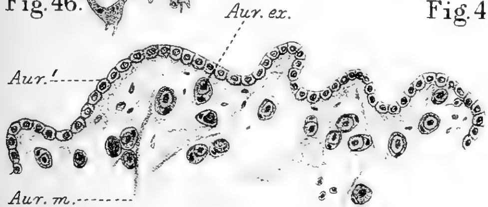


Fig. 49.

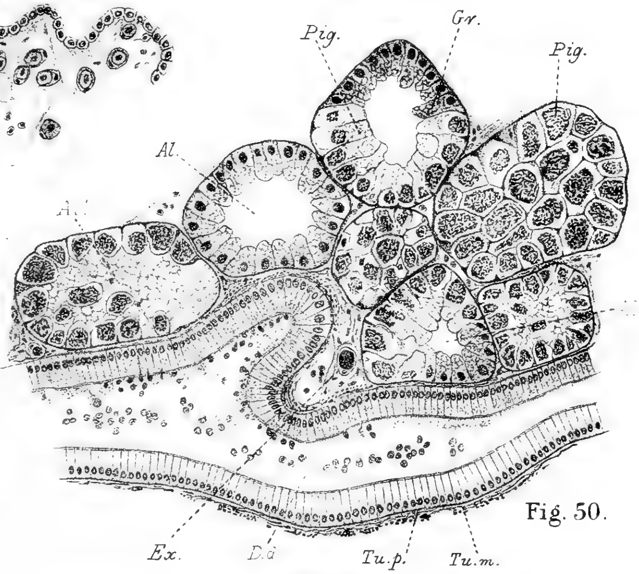
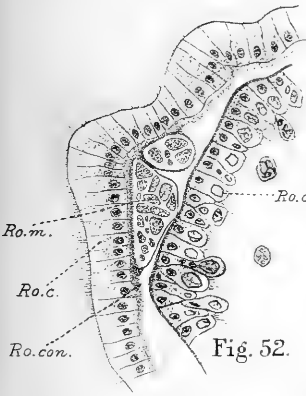


Fig. 50.



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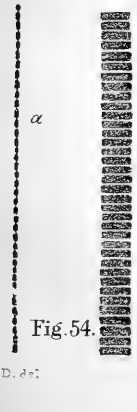

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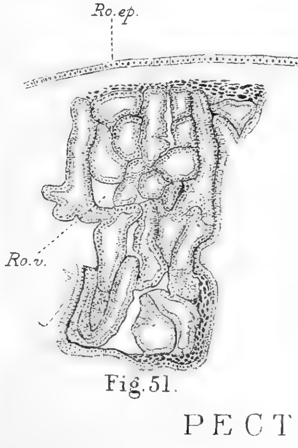

Fig. 51.

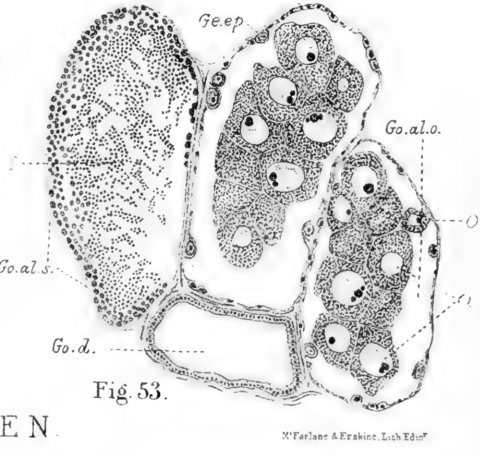

Fig. 53.

W.J.D. del.

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