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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.

XX.

BUCCINUM

(THE WHELK)

BY

WM. J. DAKIN, D.Sc., F.L.S.
ASSISTANT LECTURER IN ZOOLOGY, UNIVERSITY OF LIVERPOOL

(With 8 Plates)

Price Four Shillings and Sixpence

LONDON
Williams & Norgate
June, 1912

[redacted]

L.M.B.C. MEMOIRS.

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BUCCINUM.

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AUTHOR'S NOTE ON THE USE OF THIS MEMOIR AS A GUIDE TO DISSECTION.

As the L.M.B.C. Memoirs are read mainly in Universities, it is thought advisable to indicate how this Memoir may be used to advantage by the students of a general zoological course. This is the more necessary since a few of these Memoirs have become original treatises and contain a considerable amount of detail which may be passed over by the ordinary student. In a practical course, such as that for the Final B.Sc. examination, where the following molluscan types are examined:—Chiton, Patella, Buccinum, Helix, Doris, Aplysia, Pecten, Anodon or Mya, and a Cephalopod—Buccinum would be used to contrast with Patella and with Helix as the type of a marine Prosobranch.

Whelks narcotised in sea-water containing cocaine should be used for dissecting. The shell should be removed at once by breaking away with bone forceps. The animals should then be preserved in 5 per cent. formalin; some should also be preserved in alcohol for dissection of the nervous system. The vascular system should not be neglected. Injections are easily carried out if the whelks are obtained alive and narcotised in the laboratory. The pages of the Memoir that are of most importance to the student should then be taken in the following order:—

I. General organisation and shell ....p. 3-7
Foot and operculum, p. 10-15

II. Cut open the pallial cavity by a slit down the right side close to the rectum.
Pallial cavity ......p. 17-19 Mucous gland ....p. 26-28
Respiratory organ p. 21-22 Osphradium ....p. 77-78

III. Examine gonads from exterior ....p. 89-93

IV. Cut into renal organ along right side ....p. 83-88

V. Dissect alimentary canal, removing proboscis ....p. 28-35

VI. Dissect proboscis ....p. 43-50

VII. Dissect nervous system ....p. 65-73

VIII. Blood system on injected animal ....p. 56-65

MICROSCOPIC WORK.—Confining the histology to a few of the more special points that can be studied to advantage in the whelk, the following permanent preparations should be made:—

Eye ....p. 73-76 Radular sac ....p. 52-54
Osphradium ......p. 77-82 Cartilage of tongue, p. 51
Radular muscles, p. 50 Gill ....p. 22-26

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-five 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 larger Biological Station and Fish Hatchery, on a more convenient site at Port Erin, has since been erected, and was opened for work in July, 1902.

In these twenty-five years' experience of a Biological Station, where College students and 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. 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 XX. have now been published. No. XXI., Pagurus, by Mr. H. G. Jackson, is nearly ready, and will appear in Autumn.

Memoir I. Ascidia, W. A. Herdman, 60 pp., 5 Pls., 2s.
,, II. Cardium, J. Johnstone, 92 pp., 7 Pls., 2s. 6d.
,, III. Echinus, H. C. Chadwick, 36 pp., 5 Pls., 2s.
,, IV. Codium, R. J. H. Gibson and Helen Auld, 26 pp., 3 Pls., 1s. 6d.
,, V. Alcyonium, S. J. Hickson, 30 pp., 3 Pls., 1s. 6d.

Memoir VI. LEPEOPHTHEIRUS AND LERNÆA, Andrew Scott, 62 pp., 5 Pls., 2s.
" VII. LINEUS, R. C. Punnett, 40 pp., 4 Pls., 2s.
" VIII. PLAICE, F. J. Cole and J. Johnstone, 260 pp., 11 Pls., 7s.
" IX. CHONDRUS, O. V. Darbishire, 50 pp., 7 Pls., 2s. 6d.
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" XI. ARENICOLA, J. H. Ashworth, 126 pp., 8 Pls., 4s. 6d.
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" XIV. LIGIA, C. G. Hewitt, 45 pp., 4 Pls., 2s.
" XV. ANTEDON, H. C. Chadwick, 55 pp., 7 Pls., 2s. 6d.
" XVI. CANCER, J. Pearson, 217 pp., 13 Pls., 6s. 6d.
" XVII. PECTEN, W. J. Dakin, 144 pp., 9 Pls., 4s. 6d.
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" XIX. POLYCHAET LARVAE, F. H. Gravely, 87 pp., 4 Pls., 2s. 6d.
" XX. BUCCINUM, W. J. Dakin, 123 pp., 8 Pls., 4s. 6d.
" XXI. PAGURUS, H. G. Jackson.
DORIS, Sir Charles Eliot.
ACTINIA, J. A. Clubb.
CUCUMARIA, E. Hindle.
HALICHONDRIA and SYCON, A. Dendy.
OYSTER, W. A. Herdman and J. T. Jenkins.
SABELLARIA, A. T. Watson.
OSTRACOD (Cythere), Andrew Scott.
ASTERIAS, H. C. Chadwick.
SAGITTA, E. J. W. Harvey.
BOTRYLLOIDES, W. A. Herdman.

In addition to these, it is hoped that other Memoirs will be arranged for, on suitable types, such as Pontobdella, a Cestode and a Pycnogonid.

W. A. HERDMAN.

University of Liverpool,
May 30*th*, 1912.

AUTHOR'S PREFACE.

A Memoir on the Whelk has long been desired by many University teachers who have regularly included *Buccinum* as a type of the Monotocardia in their laboratory courses. It is hoped that the present treatise will enable this very easily procured gastropod to be used to better advantage by students.

Most of the material made use of in the investigation has been obtained from Port Erin; and I should like to express my thanks to Mr. H. C. Chadwick, the Curator of the Biological Station, for much kind help in this connection.

I wish also to take this opportunity of acknowledging the great aid Professor Herdman has constantly given me by his advice and by his careful editing of my work; and, further, to thank Mr. H. G. Jackson, Miss C. M. G. Lewis and Miss E. L. Gleave, amongst my past and present students, for their help from time to time during the progress of the work.

W. J. Dakin.

L.M.B.C. MEMOIRS.

No. XX. BUCCINUM.

(The Whelk)

BY

WM. J. DAKIN, D.Sc., F.L.S.

CLASSIFICATION.

The whelk belongs to that class of the cephalophorous Mollusca, the Gastropoda, which includes also the limpets, land snails, and nudibranchs. The group is characterised by the possession of an asymmetrical body, a well developed head bearing eyes and tentacles, a foot for creeping, and a shell consisting of one piece only (univalve). In some cases the shell is reduced considerably, and it may even disappear completely in the adult (e.g. Nudibranchiata).

The Gastropoda may be conveniently divided into the. two sub-classes:—Streptoneura and Euthyneura. The first of these groups is defined by the nervous system being involved in the torsion of the body so that the visceral loop joining the visceral and pleural ganglia is twisted into a figure of eight. The morphological right side of the loop becomes carried over the alimentary canal to the topographical left side, and the left half, under, to the right side. This sub-class is also named Prosobranchia from the fact that, in most genera, the gills lie anterior to the heart.

The whelk is a representative of the Streptoneura, and the common land snail is a type of the other group, Euthyneura; the exact position of *Buccinum* can be seen in the scheme given on the next page.

Class GASTROPODA.

Body asymmetrical, well developed head, well developed foot, usually with flat creeping sole. Shell in one piece, usually coiled in a spiral, but may be reduced and completely disappear. Pallial complex situated on the right or left side in a more or less anterior position. One half, usually the morphological left, of the pallial complex reduced, and may be absent.

Sub-class I. Streptoneura (=Prosobranchia).

Sexes separate. Visceral loop twisted into figure of eight. Pallial complex placed anteriorly. In most, only one gill, which is situated in front of heart. Chiefly marine. Shell very rarely absent.

Order I. Diotocardia (=Aspidobranchia).

Order II. Monotocardia (=Pectinibranchia).

Heart with one auricle. One gill with leaflets on one side of an axis. Well differentiated osphradium. Eye a closed vesicle. Single kidney. Siphon and penis usually present.

Sub-order I. Architaenioglossa.

Sub-order II. Taenioglossa.

Sub-order III. Stenoglossa.

Pectinibranchs with much concentrated nervous system. Proboscis, siphon, and penis always present.

Tribe I. Rachiglossa.

Radular formula. I.I.I.

Fam. Buccinidae

Gen. *Buccinum.*

GENERAL DESCRIPTION.

The body of the whelk is divisible into three obvious external regions, head, foot, and visceral mass (Pl. I, fig. 7). A large part of the animal can be extended beyond the mouth of the shell, but the visceral mass always remains hidden, and the entire animal can be retracted when disturbed. The integument of the visceral mass is produced to form that characteristic molluscan structure—the mantle (Pl. I, fig. 7, *Pall.*). The mantle forms a continuous cloak round the body, its free edge being just visible at the shell mouth when the animal is extended. It encloses a space, the mantle cavity, which is best developed on the dorsal and anterior surface. The shell is secreted chiefly by the epithelium of the mantle, particularly of the mantle edge. The organs in the mantle cavity will be referred to later.

The head of the whelk in an extended condition bears anteriorly two appendages, the tentacles (fig. 7, *Tent.*). These are compressed dorsoventrally at their base but are produced to a fine conical lip. They are capable of considerable extension and contraction, but cannot be introverted. At the base of the tentacles and on their outer sides are a pair of cephalic eyes, situated on slight lateral prominences.*

Below the tentacles and in the middle line is a conspicuous opening, an apparent mouth. This is, however, not the true entrance to the buccal cavity. The latter opens at the extremity of a retractile snout but has been carried backwards, owing to an ingrowth of integument, and consequently the true mouth is only seen when

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* One specimen of *Buccinum undatum* found at Port Erin possessed three tentacles—perfectly normal in shape and each with an eye at the base. From the position it is probable that a second tentacle and eye was present on the left side. A similar case in *Patella vulgata* has been recorded by Bateson.

the invaginated tube is everted. This eversible tube is the proboscis, and it can be extended about two inches outside the opening of the apparent mouth.

The Foot forms the greater part of the mass seen when the animal is fully extended (Pl. I, fig. 7). It has a very different appearance in life from that seen even in the best preserved dead specimens, where the foot is hard and always somewhat contracted. It is formed of a complex and powerful mass of muscles, and when fully extended is perfectly smooth, without any trace of wrinkles, soft and velvety to the touch, and capable of much change of shape. It has a perfectly flat ventral surface, with a blunt anterior and a tapering posterior end (Pl. II, fig. 9). The ventral surface or sole is used for creeping, but I have also seen the anterior part used for holding food matters. When a whelk supports itself above the water-line in an aquarium tank, it does so solely by means of suction. Some little force is required to detach it, but the sole is simply slimy and no adhesive substance is secreted.

Upon the dorsal but posterior region of the foot is situated a horny disc, the operculum, used for closing the aperture of the shell when the animal is withdrawn.

Running transversely across the anterior part of the foot is the deep pedal groove. This will be described in detail below, in the section on the foot.

The Shell.

The shell of the whelk (Pl. I, figs. 1 and 2), secreted by the mantle, consists of a single valve which is coiled spirally owing to the varying conditions under which different parts of the mantle edge secrete shell substance. In most cases the twist is of such a nature that if the shell is held by the apex with the aperture away from the observer and turned downwards, the aperture will lie to the right of the columella. Shells coiled in this manner are "dextral," but one occasionally finds a "sinistral" whelk with the spiral reversed and the asymmetrical viscera developed on the opposite side of the body.

The shell may be regarded as a long cone coiled into a spiral. Text-fig. 1 shows the terms in use for the

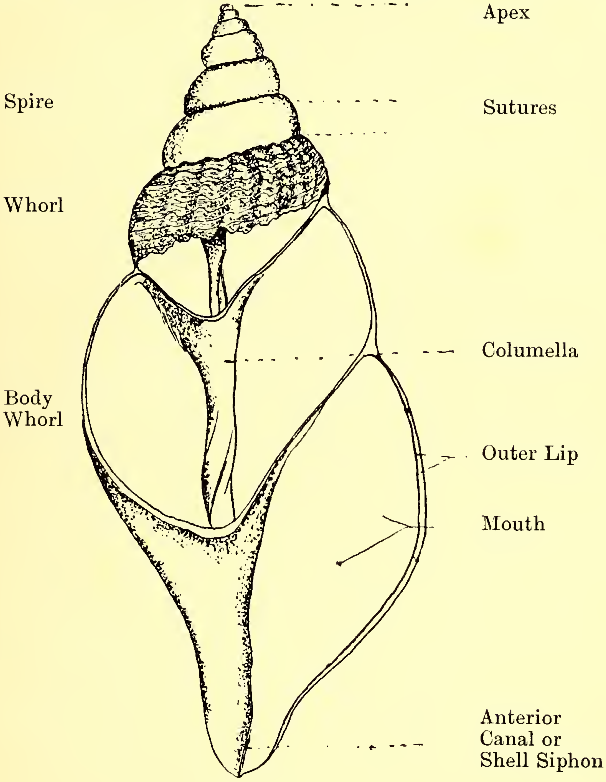

Fig. 1.

different parts. The **apex** is the oldest part of the shell and often in gastropods presents important characters, such as being coiled in the reverse direction.

The **whorls** are in close contact and are about six or seven in number in an average adult specimen. The last turn of the shell is known as the **body whorl** and is extremely large. The successive whorls of the shell in the female show a greater enlargement than is the case in male shells. The lines marking the point of contact of two successive whorls are known as the sutures. The mouth of the shell is produced into a short anterior canal or shell siphon (fig. 1, Pl. I) in which lies a prolongation of the mantle, the pallial siphon (fig. 7, *Siph.*). This condition is characteristic of carnivorous gastropods. The pallial siphon can be extended some distance out of the shelly canal, into which it is retracted when the body is withdrawn. In some gastropods there is also an anal or posterior canal which is represented by the perforation in *Fissurella* and the series of holes in *Haliotis.*

The outer surface of the shell is covered by a horny layer which can be stripped off quite easily. In worn specimens it is frequently absent in patches. This layer, the periostracum (Pl. I, fig. 4) gives the shell a somewhat brown appearance and a furry surface. It will be referred to in detail below. The external surface of the whorls is marked by very distinct grooves and ridges which run regularly in a longitudinal direction, and can be traced round all the whorls to the apex of the shell. They correspond to the lines radiating from the umbo of a lamellibranch shell. In *Buccinum* these lines are arranged on crests and troughs; and are in groups of about six ridges between two crests. The crests become much more distinct as one passes from the mouth towards the apex of the shell, where they are more crowded.

Running roughly at right angles to the former system of longitudinal crests, and therefore transversely to the direction of growth, is another system. This is made up of two sets of markings—lines of growth and broad waves or corrugations. The lines of growth are rather indefinite striae, not nearly so distinct as the ridges of the first system, except near the mouth of the shell and particularly on the shell siphon. The corrugations on the other hand are much more definite on the earlier whorls, and on the last or mouth whorl of an adult shell they are only well marked near the suture line.

These transverse corrugations relieve the monotony of the plane surface and are one of the first characters which strike the observer when comparing the shell with that of *Fusus*.

A longitudinal section taken through the body whorl of the shell shows the following structure:—(*a*) an outer wide layer of irregular columns; (*b*) a middle and narrower layer, also composed of columns, which are, however, regular in shape and arranged at almost a right angle to the surface of the shell; (*c*) an inner layer characterised by delicate oblique cross lines.

The outermost layer begins at the outer lips of the shell mouth, the middle layer commences a little further inside, and it is soon followed by the inner layer. According to Tullberg, who seems to have made a careful study of the structure, a fourth and more internal layer still, occurs in the older whorls and increases in thickness as one approaches the apex of the shell. This is not seen in the micro-photograph, which is from a section through the wall of the body whorl. Text-fig. 2, after Tullberg, indicates the position of origin of the layers.

In addition to these layers of shell substance, there is a very well developed periostracum which can be quite easily peeled off from the shell and examined without sectioning.

The Periostracum is a chitinous layer, yellow in colour, and raised on the external surface into a number of papillae which give the shell the appearance of being covered with a velvety tissue. These papillae are all directed backwards towards the apex of the shell. In sections (Text-fig. 2) the periostracum appears to be made up of layers lying obliquely to the surface. A spine is simply a prolongation of one of these layers.

The outer layer (*a*) of shell (Text-fig. 2, *a*) is marked by the possession of more organic substance than the other layers. The calcareous substance crystallises irregularly as mentioned above, and the appearance can be understood better perhaps from the photograph (Pl. I, fig. 6) than from any description.

The middle layer, Text-fig. 2 (*b*), is, as we have seen above, marked in longitudinal sections by parallel lines running perpendicular to the surface of the shell. In transverse sections, however, the appearance of this layer is, as Tullberg remarked, just like the inner layer (*c*) in longitudinal section. This structure will be understood better when the remaining two layers (*c* and *d*) inside it are examined in transverse section. It will then be seen that the layer (*d*) is marked like the middle layer (*b*), and thus both (*b*) and (*d*) seem built of parallel columns in longitudinal sections, whilst they are marked by oblique lines in transverse section. The layer (*c*) is apparently built up of parallel columns in transverse section. The reason for this strange appearance is that the three inner layers (*b*, *c*, and *d*) are built up in exactly the same way

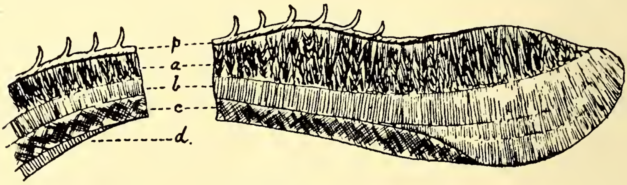

FIG. 2.

of small plates which are arranged in rows with the plates at an angle to each other. Whilst, however, the rows of the layers (*b* and *d*) are situated in a line at right angles to the direction of the whorls, the other layer has the rows running almost in the direction of the lines of growth. It follows that in a longitudinal section of the shell, the plates of layers (*b* and *d*) are seen from their cut faces and appear as columns, the cross striation marking the cut faces of the plate. The plates of layer (*c*) are, however, cut so that they are seen in side view, and the oblique running lines mark the edges of the plates. We might therefore divide the shell into two layers, an outer and an inner, the latter with three subsidiary strata built up in the same way, but, as the geologists would say, unconformable. We have already seen that at the apex of the shell there are a number of partitions cutting off small chambers. These are formed entirely by layer (*d*) of the shell.

Formation of the shell layers and periostracum.—The shell is formed by the entire surface of the mantle, but chiefly by the mantle edge. The periostracum and the three outer shell layers are formed solely by the edge, each of them farther from the actual margin, whilst the innermost layer (*d*) can be increased in thickness throughout life by the mantle immediately below it. The structure of the mantle edge, with the shell secreting cells, will be given in the section on the mantle.

There is probably little doubt that the actual crystallisation of the shell substance into the structure seen in sections takes place outside the secreting cells, and is determined to a certain extent by the constitution—a mixture of conchiolin and lime—of the secretion. The origin of the complex shell structures must, however, be further governed by an architecture already present in the secreting area of the mantle. Such a differentiation of the secreting cells is, however, ultra-microscopic, and the sculpture of a mollusc shell belongs to the same category as the regular shape of the teeth on the radula, the form of placoid scales and the growth of the Echinus plates.

The Columellar muscle is attached to the shell by the same kind of cells that are noticed in *Pecten* and other lamellibranchs. During life a movement of the muscle takes place, but there is no actual movement of the muscle fibres. A growth of new fibres takes place in front, and resorption behind, so that as a result the whole structure appears to move forwards.

THE FOOT.

The ventral creeping foot is exceedingly well developed in Buccinum. It is muscular, and capable of very considerable expansion and contraction, so that whilst soft and almost translucent when expanded, it becomes opaque and tough as cartilage and difficult to deal with in dissections when contracted. The flat and smooth ventral surface, or sole, has, when the foot is expanded the shape indicated in fig. 9, Pl. II. Thus the anterior margin of the foot is broad, and the width remains constant for some distance backwards until towards the posterior end it gradually narrows away to a point. Running parallel to the anterior margin of the foot is a deep groove (fig. 9, Pl. II, *Ped. gl.*), which cuts off an anterior narrow ridge from the major portion of the foot; and into this anterior groove open numerous glands. The molluscan foot is usually well provided with glands, and these may be divided into (*a*) scattered gland cells covering the foot, and (*b*) specialised compound glands.

The latter class includes the byssus gland of the lamellibranchiata. In the gastropoda the specialised glands may be divided into an anterior foot gland, often opening anteriorly into a transverse groove, and an unpaired median gland opening into a cavity situated in the middle line of the foot. It is very probable, however, that both these are parts of the same system, and it is generally believed that one or other is homologous to the byssus gland of the lamellibranchs. The median unpaired opening is absent in the whelk, but the anterior glands are very well developed, and the pedal groove can be observed quite early in the embryo. The portion of the foot anterior and dorsal to the pedal groove, as well as the anterior part of the ventral surface, may be used as a clasping organ, and in this way the whelk can to a certain extent retain its hold whilst using the proboscis and radular apparatus to bore through a molluscan shell or a crustacean exoskeleton.

As stated above, the foot is highly muscular. It is almost entirely composed of muscle fibres, and moreover the greater part of it is one muscle—the columellar muscle of the shell, which arises from the columella (Pl. I, fig. 3), and in average-sized specimens from the inner surface of the 5th whorl, and is inserted into the under surface of the operculum, and thus must pass through the foot in order to reach this point. In the foot it is crescentic in section, the convex side being dorsal and very distinctly marked off from the narrow band of more superficial tissue. The whole muscle lies here near to the dorsal surface of the foot. The attachment to the operculum is on the ventral side and forms an elliptical area which is situated eccentrically.

The columellar muscle of the gastropods has been homologised with the adductor of the lamellibranchs by those authors who have considered the operculum homologous with the other valve of the lamellibranch shell; and with the retractor muscles of the foot, by those who consider the operculum as representing the byssus of the lamellibranchs. Both theories are untenable. The operculum is probably a new structure, and the search for homologies is sometimes carried too far.

The foot exhibits very great changes in size, according to whether it is fully expanded or completely contracted. Whilst the whelk is creeping about, the foot is almost constantly changing in shape, and if not in total volume the size of different regions at least varies. This power of change is due to the vascular supply and the muscular structure. The pedal arteries form a very complete network extending throughout the foot. Blood runs back through a large central sinus. The expansion takes place through the forcible intrusion of blood into the foot. If the foot of an expanded animal be suddenly cut off with a very sharp scalpel, the sudden outflow, or jet of blood, seen as one severs the sinus, is most striking. This is due to the muscular contraction which begins immediately the foot is touched with the knife. The blood, in fact, has most important functions to perform in effecting both the expansion of the foot and the extrusion of the proboscis.

The creeping action of the gastropod foot has already attracted considerable attention. In most cases when the animal is in motion a series of waves can be seen coursing along the foot. These may be in a direction from behind forwards—*direct* (*Aplysia*, *Doris*, etc.,) or in the reverse direction anterior to posterior—*retrograde* (*Littorina littorea* and others). In some gastropods again the foot is divided into two longitudinal halves and these move alternately, both exhibiting systems of waves. In addition to the above types there are cases (Parker) where there seem to be no waves at all and the foot glides like a Planarian over the substratum. In *Buccinum* the waves can only be detected at the edges of the foot, but in addition to this motion the whole of the anterior part can be moved forward and then attached whilst the posterior portion is pulled up to it. This is particularly well seen when the mollusc is removed from the water. The actual forward motion of the foot is caused by muscular contraction pulling forwards all those regions of the foot temporarily raised,—at least when compared with the rest of the foot. These regions are the waves, the crests being for the time the fixed portions.

The Operculum is a disc of chitin with a deposit of calcium carbonate, placed on the dorsal surface of the posterior part of the foot (Pl. I, fig. 7, *Op.*, and fig. 5). It is carried on a slight elevation, the "opercular disc," and when the animal is withdrawn into the shell fits into the mouth, closing the orifice completely. The operculum is pulled to with considerable force, for, since the columellar muscle is attached to this plate and the direction of pull is almost exactly along the muscle, the whole force of which the muscle is capable can be exerted. The amount of lime in the operculum of *Buccinum* is but small, and the structure is horny in appearance, lacking the strength of some other gastropod opercula which may be thick and extremely hard.

Seen from its superior surface, it is marked by very distinct lines of growth which are arranged concentrically round an eccentrically placed "marginal nucleus." The attachment to the foot is also eccentric, the oval area lying quite to one side, the side further from the nucleus and anterior when the foot is uncontracted. Round the area of attachment the tissue of the opercular disc forms a collar which projects for a little distance, sheathing the unattached marginal regions of the operculum. This "opercular lip" is deepest on the posterior border where there is a greater width of unattached operculum. When creeping, the operculum is arranged, as we have seen, transversely across the foot. The anterior margin in this position is the *internal* border, the posterior margin the *external* border when the operculum is applied to the shell mouth.

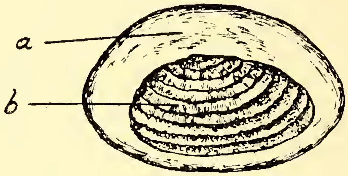

Fig. 2a.

If the operculum is removed from the foot and the attached or ventral surface examined, a very different system of striae will be seen. The operculum is, as a matter of fact, composed of several layers, and the markings on the superior and inferior surfaces are therefore quite independent of one another. The area of attachment, as already mentioned, is situated towards the anterior margin, and entirely to one side, therefore, of the nucleus. This area is marked by about ten bands (in adult specimens), arranged concentrically, but with only part of any band showing, the remainder being outside the area of attachment. Furthermore, these bands are arranged in an imbricating manner (Text-fig. 2a, *b*), each one nearer to the centre overlapping its more marginal neighbour. The area outside the region of attachment is covered with a somewhat glossy horny layer, which hides the concentric bands as stated above. This glossy ventral layer is broadest under the posterior margin (Text-fig. 2a, *a*). The operculum is composed of three layers, a very delicate superior layer, a median layer of considerable thickness which is itself formed of numerous laminae arranged at an acute angle to the plane of the operculum, and a third and most ventral layer, the glossy one described above. The thin superior layer is formed by a pad of cells situated in a cleft *below* the anterior lip of the opercular disc. The middle layer is secreted by the cells of the disc at the margin of the region of attachment, and chiefly anteriorly. As a matter of fact, the epithelium of the foot is perfectly continuous underneath the operculum, and it is by means of these cells that the muscle fibres are attached to the operculum. The most ventral layer of all is produced by the cells of the opercular lip. It will be noticed that this lip is much deeper and more obvious altogether posteriorly where the glossy layer is widest and best developed.

It is possible without more than decalcification to cut sections through foot and operculum. These will show quite easily the positions of the various secreting cells. The secreting cells are characterised by their great depth. They are narrow and about four times as deep as the other epithelial cells of the foot in the vicinity.

The pedal groove (Pl. II, fig. 9, *Ped. gl.*; fig. 10, *Ped. gr.*) is a deep incision running transversely across the anterior margin of the foot. It appears quite early in the larva, and is relatively very large at this period. In transverse sections of the groove (Pl. II, fig. 10), or longitudinal sections of the foot, a region round the base of the groove can be seen with the unaided eye to be different from the rest of the foot. Sections stained with methyl-blue-eosin are very characteristic and make obvious the fact that this peculiar region is composed of numerous compound glands.

The groove is, in fact, nothing but a slit-like common opening of a very large number of glands. The foot in the region of the groove is bounded, as elsewhere, by a layer of deep epithelial cells with characteristic striated cuticular margin and cilia. These ciliated cells are compressed laterally and separated by gland cells. Exactly the same type of cell lines the groove, and there is no change even at the bottom of it, except that the cilia are longer and much better developed than elsewhere. Here the epithelial cells are much compressed and the nuclei are drawn out into long spindles.

Between the cells open the compound glands. Below the epithelium is the muscular tissue, built up mainly of transverse running fibres, so that their cut ends appear in section (fig. 10, *Ped. mus.*). There are, however, scattered oblique and longitudinal fibres. In the region of the groove the muscular tissue remains absent, and its place is taken by the glands. Thus the very distinct demarcation of the gland is due as much to the absence of muscles here as to the presence of the gland cells. The glandular tissue (fig. 10, *Ped. gl.*) is very characteristic. There is no blue staining contents characteristic of the mucous gland cells or similar cells in the mantle and pedal epithelium. Instead, there are packets of very thin-walled cells situated some considerable distance below the epithelium.

The packets are bounded by very thin connective tissue sheaths, but this is so delicate that it may seem no more than the outer walls of the cells which are arranged to form the packet.

The cells are intensely vacuolated. From each packet a narrow path of the same cells runs to the epithelium. These cells, however, do not enclose any canal. It appears as if the secretion must reach the groove by passing through the cells. Usually in sections there are no traces of secretion in the groove, and in living specimens no mucus or other fluid appears coming from the groove. What is, then, the function of the gland? It is homologous with the pedal pore of many other gastropoda; once considered an aquiferous pore by which water entered the animal. The gland secretes the substance of which the egg capsules are formed. This fact, noted in 1899 by Cunningham to apply to *Buccinum* and *Murex*, has since been found to be true for *Purpura* by Pelseneer.

THE MANTLE AND PALLIAL CAVITY.

The pallial cavity proper is the space between the mantle and the dorsal surface of the body of the animal. Its floor is formed by the body wall, its roof by the mantle. It will be advisable to refer in a general way to this part of the animal in a separate short section, inasmuch as the cavity contains several important organs belonging to different systems.

These organs considered together may be termed the Organs of the Pallial Complex. Three of them are structures developed largely from the mantle itself—the ctenidium or gill, the osphradium, and the mucous gland (Pl. II, fig. 8). Furthermore, there are to be considered the Rectum and Anal opening (fig. 8, *Rect.*), the Renal opening, and the male and female genital openings. The mantle itself is thick and muscular, and this applies most markedly to the free edge. The edge is slightly recurved outwards, and just behind the extreme margin and on the outer surface is a delicate band of yellow pigment.

If the mantle is slit down the extreme right side on the *left* of the rectum (and the oviduct in the female), and turned over to the left, the organs of the pallial cavity can be easily made out. On the extreme left, and arising from the inner surface of the mantle, are two ridges which form the side walls of a groove, the pallial siphon (fig. 8, *Siph.*). These side walls and the basal part of the groove are continued so as to form a truncated cone with a gutter down one side of it. This pallial siphon lies in the shell siphon, but can be extended a considerable distance when the animal is active. Water entering the mantle cavity passes in by means of this tube, which is characteristic of the carnivorous gastropods. One would imagine from observation of the living animal that the siphon was connected with some important system of sense organs. It is continually in motion from side to side, and extends much further from the animal and is more active than the tentacles.

Examination of the mantle cavity in this light reveals an interesting series of organs. The osphradium, which is a darkly pigmented structure on the left side, is situated right across the end of the siphon (fig. 8, *Osph.*). Thus all water entering the pallial cavity must pass over it *before reaching the other organs.*

The osphradium is a narrow organ composed of two series of leaflets arranged along the sides of a central axis. It will be discussed further in the chapter on the sense organs. To the right of the osphradium is the gill (fig. 8, *Ct.*). It is separated from the osphradium by the ctenidial axis which can be seen as a white ridge running from the most distal part of the gill to the inner end of the pallial cavity. The gill itself is composed of leaflets arranged on one side of this axis only, the topographical right. Between the ctenidium and the cut side of the mantle the inner surface of the latter is occupied by the large mucous or Hypobranchial gland (fig. 8, *Mu. gl.*), which extends therefore from gill to rectum. The gland is made up of a number of deep lamellar foldings of the mantle, about twenty in number. The structure of this organ is considered elsewhere.

The Anus (fig. 8) is situated at the apex of a prominent papilla on the right side (topographical).

The vaginal portion of the oviduct is conspicuous in ripe females as an opaque white cylinder on the extreme right. Its opening into the pallial cavity is not so prominent as the anal opening by reason of the lowness of the papilla. In male specimens the pallial cavity will be filled by the large penis which usually lies twisted backwards. All these organs terminate about the same distance from the mantle edge and thus leave free a wide region, the inner surface of the thickened margin.

The Renal opening is a slit-like pore, situated to the left of, and slightly above the rectum on the posterior wall of the mantle cavity, in fact on the membrane separating this cavity from the renal organ. The long axis of the slit is dorso-ventral in direction.

The Mantle Edge.

A great part of the mantle, whether at the thickened edge or in the region of the ctenidium and other organs of the pallial complex, is composed of a modified connective tissue. One sees in sections practically nothing but thin cell walls with nuclei adhering to them, and here and there fragments of muscle fibres. This characteristic mantle connective tissue (figs. 31, *x con.* and 45, *Pall. gl.*) is seen very well in the thickened edge, where it occupies about $\frac{3}{5}$ of the total thickness. Against the epithelial layer, which bounds the surface of the mantle, and underlying this everywhere, is a thick sheet of compact fibrillar connective tissue of the more normal invertebrate type (fig. 45). Running through this layer are muscle fibres of which the circular are near to the surface whilst longitudinal fibres occur more frequently nearer the central connective tissue mass. The most important feature of the mantle edge is the epithelium, for this is concerned here with shell building. The epithelium covering the free inner surface of the mantle is formed of columnar cells whose height is several times their breadth. These cells are typical ciliated cells, so that the epithelium presents here a ciliated surface. The ciliated cells are separated everywhere by mucous cells. These ciliated cells extend round the edge of the mantle to the shell side. On this side of the mantle (and in that region where the mantle forms the roof of the pallial cavity) there is a remarkable gland running across and opening to the surface not far from the mantle edge. The gland is situated deep below the epithelium imbedded in connective tissue. The actual gland cells communicate with the surface by long processes which are so crowded together that, just below the epithelium and away from the gland cells, they appear like the fibres of a broad nerve. The resemblance is quite striking in methyl-blue-eosin stained sections, for the stain is not unlike a nerve stain. Another very striking feature of the gland is that, instead of the fibre-like communication to the surface opening between epithelial cells, the epithelium appears to be absent for a short space and its place taken, in fact, by the gland cell processes themselves.

This glandular mass in the *Buccinum* mantle was noticed by Tullberg, who discusses its function without, however, coming to any definite conclusion. He states that it might very well be a gland for the secretion of the Periostracum, and this is supported by the fact that the gland is absent on the mantle below the visceral mass where no Periostracum is formed. Against this, however, he adds that the gland is too large for this function alone and that it would be peculiar to find a special gland for the secretion of the Periostracum, whilst the shell itself is formed by the general epithelium of the mantle.

In my opinion the objections that Tullberg brought forward are not important. In the lamellibranchs the Periostracum arises in a groove from a very definite pad of cells, certainly epithelial in position but still differentiated enough to form a special organ. Hence there is no reason why the thick Periostracum of the whelk should not be formed by this gland. In any case no other function has been ascribed to it. The comparative anatomy of this organ is being followed up by the author.

The shell side of the mantle from the opening of the gland inwards is faced by epithelial cells differing from those already noted in the absence of cilia. These are the shell secreting cells. They are marked, particularly near the gland, by the possession of granules of yellow pigment.

RESPIRATORY ORGAN (CTENIDIUM).

There is only one ctenidium present in *Buccinum*, as in most of the higher Gastropoda. This is the morphological right gill, but is situated now on the left side of the pallial cavity. It has already been referred to as being visible through the thickness of the mantle. This ctenidium extends from a point, in line with the anterior limits of the osphradium and mucous gland, as far back as the pericardium (fig. 8, *Ct.*). It is composed of a large number of flattened leaflets which are packed parallel to one another and vary in size, so that they become successively smaller as either end of the ctenidium is approached.

These leaflets are roughly triangular in shape. The axis of the ctenidium lies close to the osphradium (fig. 8, *Ct. ax.*). The respiratory leaflets are disposed along one side only and are further attached by the whole of their bases to the mantle (see Text-fig. 3, p. 25).

The ctenidium is therefore *Monopectinate.*

The efferent branchial vessel runs along under the ctenidial axis and thus the area of each leaflet adjoining the axis may be known as the efferent end and the free side, the efferent margin of each leaflet. Branchial lacunae extend up the afferent margins of the leaflets from the afferent branchial sinus which lies in the mantle immediately below the point of attachment of the afferent edges of the lamellae.

The ctenidial axis (fig. 8, *Ct. ax.*) is conspicuous as a smooth ridge running along the inner surface of the mantle as far as there are ctenidial leaflets.

It is made of the same peculiarly vacuolated connective tissue (fig. 39, *Ct. gl.*) seen in the mantle at the base of the ctenidial leaflets. Towards the side to which the branchial lamellae are attached the place of this tissue is taken by longitudinal muscle fibres (fig. 39, *Ct. mus.*). This layer increases in thickness towards the middle of the ridge.

The ctenidial nerve (fig. 39, *Ct. n.*) runs along the axis not far from the osphradial side, and gives off branches at intervals, which pass to the leaflets.

HISTOLOGY.

The microscopic structure of the ctenidial leaflets is interesting by reason of the histological differentiation of the different areas. Each leaflet consists of a double bounding layer of epithelium enclosing a flattened cavity, which is a blood space. Underlying this epithelial layer (figs. 31, 32, 33, *ct. e.'*, *ct. e.''*, *ct. e.'''*) there is an internal connective tissue layer with muscles, lining the blood space just mentioned. Between these two layers a supporting tissue is developed which is much thickened near the ctenidial axis and runs along the efferent margin of each leaflet (figs. 31, 32, 33, *Sup. m.*).

This supporting tissue, which in its thickened parts is apparently hyaline, has been regarded as cartilaginous or chitinous; this will be referred to below.

The relation of the various structures enumerated can be made out best in a section transverse to the leaflets and perpendicular to the mantle. Such a section, running through the efferent margin, is figured on Pl. IV (figs. 31, 32, 33).

The external epithelium, which bounds the lamellae, differs considerably in the various regions. Taking the section through a point near the efferent margin, there is first the free edge to be considered. The epithelium here is composed of somewhat deep and regular columnal cells bearing cilia (fig. 33, *ct. e.'*). This epithelium diminishes in thickness and becomes more irregular than indicated in the figure as one leaves the free margin. The cilia are also lost and the cells appear glandular (fig. 33.) Following on this region the cells again become more deep, more regular and with deeply staining cytoplasm. They all bear well developed cilia, so that the whole area occupied (fig. 32, *Ct. e.'''*) by them is very conspicuous by reason of the marked contrast with the glandular cells lacking cilia on either side of it. Passing this area towards the mantle, the cells become once more glandular and without cilia. The epithelium here is often thrown into folds through contraction, probably on fixation (fig. 31, *Ct. e.″*), but this in all probability can take place in life since there is a plentiful supply of muscles in the sub-epithelial layers.

Immediately under the epithelium there is a supporting membrane. This is very delicate and almost indistinguishable under the greater part of the area of the leaflets, but thickens considerably, so that it becomes the outstanding feature in stained sections, near the efferent margin (fig. 33, *Sup. m.*). It is this substance that has been termed cartilage or chitin. It is clear, however, that this supporting membrane must be considered in conjunction with the connective tissue on its internal face, that is, bounding the blood cavity. This layer is distinctly peculiar. Seen in transverse sections, all that can be observed are a few nuclei with very little surrounding cytoplasm (fig. 32, *Ct. con.*). If, however, a section is cut very slightly tangential to the leaflet, it may be possible to secure the layer itself. It then appears made up of squamous cells, often with the corners drawn out (fig. 34). If these cells touched, making up a definite membrane, it would be difficult to distinguish them from an endothelium. Instead of this, they are more or less scattered, and at odd places there is a crowding together to form islands of pseudo membrane. This tissue is thus very characteristic. Now the supporting membrane is in close contact with these cells, and moreover, in places it is quite continuous with the matrix surrounding them. This brings out strongly its resemblance to the matrix of ordinary connective tissue both in structure and in staining. Hence I have come to the conclusion that the supporting structure, thickened at the efferent margin, is really a connective tissue, free from cells or fibres, and that the cells which have formed it occur on its inner surface.

The relative areas covered by the different structures are indicated in Text-fig. 3.

The connective tissue supporting skeleton extends from the axis along the efferent border to the angle. At first it extends from the free edge of each leaflet to the mantle, but it gradually becomes reduced. The area of ciliated cells increases quickly and then extends to the angle of efferent and afferent edges, occupying in sections from about a third to one-sixth of the length of the leaflet (measured from efferent margin to mantle side). The glandular cell area is nearest to the mantle. It increases steadily in thickness as the afferent edge of the leaflet is approached and is widest in that region.

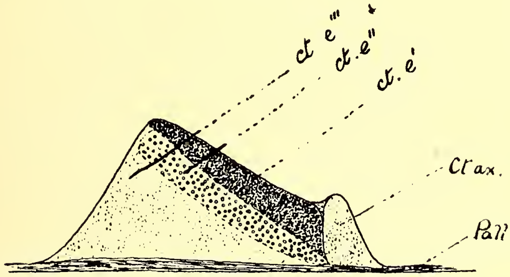

FIG. 3. *ct. e.'''* Area of Glandular Cells. *ct. e.''* Area of Ciliated Cells. These differ from the reference letters on Plate IV.

One further detail remains to be described. Peculiar characteristic bridges run across the blood cavity in the leaflet. Each of these appears to be formed of muscle fibrils which diverge at their extremities (fig. 34, *Ct. mus.*). The cell in which these muscular fibrillae have been formed remains, and is usually quite obvious with its residual cytoplasm and nucleus in the centre of the bridge.

Thus it is possible by contraction of these numerous muscle strands to approximate the two surfaces of the leaflets, and hence to force out the contained blood.

Another peculiar histological structure may be referred to here. The epithelium of the lamellae is simply the folded epithelium of the inner surface of the mantle. The outer epithelium bounding the mantle externally is, of course, not folded here or elsewhere (fig. 31, *Pall. ep.*). Between these two layers there is the very characteristic median stratum of connective tissue made up of extremely large cells with delicate walls, feebly staining nuclei and practically no contents (fig. 31, *X. con.*). What function this layer may play has so far not suggested itself.

MUCOUS GLAND.

The mucous gland is the most conspicuous organ in the pallial cavity, both by reason of its secretion as well as by its structure. It is a modified region of the mantle between the ctenidium and the rectum where gland cells predominate, and the inner wall of the mantle is thrown into deep folds which run transversely, overlapping slightly and hanging down into the pallial cavity.

The mucous gland is really the inner wall of the mantle whose cells are elongated and specialised as gland cells. The anterior folds of the gland are directed backwards, the most posterior ones forward (fig. 8, *Mu. gl.*). They are much thicker than the ctenidial leaflets and are separated by much greater spaces. The number varies, 20-25 being about an average for a full-sized whelk.

This region of the mantle is extremely well supplied with blood, as a glance at fig. 35 will show, and numerous vessels run down parallel to the folds from the reno-mucous vessel to the afferent branchial vessel. The secretion of the gland is either perfectly hyaline or yellow-white in colour. It is perfectly abominable to handle, and after months in five per cent. formalin it still retains its fresh appearance and consistency. It can be drawn out into long threads of surprising length (some feet) without breaking. The secretion of this matter takes place very rapidly when the animal is severely stimulated, particularly with irritating fluids. Concerning its function but little is known. It would appear in the first place to be a protective—or defensive—secretion. It does not leave the animal gradually after secretion but is produced, as we have seen, spasmodically and quickly, and raises itself in a sheet. Obviously it removes in this way any dirt, sand grains or other matter from the organs of the pallial cavity, and, moreover, protects them to a certain extent from the entrance of such materials.

HISTOLOGY OF MUCOUS GLAND.

Sections taken through the mucous gland show that we have to deal with a very much modified epithelial layer, which rests on a basement membrane of connective tissue overlying the peculiar cellular connective tissue of the mantle (fig. 40, *Con.*). This latter tissue extends into the folds, but only occurs as bridges running across at intervals and leaving great cavities between the two sheets of epithelium. The epithelium is composed of three types of cells as described by Bernard: 1, Mucous cells; 2, ciliated cells; 3, neuro-epithelial cells.

In sections, the characteristic appearance is to find cell walls running from the periphery to the basement membrane dividing the whole up into large chambers filled with mucus (fig. 40, *Mu. c.*), but in addition there is a more protoplasmic peripheral region bearing cilia and another series of cell walls. There are also two distinct nuclear regions, one of which is peripheral (nuclei belonging to the ciliated cells), and the other basal (nuclei of the mucous cells).

The ciliated cells are long and narrow, with, however, an expansion at the periphery which forms a kind of platform. The mucous cells are very large and wide, their length varies according to the amount of mucus present. Their peripheral ends are, however, often quite attenuated.

Bernard has made a very detailed study of the process of mucus formation, examining pieces of living tissue from the gland with the microscope. He concludes that before the production of mucus the ciliated cells are all in contact and form a continuous surface without grooves or openings. The mucous cells do not reach at first the level of the surface, but gradually they extend until they appear between the ciliated cells. A small opening occurs and from it the excretion pours out as a drop. The cell continues to secrete mucus.

The ciliated cells can detach their peripheral portions, which go off as ciliated spherules minus nucleus and with little protoplasm. Finally dead cells of both kinds are expelled and may be seen in the excretion.

THE ALIMENTARY CANAL.

The alimentary canal opens at the true mouth, at the apex of a long retractile proboscis (fig. 11, *Prob.*), probably not to be seen without dissection in the preserved specimens. The opening which has been noted on the surface of the head below the tentacles is not then the true mouth. At this point the body wall is turned in to form a permanent introvert of considerable length, part of which, however, is again turned on itself to form

The Proboscis. Text-fig. 4 explains this part of the body better than any description. The invaginated body wall between *a* and *d* forms both the proboscis, which can be protruded, and a proboscis sheath; part of the latter, however, can be everted (fig. *b* to *c*).

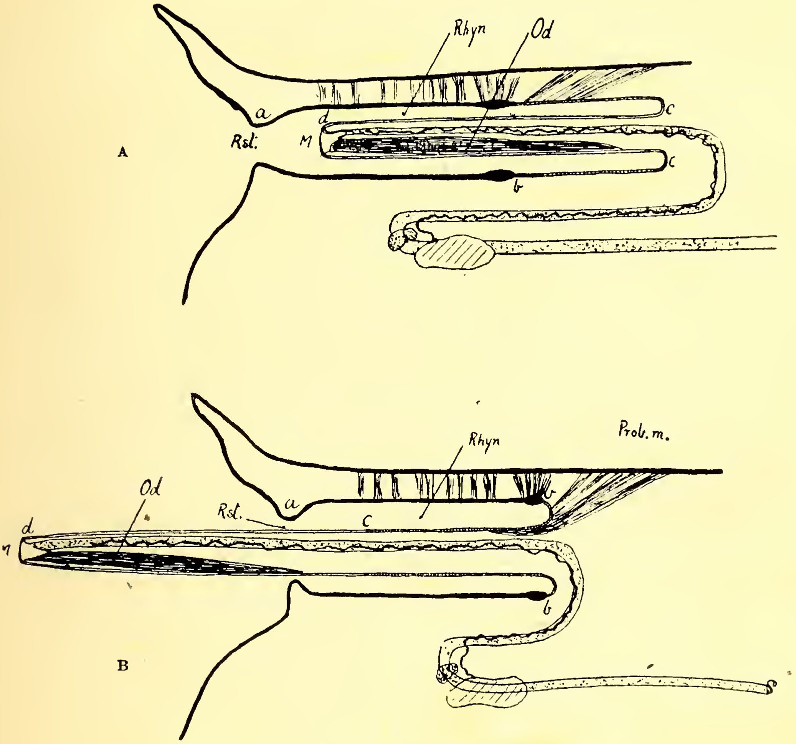

Fig. 4.

The section of the proboscis sheath *a-b* in Text-fig. 4 is connected somewhat closely to the body wall by short muscles. This region retains its position whatever be the disposition of the proboscis. A definite ring of muscle and connective tissue (usually of a reddish hue in fresh specimens) encircles the sheath at *b*, and marks the boundary of the next section *b-c*. This portion, about

1½ inch long in the adult, is thin walled, made up of muscular fibres and connective tissue, and is connected by long strands of muscle with the walls of the body cavity. Some of these strands pass backwards for some distance. Now this region can be everted in such a way that whilst forming part of the proboscis sheath in the retracted condition (fig. A), it forms the base of the proboscis in the extended position (fig. B). Thus the protrusion of the proboscis is not due to muscular action of this structure itself but to the unfolding of the hinder part of its sheath. The proboscis is nothing but a further continuation of the body wall, and the true mouth lies as mentioned above at its distal end (figs. A and B, *M.*).

The cavity (part of the external world) between the proboscis and its sheath (Text-fig. 4, *Rhyn.*, and Pl. II, fig. 11, *Rhyn.*) is known as the Rhynchodaeum, and the opening of the latter, or the false mouth, is the Rhynchostome (*Rst.*). Such a proboscis is termed a *pleurembolic proboscis* (Lankester*), from the fact that when withdrawn it is the base that is pulled and disappears first. The other and opposite type is the *pleurekbolic*, met with in the Cypraeidae, etc. The proboscis of *Buccinum* was known to the ancients, and both Aristotle† and Pliny‡ refer to it. Cuvier was the first, however (1817)§, who described it with accuracy and detail.

Pharynx.—The mouth (Text-fig. 4, *M.*, and fig. 11) opens into a muscular pharynx (Pl. II, fig. 12, *Ph.*), the walls of which are attached all round to the proboscis walls by radiating muscles. Into the floor of the

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* Lankester. Art. Mollusca, Encyclop. Britannica, 9th edit., Vol. XVI, 1883.

† Aristoteles. De Animal. hist., Lib. IV, cap. 4, §§ 7, 8, 9.

‡ Plinius. Hist. Nat., L. XI, c. 37.

§ Cuvier. Mém. pour servir à l'hist. et à l'anatomie des Mollusques.

pharynx, which bears no teeth, projects the tongue apparatus, and the muscles of this characteristic organ almost surround the anterior part of the alimentary canal. The whole structure is known as the Odontophore (Text-fig. 4, *Od.*), and consists essentially of a tongue, projecting into the pharyngeal space, covered by a flexible rasp—a membrane set with teeth—known as the radula. A description of this apparatus is given separately below.

The pharynx extends backwards for about 1 cm., and almost at the point where the radular apparatus opens into it, two salivary ducts enter laterally, one on either side (Pl. II, fig. 12, *Sal. d.*). These ducts can be seen as two delicate white tubes running along the sides of the oesophagus (fig. 12, *Oes.*), the next portion of the gut.

The Oesophagus extends from the pharynx to the stomach, and is the longest section of the alimentary canal. The most distal part, immediately behind the pharynx, is flattened dorsoventrally and runs along through the proboscis to its posterior end. Here it turns abruptly on itself and runs forward again in close contact with the proboscis sheath. The anterior direction is kept until the region is reached where the nerve collar lies hidden by the conspicuous salivary glands, and then another somewhat abrupt bend occurs (Text-fig. 4, A and B) and the oesophagus passes through the nerve ring and runs posteriorly along the floor of the body cavity. This curious looping of the oesophagus is probably due to the nerve collar which has retained its normal anterior position and compelled the alimentary canal to take the course which has been described. The part of the gut which is thus bent into an **S** is marked by longitudinal folds projecting into the lumen. None of these longitudinal folds are specialised or better developed than others. At its sides run the salivary gland ducts already mentioned. They arise in the large salivary glands, compact bodies of a yellow colour, which are situated asymmetrically about the alimentary canal and nerve collar. The latter is hidden completely except from below. The left gland lies more posterior and more dorsal than the right, and thus covers part of the latter. The ducts are formed by numerous small branches joining up in the tissue of the glands and leaving them dorsally (Pl. II, fig. 12, *Sal. gl.*). The histological structure of this organ is given below.

Neither gland alters its position during the evagination or invagination of the proboscis, and a further most important point to notice is that *neither salivary duct passes through the nerve ring.*

This is probably due to the fact that with elongation of the proboscis the salivary glands came to lie in front of the nerve collar. With the later elongation of the salivary ducts the salivary glands came to lie behind the nerve collar and moved to the position externally to the collar. This explains the fact that in the Rachiglossa the ducts do not penetrate the nerve collar, a feature otherwise common in the Monotocardia, where the glands are posterior to the nerve ring.

A little distance behind the nerve collar a narrow tube opens into the oesophagus on its dorsal surface (fig. 12). After running forwards for a few millimetres, it curves round and widens into a very thin-walled bag, usually flattened, and of a brown colour in fresh specimens, owing to the contents. The bag extends back for some distance, lying upon the oesophagus. It is the so-called gland of Leiblein (Pl. II, fig. 12, *Ln. g.*)—the poison gland of the Toxiglossa.

Both gland and oesophagus move over towards the left side as the visceral mass is reached. Just before the region of the pericardium and digestive gland is entered, a peculiar caecum is to be found on the oesophagus (fig. 12, *Ln. g.*). Its walls are rather more thick than the part described above, and resemble the short piece now left between caecum and stomach. The caecum can be easily seen in simple dissections, for the oesophagus has now left the head region and is visible without any incision whatever at the surface of the visceral mass on the left ventral edge. The caecum itself lies just behind the pericardium (fig. 12, *Caec.*).

The **Stomach**—that part of the alimentary canal into which the ducts of the large digestive glands (the so-called liver) open—is a bag of considerable size, with one surface lying against the digestive gland and the other surface against the bounding integument. Thus the stomach is clearly visible without any dissection. Curiously enough, it is attached strongly by short muscle strands to the epithelial layer of the body wall, so that the latter, which can be easily removed from the other parts of the viscera, is only pulled away with difficulty from this area.

The stomach (fig. 12, *St.*) is very irregular in shape. It is flattened, so that there are two more important surfaces, and it is elongated in an antero-posterior direction. The oesophagus opens into it ventrally about midway between the point of origin of the rectum and the posterior apex of the stomach. Just before entering the stomach the oesophagus passes under a somewhat conspicuous lobe of this organ, which is marked with radiating striae and lies between oesophagus and intestine (fig. 13, Dg.″).

The markings on the external surface of the stomach correspond to ridges which occur on the inner surface and project into the lumen. Two openings into the stomach, both on the inner surface, mark the entrance of the ducts from the digestive gland (fig. 13, *Dg. d.*). One of these is situated anteriorly close to the proximal part of the rectum, the other is just posterior to the point of entrance of the oesophagus.

The Digestive Gland is the largest structure in the visceral mass, and extends from the pericardiac region to the tip of the spire. It is brown or brown-green in colour, and soft and oily in consistency, with no very pleasant smell. This large gland, which is made up of fine branching tubules, was formerly regarded as a "liver." It is now agreed that this name is unsuitable, as the digestive functions are more comprehensive and unite the functions of the different digestive glands of the vertebrate gut. It is, furthermore, the chief organ in the body for absorption of digested food.

Originally the digestive gland of the Gastropoda was paired and symmetrical. In the adult *Buccinum* there is an obvious division into right anterior and left posterior lobes. The latter is much the larger of the two and extends from the tip of the stomach to the end of the spire. The boundary of the two regions lies at the posterior end of the renal organ. The paired nature is still further indicated by the fact that the tubules, of which the gland is composed, open into one another, and finally form two large ducts which enter the stomach, as mentioned above. The posterior part of the digestive gland is partially covered by the gonad which lies, forming a kind of arch (fig. 58), on its dorsal surface.

The Intestine (fig. 12, *Rect.*), the original posterior portion of the gut, is of shorter length than the oesophagus. Owing to the torsion which has taken place in development it runs forward dorsally to open into the pallial cavity. The intestine leaves the stomach dorsally and anteriorly and lies close to the surface until the renal organ is reached. It then plunges underneath the latter (though still on the surface of the digestive gland and outside the pericardium), and reaches the pallial cavity.

It is now some distance away from the oesophagus and ascends into the wall of the pallial cavity, taking a course along the right side at the extreme edge. In the female this distal portion, the rectum, is compressed by the oviduct. The rectum terminates in a conical protuberance at the end of which the anus is situated (fig. 8, *An.*). With the exception of glandular walls, no special anal or rectal glands are present.

Histology of the Alimentary Canal and related Organs.

A detailed account of the histology of the whelk's tissues would be far beyond the limits of this Memoir. Only some of the more typical and important structures will be referred to here.*

The Pharynx.—The pharynx in life has a peculiar pink colour, due to its muscular wall. In sections one finds the lumen of the gut lined by a layer of deep epithelial cells. As a matter of fact, the lining of the gut is very similar throughout its length, and the same kinds of cells are found in the epithelium, viz.:—(1) Ciliated cells, (2) Eosinophilous cells, (3) Gland cells. Whatever may be the function of the two latter types, it is interesting to notice that they occur throughout the whole length of the gut from pharynx to rectum.

The ciliated cells (fig. 24, *Cl. c.*) are typical tall

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* The author intends to publish shortly a series of papers dealing with Molluscan Histology.

columnar epithelial cells, with an oval nucleus situated near the middle of the length. A distinct border, due to the desmochondria at the base of the cilia, is present. With either methyl-blue-eosin, or Mallory's stain, the contents of the eosinophilous cells (small spherical granules) (fig. 24, *Ev. c.*) stain an intense red and the contents of the gland cells light blue (fig. 24, *Gl. c.*).

The most interesting part of the pharynx is, however, its muscular sheath, which underlies the epithelium. It may be divided into two layers, longitudinal fibres situated next to the epithelium, and an outer circular muscle layer (fig. 24, *Mus. long.* and *Mus. circ.*). There is no outer layer of epithelium bounding the cavity in which the pharynx lies, for this is simply a haemocoele. The muscle fibres are extremely thick, and each is surrounded by a capsule of connective tissue. This matrix is, however, so reduced that it has rather the appearance of very thick cell walls, where the muscle fibres are cut transversely. The fibres themselves resemble the cell contents, for they are almost round in transverse section; the angular shape really possessed by them is probably due to crowding and pressure. The structure of the fibres is extremely distinct in this pharyngeal musculature, and one sees a beautiful peripheral arrangement of fibrils surrounding a large central granular sarc, in which may sometimes be seen the nucleus. A better or more easily procured example of this type of muscle fibre could hardly be imagined. These large fibres with their great sarcoplasmic centres give the reddish pink tinge to the pharynx, a colour which is hardly ever present in molluscan muscles, and in the whelk in one other place only, the muscles of the odontophore.

The Gland of Leiblein.—So far as I am aware, no description of the structure and chemistry of this gland exists. In life the gland possesses brownish contents which can be seen through the delicate walls. It is homologous with the so-called poison gland of the Toxiglossa, and, as stated above, belongs normally to the ventral side of the oesophagus. Its opening has been brought to the present dorsal position by the torsion of the alimentary canal in this region.

The walls of the sac are formed of a delicate layer of connective tissue (fig. 30, *Con. t.*), which is, at the same time, a supporting membrane for a stratum of peculiar cells which line the cavity. These are extremely long pear-shaped cells which are attached to the basement membrane by their narrow ends. They have the appearance of loosely adhering cells, sometimes looking like contracted Infusoria, attached by narrow stalks and protruding swollen sac-like portions into the lumen of the gland (fig. 30, *Gl. c.*).

The cells themselves are of all sizes, and vary from ordinary columnar epithelial cells to the elongated pear-shaped kind. There is no doubt that all the cells are of one category, and the differences observed are merely those of growth. In all cases the nuclei, which are elliptical in shape, are to be found near the bases of the cells. The cells are well filled with protoplasm and crowded with brownish yellow granules. In the sections so far examined the lumen of the gland has contained numerous cell remains, and it is evident that dehiscence of the whole cell, or at least part, takes place when filled with the brown granules.

The function of this gland is at present problematical, and I do not know on what evidence the term poison gland, as applied to the homologous structure in the Toxiglossa, has been given. It could hardly function as a poison gland in the whelk, opening, as it does, so far back. It is in all probability a digestive gland, but it might function as an "antiseptic."

The Salivary Glands possess an extremely compact structure. They become brittle in preserved specimens, and are most difficult to cut when embedded in paraffin.

Sections show that after the salivary ducts break up in the gland, the branches dividing into finer tubules in their turn soon end through complete occlusion of their cavities. Sections of the ducts with their columnar cells bearing cilia (fig. 26, *Sal. d.*) are met at irregular intervals, but the greater part of the tissue is composed of groups of large intensely vacuolated cells (fig. 26, *S. gl. c.*). These large cells become continuous with the epithelium of the ducts, but, unlike the gastric gland cells, they are so large that the cavity of the ductule soon ceases to exist when the walls are formed of them. In most of the cells a trace of protoplasmic contents at least remains, and there is a distinct nucleus. The rest of the cell is either one large vacuole with colourless non-staining contents, or is filled with bodies of irregular shape and very variable size, which stain intensely with eosin (fig. 26, *S. gl. c.'*).

In some gastropods the secretion of the salivary glands contains a large amount of free sulphuric acid, which is supposed to aid in the boring of calcareous shells. No marked acid reaction could be obtained with the whelk secretion. Griffiths finds that the gland has the same function as that of *Patella*, and contains a ferment capable of transforming starch into glucose.

The Oesophagus.—The section figured has been cut not far from the caecum (Pl. III, fig 25). It has already been mentioned that longitudinal ridges run along the lumen of the oesophagus. These can often be seen from the exterior, but *not* because the external surface is thrown into folds. It is only the internal layers that are folded, so that as a result the walls are alternately thick and thin. There is no external epithelial layer bounding the alimentary canal, for it runs through a haemocoele and not a true body cavity bounded by an endothelial layer. One finds, therefore, most externally, an attenuated connective tissue layer (fig. 25, *Oe. con.*). This gives place to compact dense connective tissue, through which run many muscle fibres (fig. 25, *Oe. con.'*). Externally, the circular or transverse muscle fibres predominate, internally one finds longitudinal fibres, and this layer is particularly thick and forms the main substance of the folds. The connective tissue sheath is divided, therefore, into two distinct layers by reason of the muscles which run through it. The inner layer with the longitudinal muscles varies in thickness according as to whether it is under a groove or a fold, and forms the support for the epithelium which lines the gut.

The Epithelium is composed of regular columnar epithelial cells, the height of which is about twelve or more times the thickness. There are three kinds evident, viz.:—(1) Ciliated cells, (2) Eosinophilous cells, and (3) Gland cells, and their frequency is in the order given above, the gland cells being least numerous.

The ciliated cells are very narrow basally, but increase in thickness towards the lumen, and their surfaces form a distinct unbroken plane. They are typical ciliated cells and show very distinctly the double row of desmochondria at the base of the cilia, and the connecting fibres in the cytoplasm.

Between these cells occur the eosinophilous cells in great numbers. They are more common here than anywhere else, and are crowded with small granules which show a most marked avidity for eosin. The gland cells stand out very distinctly in methyl-blue-eosin stained preparations, for their contents appear light blue, whilst the epithelium generally is a dense red, a granular red!

They do not occur in very great numbers. In some sections the lumen of the oesophagus is filled here with the blue stained contents of these gland cells and the red stained extruded cells. Eosinophilous granules also abound in the secretion.

The Caecum.—The caecum differs from the part just described in having the simple folds of epithelium and connective tissue thrown into most complex secondary folds. Thus the lumen is split up and reduced in size, and the connective tissue is reduced to a thin layer between the folds of epithelium.

Another important and obvious distinction is that the eosinophilous cells have become much reduced in number, and hence the lining epithelium has almost lost the granular densely stained appearance. A few scattered gland cells are to be found. What the function of this caecum may be it is difficult to say, for the walls are not in the least like the walls of a gland, and gland cells are reduced in number.

The Stomach.—In structure the wall of the stomach does not differ essentially from the rest of the alimentary canal. The cavity is lined by a layer of columnar ciliated epithelial cells (hexagonal in transverse section), which are perhaps not so long nor so slender as the cells of the rectum, but resemble them closely. Amongst these cells are scattered eosinophilous cells of the same character as those found elsewhere in the walls of the gut. Gland cells occur but rarely. The nuclei of the epithelial cells are to be found nearer to the basal membrane than those of the cells of the remaining parts of the digestive tract. Underlying the epithelium is a thin but distinct basal membrane, and below this a layer of connective tissue with muscle fibres.

Numerous large blood spaces occur in the connective tissue, so that it may practically be said that the stomach lies in a blood cavity.

The conspicuous grooves, which have already been referred to as occurring on the inner surface of the stomach, are produced by variations in height of the epithelial cells. In this respect the epithelium agrees with the same layer in the stomach of the lamellibranch *Pecten*.

The Digestive Gland.—This large gland has been known as the liver, the Hepatopancreas, and the Gastric Gland. It is now regarded as a "pancreas," but with additional functions, such as storing pigment and fat. The term liver should certainly be abolished and replaced by the name "digestive gland."

The gland is tubular, and is formed by repeated division of the ducts which open from the stomach. These numerous branches ramify still further, and eventually end blindly as caeca. The gland, like that of *Pecten*, is composed almost entirely of these caeca and ductules, and the connective tissue which encloses each ductule and caecum, and is therefore to be seen between them, is reduced to a minimum. There are numerous blood lacunae penetrating between the caeca.

The appearance of stained sections is very characteristic, for almost all the gland cells are crowded with large, oily-looking granules, which stain vividly with eosin (fig. 29, *Dg. gr.*). They are so numerous, in fact, that details of cell structure are almost entirely obscured. Commencing from the opening of a ductule into the stomach, and passing towards the blind end of one of its branches, the following changes are to be noticed in the character of the cells. The walls are at first made up of ciliated columnar cells (fig. 29, *Dg. c.′*), which resemble those of the stomach. The protoplasm is distinctly seen here, since there is little or no secreted or absorbed substance. These cells are gradually replaced by more and more vacuolated ones (fig. 29, *Dg. c.″*), containing the intensely staining bodies. Cilia disappear, and finally the typical broad cells almost meet in the centre, so that the cavity becomes very narrow, almost occluded, as the end of a caecum is reached.

There are usually said to be three kinds of cells present in the digestive gland of molluscs—ferment cells, granular cells (liver cells), and lime cells. It is extremely difficult to make out these different types in the whelk. Very occasionally cells are met with which are possibly lime cells, but most cells are alike in containing the oily or fatty bodies already referred to. Whether it is really possible to draw a distinction between ferment cells and granular cells is very doubtful. It is probable that both are merely stages in the life of the same cell.

Intestine.—The intestine differs hardly at all in structure from the oesophagus. There is the same layer of very tall and narrow epithelial cells, with long cilia. Gland cells, however, are far more numerous. The eosinophilous cells are present in considerable numbers as before. The lumen contains large quantities of the granules from the latter cells, and considerable numbers of extruded cells or parts of cells.

THE ODONTOPHORE.

The complex odontophore of the whelk was examined by Geddes in 1878. He does not describe the structures in detail, but gives figures of some dissections.

In order to expose this organ, the proboscis should be removed and pinned down with the dorsal surface uppermost. If a cut is made down the middle line and the flaps folded back, the whole apparatus lies somewhat as figured in Pl. III, fig. 19, the oesophagus resting on the odontophore.

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Now the odontophore consists essentially of a band (the radula), to which are attached a large number of muscles. This band is fixed, pulley-like, on a grooved support, which we shall call the odontophoral cartilage. The whole structure is bound together by two delicate sheets of transverse muscle fibres. One of these will be seen immediately the oesophagus is removed, and lies dorsally, forming a roof over the radula and cartilage (fig. 19, *d.m.s.*). Two dorsal protractor muscles (fig. 19, *d. pr. m.*) run from the anterior end of the proboscis walls to the odontophore. In addition to these, the walls of the buccal cavity are muscular, and there are two delicate ventral protractor muscles (fig. 18, *v. pr. m.*). It seems probable that protrusion of the odontophore (it can be brought up to the mouth opening), is aided by blood pressure, in addition to muscle action.

A conspicuous central dorsal muscle (figs. 19 and 16, *C.d.m.*), which is attached to the extremity of the radula (dorsally), extends back over a large number of other muscles, all of a faint red tint, to become attached to the floor of the proboscis. At the sides of these muscles are two peculiar straps, consisting of a connective tissue matrix with numerous muscle fibres (figs. 16, 18, 19, 20, *L.t.b.*). These are extremely important structures, and run back a considerable distance, to branch finally and become attached to the floor of the proboscis. They will be termed the *Lateral odontophoral bands.* These bands form the meeting place at their anterior extremities for a number of dorsal and ventral muscles and the odontophoral cartilage. Thus many of the muscles of the radula are not attached to the walls of the proboscis directly, but to two lateral musculo-connective tissue bands. Neither Geddes nor Oswald have figured this muscle connection with the lateral bands correctly.

The odontophoral cartilage is formed of two long band-like lateral cartilages, which are much thicker at their anterior ends and somewhat **L**-shaped in section. They fuse ventrally at their anterior ends, and thus by reason of their shape form the walls of a gutter or groove open dorsally (figs. 20, 18 and 23). In addition, they are united posteriorly by the sheet of transverse muscle fibres, the companion structure to the dorsal sheet already noticed (fig. 18, *V.e.m.*).

Upon this odontophoral cartilage lies the radula. There is usually about 20 mm. of it on the dorsal surface, and 10 mm. on the ventral.

The muscles of the odontophore may be divided into:—

I. Muscles attached to radula, (*a*) dorsally, and (*b*) ventrally;
II. Muscles attached to odontophoral cartilage;

or

I. Protractors, (*a*) of Pharynx, and (*b*) of Radula and Cartilage.
II. Retractors, (*a*) dorsal, and (*b*) ventral.

The protractors of the Pharynx consist of two muscles which run dorsally from the anterior end of the proboscis to the posterior end of the pharynx. By contraction of these muscles the pharynx can be moved forward.

The protractors of the Odontophore have already been referred to. They are first a pair of muscles which run from the walls of the proboscis to the sides of the odontophore, really to the lateral "cartilages" of the odontophore, and a pair which are situated ventrally and anteriorly (figs. 18, 21, *V. pr. m.*). These are also inserted in the odontophoral cartilages. In addition to these might be included the muscles of the buccal cavity walls, which are attached to the radular sheath. The action of all these muscles is to pull forward the radular apparatus.

The Retractor muscles are much more complicated, and are at first somewhat difficult to follow. There are two series of these muscles, dorsal and ventral, lying above and below the odontophoral cartilage respectively. The dorsal retractors are much more numerous, and larger than the ventral, and, as will be seen later, this is to be correlated with the movements of the radula and the arrangement of teeth on the same.

The first retractor to be observed is the most dorsal unpaired median band (fig. 16, *C.d.m.*), which is attached to the end of the radular sac, and after running back some distance is inserted into the walls of the proboscis.

Before referring to the other dorsal retractors attached to the radula, mention must be made of two curious muscles which run from the end of the radular sac, at the point of insertion of the central dorsal muscle, to the two cartilages (fig. 16, *c.c.*). They are thus fixed to two apparently unstable points. The action of these dorsal occlusor muscles and the median dorsal muscle is interesting, for the contraction of the former will bring the two cartilages together, closing the gutter and preventing the radula from slipping up over the sides, whilst the contraction of the median muscle will pull back the radular sheath and even the pharynx.

There still remains a large number of retractor muscles attached to the dorsal portion of the radula. Of these, two on each side arise from the anterior ends of the *lateral odontophoral bands* (or the posterior ends of the odontophoral cartilages), and are inserted laterally to the radular sheath (fig. 16, *l.r.r.′*, *l.r.r.″*). The others all arise on the floor of the proboscis wall some distance posteriorly. They comprise (1) the median muscle lying under the centre dorsal muscle (fig. 16, *c.d.m. inf.*), (2) the paired muscles (fig. 16, *r.′*, *r.″*), and (3) the paired muscles (fig. 16, *V. r.*).

Altogether, there are four or five pairs of muscles running together in this way, and all are attached laterally and ventrally to the radular sheath some distance forwards.

The Ventral Retractors are much inferior in strength and number to the dorsal muscles. Like the latter, they are attached both to the floor of the proboscis sheath and to the anterior ends of the lateral odontophoral bands. In fig. 18, the ventral muscles are supposed to be seen *through* the odontophoral cartilage, all the dorsal muscles and dorsal part of the radula having been removed. It will be seen that on each side there is a bi- or tri-partite muscle, the lateral ventral retractor, which runs from the lateral tongue band, and is attached in front to the sides of the radula (figs. 17 and 18, *v.v.m.*). In addition to these there are two median ventral muscles (fig. 17, *m.v.r.*), which lie in close contact with the ventral sheath of circular-muscle fibres (fig. 18, *v.e.m*), and then run back to be inserted in the same region as the dorsal retractors, the floor of the proboscis.

In regard to the mode of action of the apparatus, Huxley came to the conclusion that the "cartilages" which support the radula were perfectly passive and that the radula was pulled backwards and forwards, as a strap over a pulley or a polished surface, so that it scraped the object like a rasp or file. This was the result of observations on some living gastropoda. Geddes held the opposite view, a view formerly hinted at by Cuvier, to the effect that the action of the radula was due to the muscles pulling the whole tongue up and down.

My observations lead me to support Oswald, who asserted that both these movements played a part; but those described by Huxley seem, at the same time, to be the most important.

The mere fact of the attachment of the muscles to the odontophoral cartilage shows that this is not altogether passive. Again, the effect of the dorsal retractors pulling on the radula would be to cause the cartilage to move dorsally, but this would only happen to any extent *if the radula were fixed securely against the cartilage.* Most of the muscles, however, are inserted in such a way that much power would be lost if they were only moving the cartilages; in fact, it would be difficult to account for their positions. Furthermore, there can be little play for the cartilage in the securely bound up odontophoral mass. One would conclude, therefore, from the anatomy alone that the rasping movements of the radula over the cartilage were the most important, whilst at the same time this structure was not altogether passive. Any doubt, however, was dispelled by one of the whelks actually attacking the finger of the author and rasping away for a few seconds on the skin. The median teeth of the radula are so placed that at the point of reflection of the latter over the tongue they point upwards. It is not easy to see how they could be of much use in boring if they remained in this position. One sees here perfectly clearly the reason for the powerful dorsal musculature. When the radula is pulled by the ventral muscles the teeth slip backwards over the object with little friction since they are pointing the other way, but when the dorsal muscles contract, the teeth are directed against the object and much resistance has to be overcome.

The action of the radula can, as a matter of fact, be easily demonstrated in whelks that have been narcotised. If the proboscis is removed from one of these animals and squeezed between the finger and thumb gently, the odontophore will be protruded, and the application of a little pressure to a spot which can be found by trial will cause the radula to move backwards and forwards over the cartilage.

The action of the muscles, so far as I have been able to determine, is as follows:—By contraction of the dorsal retractors, the radula is pulled so that the teeth rasp the object. At the same time the occlusor muscles come into action and hold the sides of the cartilage together, so as to maintain the groove. I find no evidence whatever to show that by contraction of these muscles the radula comes to lie *on* the sides of the cartilages as stated by Oswald. On the other hand, the position of the lateral teeth show the necessity of the groove, for as they pass from the plane ventral surface of the tongue to the gutter-like dorsal surface, they "bite" inwards, and so the net result is a tri-partite attack on the object.

The ventral muscles now come into play and draw the radula easily backwards. There would be no point in the arrangement of the lateral teeth whereby they can rotate inwards and act in a most efficient manner, if movements of the radula over the cartilage were not the usual method of attack.

The radular teeth (fig. 14) are, in accordance with the Rachiglossan formula, three in number, one median and two lateral. The median teeth, known as the central or rachidian, are placed with their anterior margins exactly transversely across the radula and possess a number of similar denticles which will be referred to again below. A thickened yellow band marks the position of the tooth itself. All the teeth are fused to the chitinous radular band. The lateral teeth are set obliquely, and almost alternate in position with the centrals. The inner end of a lateral tooth lies almost opposite the base of a central tooth, whilst its outer end is opposite the next posterior central. Furthermore, the lateral teeth are not exactly on the same plane as the centrals, and as the radula passes into the lingual groove they are caused to rotate until their denticles are directed towards the middle line. The denticles of the lateral teeth are much larger than those of the centrals and vary in shape, the outermost being by far the most powerful.

On the whole, the radular teeth are very regular and characteristic in the gastropoda, and are commonly used for purposes of classification. The teeth of *Buccinum undatum*, however, make a very striking exception to this rule, since the number of denticles on both the central and lateral teeth varies in an extraordinary manner, giving an excellent example of meristic variation. The three first radulas taken from Port Erin whelks varied in number of denticles as follows:—

Lateral teeth:—4. 4. 4.
Central teeth:—6. 7. 8.

Bateson records that from 27 specimens the variations were as follows:—

Lateral	- 4.	4.	4.	4.	4.	3 & 4.	3 & 4.	4 & 5.
Central	- 5.	6.	7.	6-8.	9.	6.	7.	8.
Cases	- 8.	12.	2.	1.	1.	1.	1.	1.

It will be seen that even the bilateral symmetry may be destroyed, the opposite lateral teeth having a different number of denticles. Furthermore, though in almost all cases the teeth are the same on the one radula, there have been observed specimens where the number of denticles on the anterior central teeth was less than the number at the posterior end of the radula.

Histology of Odontophoral Cartilage and Radular Muscles.

The cartilage of the molluscan radula (fig. 23) represents probably the earliest development of cartilage in the animal kingdom, and by reason of its distinctness and ease of preparation it is a good example for the study of invertebrate cartilage.

The most external bounding layer is a delicate connective tissue, which encloses the cartilage cells. The cartilage itself has the appearance of a plant tissue. It seems at first sight to be composed of very large irregular cells with small round nuclei and extremely definite and deeply staining cell walls. The cells (fig. 22, *Cart.*) are 18μ in diameter, turgid with fluid, and contain a delicate fibrillar protoplasm which does not stain intensely owing to its attenuated state. The nuclei (fig. 22, *Nuc.*), which are perfectly spherical, are only 4μ in diameter. A nucleolus is usually present and many small granules of chromatin. The apparent cell walls are in reality the intercellular matrix formed by the cells. This is small in quantity and is formed in such a regular manner that it has the appearance of cell walls rather than a matrix. This pseudo-wall, if followed, often appears to be continuous round two or more cells (fig. 23). The more cells round which it is continued the thicker it is, and hence in places there appear to be septa running into the mass and forming at the same time the bounding walls of contiguous cells. The cartilage of the molluscan odontophore has often been referred to by writers, but has apparently never been examined in any detail. It has been compared to cellular or vesicular connective tissue, or called cartilage without micro-chemical tests. Josef Schaffer seems to be the only worker who has examined it in any detail, but his paper has appeared only as a resumé without illustrations. The main conclusion is that the "cartilages" vary towards or away from a distinctly real cartilage, and that the development of a low or high type of cartilage is to a certain extent independent of the phyletic position of the animal. The Buccinum cartilage is most certainly a real cartilage. Micro-chemically it reacts in a slight but distinct manner to thionin, giving the characteristic muco stain. It is therefore to a certain extent a muco-cartilage.

The odontophoral cartilage is not entirely composed of cartilage tissue, as the dorsal portions of the walls of the groove (fig. 23, *Ling. con.*) are of a very compact connective tissue, composed of a matrix resembling the intercellular matrix of the cartilage area, but penetrated by a large number of muscle fibres.

The muscle fibres (fig. 22) of the radula are also striking in structure. They are red in colour, and contain much sarcoplasm. Each muscle cell is a spindle-shaped structure of considerable length. In section it is circular, and the diameter of these fibres is considerable, 15μ. The sarcostyles (fig. 22, *Mus. col.*), or actual contractile elements, are arranged round the periphery of the muscle cell, and the large remaining central space is occupied by the sarcoplasm. Thus in any transverse sections of these muscles, the fibres are represented by circular discs, the centre of which is granular protoplasm, whilst the periphery is either a dark staining circle or this may have been resolved by the stain into a number of segments—each a transverse section of a sarcostyle. The sarcostyles do not run quite longitudinally along the muscle fibre or cell, but wind spirally round it. Thus a delicate double striation is present, but cannot be seen unless one focusses completely through a fibre.

The Radula, with its teeth, is being formed continually by the cells of the radular sac in which its posterior dorsal extremity lies, and as the teeth of the anterior region are broken away in action, new regions move forwards and take the place of the old. The radular sac is a delicate cellular caecum continuous anteriorly with the epithelium of the pharynx. It ends blindly at the point to which is attached the centro-dorsal retractor muscle (figs. 19 and 16, *C.d.m.*). The cells forming the wall of the blind end are known as **Odontoblasts.** These secrete the teeth and the basement membrane which bears them. In *Buccinum* the odontoblasts are very numerous and exceedingly narrow.

Their length, however, varies in a regular manner according to position, so that cushions of cells are formed. Transverse and longitudinal sections are both required to elucidate the structure of the radula sac. The transverse section (Text-fig. 5, A) gives the key to the structure, for it is seen that the radula near and up to the point of origin is so fixed that the lateral portions with the lateral teeth are turned up at right angles to the median area. The cells of the radula sac are longest at the extreme end, where the radula is formed. As a matter of fact, the external surface of the sac at this point forms a perfect circle in transverse sections (Text-fig. 5).

The cells of the lateral and basal walls of this circular sheath are of medium length. The cells of the dorsal wall are of extraordinary size and extend down into the cavity, forming a deep ridge, which extends for some distance from the blind end. This odontoblast ridge lies, of course, in the gutter formed by the radula. Thus one sees that the cells of the lateral and ventral walls are directed towards the basal ventral plate of the radula, whilst the dorsal ridge cells are directed towards the teeth, both median and lateral.

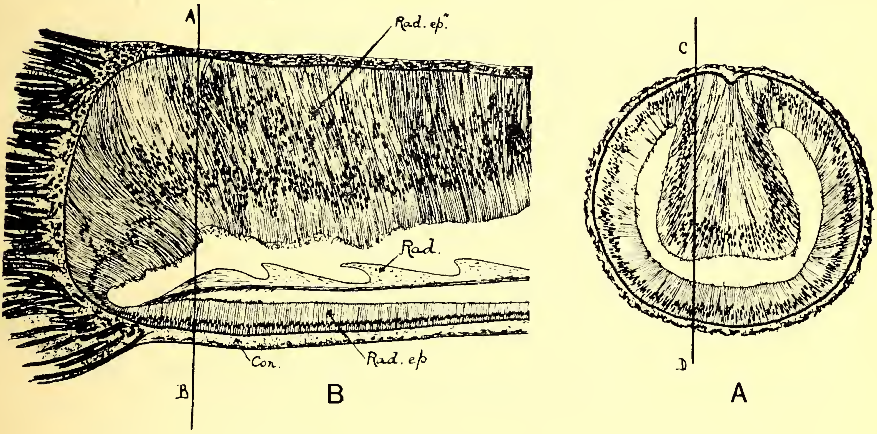


Fig. 5.

As one passes towards the pharynx the depth of all the cells decreases, the dorsal ridge passes away and gradually the ordinary epithelial type is reached continuous with the epithelium of the pharynx.

The nuclei of the odontoblast cells are oval, more or less elongated and contain numerous small granules. The most characteristic feature of the odontoblast, however, is the free end of the cell. The secretion leaves it in the form of numerous cilia-like processes which, in a Mallory-stained section, are at first red in colour. They soon become blue or purple as one passes from the cell, and then lose their individuality in a homogeneous blue stained mass of chitin, which forms the basis of the ribbon and teeth. The fibrous ground can be detected everywhere in young teeth stained with Mallory's connective-tissue stain. In the whelk the teeth are absolutely continuous with the basal membrane of the radula, and it is almost impossible to make out any line of junction or to say which cells have participated only in the fabrication of the teeth. The ventral and lateral cells of the blind end have, however, most certainly played the greater part in the formation of the ribbon membrane and the dorsal cells, the teeth.

One point, however, of great importance is that the ventral and lateral cells are still connected with the radula by the cilia-like tags some considerable distance away from the blind end, and the same applies to the dorsal cells. This probably indicates that when the point of the radular membrane (in this attached region) was at the extreme posterior end of the sac, the cells below it were there too. In other words, just as the radula is secreted and pushed forwards, so do the odontoblasts move forwards with it, and new ones are formed at the blind end of the sac. There are at present two views on this subject. One is that the odontoblasts, very many of which secrete one tooth, remain functional after that tooth has been formed and go on secreting the next, and so on. The other view is that the odontoblasts have performed all they are capable of in secreting one tooth and that they pass forwards to be replaced by new cells. Obviously they have to become much smaller. The sections of the whelk's radular sac favour, then, the latter theory. The very young teeth are probably entirely formed of chitin. Certainly there is no differentiation given by stains. They very soon become hardened by the deposit of mineral salts, but they differ, as do all other Odontophora, very considerably from the Docoglossa, where the teeth contain a remarkably large proportion of silica. According to Miss Sollas, the composition of the teeth of *Littorina* is :—Ash 3·7 per cent. containing iron, calcium and magnesium, while the rest is organic matter, the basis being chitin. In the Docoglossa, on the other hand, the mineral matter may amount to as much as 27 per cent. (*Patella vulgata*)—silica hydrate being present in large quantity.

Outside the odontoblast layer is a very compact connective tissue layer, and it is in this connective tissue that the muscles, which are attached to the radula, terminate. The muscles are of the type described above. Their terminations can be followed very beautifully indeed in sections stained in Mallory, for the muscles are bright red, and the connective tissue bright blue.

BLOOD VASCULAR SYSTEM.

The vascular system of some molluscs has attained a high degree of complexity. This is especially the case with the Cephalopoda and some of the Prosobranchiata, and the whelk amongst the latter may be taken as showing a good example of a well developed molluscan blood system. It seems that, at the present day, in many zoology courses there is a tendency to pay little attention to the vascular system of the molluscs. The cephalopods receive perhaps adequate treatment, and possibly the snail (*Helix*) has some attention.

In most cases, however, beyond the heart and large vessels leaving it, very little is investigated. Now in the whelk it is quite easy to demonstrate all the more important facts in connection with the circulation, and if a little care is used in injecting, there is no reason why this method should not be adopted in the ordinary laboratory classes for senior students. Very few complete accounts have been given of prosobranch blood systems, and it is hoped that this description will serve as an aid in the study of an excellent and exceedingly common type.

A great part of both the venous and arterial systems can be made out from the surface, without any dissection. All the vessels shown in figure 35 on Plate V can be seen, with the exception of the dotted trunks which run in the foot. This means that a cold injection mass may be used, without troubling to employ any of the complicated and unsuccessful mixtures which have been invented in order to attain solidification or coagulation in the vessels.

Directions for Injection.

For students' purposes, two very simple injecting masses will suffice:—

1.—*Cold Injecting Mass.*—Use one of the familiar collapsible tubes of artists' oil colours. Chrome-yellow is a convenient tint. Squeeze this into a dish and dilute with turpentine, stirring until a slightly thick but uniform mixture is produced.

2.—*Hot Injecting Mass,* for studying the deeper vessels.—Melt down one or two pieces of ordinary table jelly in an evaporating dish, adding water if necessary. Add to this some carmine, rubbed down with a small quantity of water in a mortar and stir until a uniform mixture is obtained which will solidify on cooling.

It is absolutely essential that the whelks to be injected be dead, and further that they have died in a thoroughly lax uncontracted state. The best means is to allow the whelks to expand in a small quantity of sea-water and then add carefully a few drops of a 2 per cent. solution of cocaine in 90 per cent. spirit; and continue adding gradually a little of the cocaine solution. It will be found that three days are necessary before the animals become irresponsive to stimuli. By that time the water is probably in very bad condition, but the whelks will not be seriously affected by this, so far as injection is concerned. The shell should now be removed piece by piece with a pair of bone forceps, and great care must be taken that the soft tissues are not damaged. The columellar muscle should be detached from the shell with a scalpel.

On the external surface the position of the mucous gland and the gill should be made out. Those two organs of the pallial complex with the osphradium can be seen through the mantle. The pericardium has been already seen, lying at the side, and under, the kidney.

Injections can be made from three places.

1.—The syringe should be inserted into the efferent branchial artery, with the point towards the heart. This vessel can be seen quite easily, forming the ventral boundary of the gill. If the paint mixture is used, a very clear view will be obtained of the branchial vessels, the vessels of the mucous gland, and the reno-mucous vessel (fig. 35, *Mu. gl.*, *Br. v.*, *R. sin.*). The auricle will be filled, and probably the efferent renal vessels (fig. 35, *Ren. eff.*).

2.—The point of the syringe should be plunged into the foot, so that it reaches somewhere in the space in which the alimentary canal and poison gland lie. This injection will fill the extensive venous sinus, and then the veins bringing blood back from all parts to the renal organ. They can be seen by removing the auricle and ventricle from the pericardium, and by slitting the renal organ along its left ventral margin and thus laying bare its internal surface.

3.—The syringe should be inserted into the aorta (figs. 35, 36, *Ao.*) at the point where it leaves the ventricle. This injection should be performed with the hot jelly, but it is the most difficult one and often fails. The arterial system is injected by this means.

THE HEART.

Buccinum possesses (as do all Monotocardia so far as is known, except *Cypraea*) only one auricle (the left one of the lower Gastropods).

The auricle and ventricle lie in the pericardial cavity, which is bounded by the renal organ and the digestive gland, the auricle being anterior.

The auricle is a very thin-walled sac, capable of considerable extension. It is somewhat like a pear in shape with the pointed end situated ventrally, and into this end opens the efferent branchial vessel.

There are two other openings into the auricle which are situated at the dorsal end. One of these at the anterior edge of the pericardium is the opening of the nephridio-cardiac vein, the other, which is situated on the posterior surface, is the opening into the ventricle. The latter, the auriculo-ventricular passage, is guarded by a valve so that blood is prevented from passing backwards from ventricle to auricle.

It will be noticed that the nephridio-cardiac vein opens directly into the auricle and not into the efferent branchial vessel. It is often somewhat difficult, however, to determine whether the vein enters near the opening of the branchial vessel and lies along the anterior margin, or whether it enters more dorsally.

The ventricle is very different in appearance from the auricle. It is roughly spherical, with very thick spongy walls, but the cavity is so much reduced by crossing muscles that the consistency of the whole is very like that of a sponge. Injections into the ventricle hardly ever succeed, because most of the injecting fluid oozes out at the point of insertion of the syringe.

ARTERIAL SYSTEM.

From the ventral pole of the ventricle a single vessel arises, the Aorta (figs. 35, 36, *Ao.*). This is of very short length for it divides almost immediately into two branches, the anterior or Cephalic aorta (figs. 35, 36, *A.c.*), and the posterior or Visceral Aorta (figs. 35, 36, *A. vis.*). The Anterior Aorta gives off immediately a small vessel (fig. 36, *a.′*) which sends branches to the oesophagus and the columellar part of the spire and then plunges below the floor of the mantle cavity into the large sinus in which lie the oesophagus, salivary glands and proboscis. The aorta lies at first at the left side but soon crosses over the oesophagus and runs under the salivary glands. Just after entering the body cavity, it gives off a vessel on the right side which passes to the columellar muscle (fig. 36, *A. col.*) and branches on its surface. The next large vessel leaves the under surface of the Cephalic Aorta (fig. 36, *A. pall.*) and passes through the muscles to reach the surface of the mantle. It divides into two main trunks, of which the ventral one reaches the surface on the under side of the animal, and the dorsal vessel just below the osphradium (fig. 35, A. pall.′).

This dorsal pallial artery supplies the siphon, and runs round the edge of the mantle, giving off branches on both sides. Very small vessels leave the aorta at intervals and pass to the alimentary canal. The next two vessels which arise are asymmetrically placed. They leave the aorta laterally, but the left one is somewhat posteriorly situated. These vessels (fig. 36, *A. cut.*), after passing out laterally, run up the walls of the body cavity and break up into small vessels innervating the roof (the floor of the mantle cavity). The vessel on the right side, however, gives off an additional branch (fig. 36, *A. cut.'*), which bores into the wall and passes to the tissues below the ovary and rectum.

The Cephalic Aorta passes forwards until the Nerve Collar is reached and then breaks up at one point into several vessels. The point where this division takes place is hidden by the salivary glands and by connective tissue.

One large vessel runs down at right angles to the course of the Cephalic Artery. This is the Pedal Artery (figs. 36 and 35, *A. ped.*). After a short course, it divides into two branches which make their way into the foot, branch again (each in a similar way) and supply the musculature. These blood vessels are of considerable size. Here they branch, but most of their small branches, which form almost a capillary network, are not shown in the figures. It is by means of this network, and the forcible action of the blood, that the great expansion of the foot is effected.

Returning to the nerve collar region, it will be seen that another large vessel runs dorsally, also at right angles to the aorta. This artery, the Buccal (fig. 36, *A. buc.*), goes forward at the side of the oesophagus, and after giving off two small vessels to the proboscis, enters the latter with the alimentary canal. Here it breaks up into a complicated series of branches supplying the odontophore and the muscles. Two other prominent vessels (fig. 36) arise at the nerve collar, one on either side of the aorta. They both pass toward the tentacles but before reaching them, small vessels leave dorsally to supply the tissues of the "head" (fig. 36).

The right tentacular artery gives off at its origin a large branch in the male, the penis artery (fig. 36, *A. pen.*).

The Visceral Aorta (figs. 35, 36, *A. vis.*) can be seen quite distinctly without injecting. It turns abruptly after leaving the ventricle and runs close to the surface across the intestine. Half-way across it gives off a branch (figs. 35, 36, *A. g.*) on the right side, which passes to the stomach and breaks up into numerous twigs upon its external surface. The main trunk plunges into the mass of the digestive gland, immediately after crossing the intestine, and runs right through, to appear again at the surface on the other side. It now remains at the surface, just below the epithelium, and lying upon the digestive gland a little ventral to the edge of the gonad; and in this position runs to the end of the visceral mass. Branches are given off at intervals which run out at right angles to supply both the gonad and the digestive gland (fig. 36, *A. go.*).

THE VENOUS SYSTEM.

The blood which is carried to all parts of the body by the arteries, collects in lacunae and is brought back to certain more extensive central sinuses. Many of the paths which are taken are, however, so narrow and so well-marked that there almost appears to be a definite system of capillaries connecting up the arteries and veins. These channels are mere excavations, which may be lined by a pseudo-epithelium due to modified cells. The centre of the venous sinus system is the region on the surface of the digestive gland at the back of the pericardium and underneath the renal organ (fig. 37). There is a large sinus—the largest in the body—underneath the pallial cavity (fig. 37), while an important vein runs along the right margin of the mucous gland (figs. 35 and 38, *R. Sin.*). These important regions may be named as follows:—The sinus in the anterior perivisceral cavity will be termed the *Cephalic Sinus* (fig. 37, *Ceph. Sin.*), as it collects blood from the head and foot. The branched system, situated at the back of the pericardium, and under the renal organ is the *Renal Sinus System* (fig. 37), while the long vessel-like sinus which extends from the right side of the renal organ to the anterior end of the mucous gland is the *Reno-Mucous vessel* (figs. 38 and 35, *R. sin.*).

Blood returning from the viscera (digestive gland and gonad) passes by means of superficial vessels (fig. 35) to a sinus which extends along the columellar surface of the visceral mass. This sinus stretches as far as the region of the pericardium and there becomes connected with the renal sinus system (fig. 37), by means of which the blood reaches the renal organ.

Blood returning from the head, proboscis, and foot flows into the great cephalic sinus (fig. 37, *Ceph. Sin.*), and from here two paths may be taken. These leave the perivisceral cavity at the posterior extremity of the mantle cavity, and are close together. One ascends and reaches the renal organ directly. It passes along its left side, internally, so that it cannot be seen unless the renal organ is turned back as in figure 37. The other receives blood from the oviduct and rectum (figs. 37, 38) and enters the Renal Sinus System and so to the renal organ.

THE RENAL BLOOD VESSELS.

It will be convenient now to discuss separately the vessels in the renal organ. This organ forms a junction system of small vessels which is interpolated into the venous system. The blood which enters it may leave by two paths, one of which goes to the heart directly and the other by way of the gills.

The blood vessels of the renal organ of *Buccinum* are remarkably organised. This, however, is probably general in the higher prosobranchiates. For purposes of comparison it will be advisable to use the renal organ of the Lamellibranch *Pecten,* which has been carefully worked out. In this genus the renal organ is a tube, the inner wall of which is thrown into folds in order to increase the area of renal epithelium. Between these folds are blood cavities. The blood leaves the renal organ by one path only and then passes to the gills.

In *Buccinum,* the renal organ is a similar tube, but it is crescentic in section and the inner wall of the outer half only is thrown into folds. The folds are quite different from those in *Pecten* (see Renal Organ below) and the floor of the renal organ (the unfolded side) covers a large vessel of the Renal Sinus System (fig. 37). The folds of renal epithelium hang down into the lumen of the renal organ, and from them membranous extensions pass to the floor. Now, on the floor, we have the large vessel of the Renal Sinus System, and from it vessels arise which pass *through the lumen of the renal organ* to the folds of renal epithelium.

Thus a large quantity of blood enters the renal organ over the internal surface. This is a most curious position which a glance at the diagrammatic section (fig. 51, *A.*) will make clear.

This, however, is not the only path for blood entering the renal organ. We have already seen that a large vessel runs round the margin (fig. 37, *lam. v.*). From this vessel branches arise which run across in the plane of the outer surface and divide up close to this surface. The system of anastomosing channels is extremely complicated, and minute, and finally all is resolved into two outgoing paths. One of these is seen right on the surface when the renal organ is injected, and is shown in fig. 35. It consists of delicate vessels running almost at right angles to the left margin (fig. 35). These delicate vessels enter a large lymph-like gland, the nephridial gland, which extends along the side of the renal organ against the pericardium. It was supposed that the nephridial gland communicated *only* with the auricle and that blood passed to it by means of the nephridio-cardiac vein and *back again* by the same course. A detailed study of this point in the whelk has clearly shown that there is a direct path from the renal organ through the nephridial gland to the heart. The other path is more internal and is made up of another series of small vessels which open into the *reno mucous vessel* running along the right side of the renal organ (fig. 38). Thus there are two lines of communication bringing blood to the renal organ and two paths along which blood leaves.

Blood Circulation in Pallial Complex.

The blood from the " kidney " which pours into the reno-mucous vessel passes forwards into that part of the latter bounding the mucous gland. Blood from the rectal region and mantle also enters this vessel, and from it passes through the mucous gland to the afferent branchial vessel. The mucous gland is exceptionally well supplied with blood, as will be seen from figure 35. From the afferent branchial vessel a large number of filamental vessels arise which convey the blood through the gills to the efferent branchial vessel. The efferent branchial vessel collects some blood from the mantle which has passed through neither gills nor renal organ, but the quantity is small. Finally it enters the auricle.

To summarise:—

1. Blood passes from the ventricle to various parts of the system.

2. Blood is collected into sinuses and conducted to (*a*) Renal Organ, and (*b*) Gills.

3. The blood passes back to auricle through (*a*) Renal organ and gills, (*b*) Renal organ alone, (*c*) Gills alone, and (*d*) Mantle alone.

The largest quantity of blood passes through routes (*a*) and (*b*), and that passing by method (*d*) is almost negligible.

THE NERVOUS SYSTEM.

Once more we must emphasise the fact that we are dealing with an example of the most highly developed Prosobranchs. The Nervous System presents the twisted visceral loop characteristic of the Streptoneura, together with extreme concentration of the ganglia. So far as the description of the nervous system is concerned, constant reference has been made to the excellent work of Bouvier on the nervous system of the prosobranch gastropods. All the important details have been worked through again, however, and the figures differ in some minor details from those given in Bouvier's memoir.

Owing to the extreme concentration which has taken place, the nerve ganglia may be divided into two groups.

The anterior centres are situated in the cephalic region and surround the alimentary canal, forming a collar almost hidden by the salivary glands. The posterior centres lie just behind the pallial cavity in the region between that and the visceral mass. The two groups of ganglia are connected by the long visceral commissure (fig. 41, *vis. com.*). Dissection of the nervous system is a matter of some difficulty and is usually a stumbling block to some students. It is quite easy to find the nerve collar, but rather difficult to expose clearly the component parts owing to the presence of a tenacious fluffy connective tissue which obscures all.

The nerves and commissures passing into the body wall are also difficult to follow by reason of the toughness of their surroundings and their resemblance in colour to the tissues in which they are embedded.

It is best to dissect the nervous system in whelks that have been kept for a short time in alcohol. This hardens the muscle but brings out the nerves much more clearly. In addition, the action of a solution of oxalic acid is decidedly useful. It brings out the otocysts and clears up the muscular mass of the foot. In order to investigate the centres making up the nerve collar, it is best to cut through the cerebral commissure which lies above the oesophagus and then to dissect the alimentary canal carefully away. The ring of ganglia can be examined *from the inside,* and thus observed without requiring the removal of so much connective tissue.

The Anterior Centres are ten in number. They consist of the cerebral, pleural, pedal and buccal ganglia, which are paired and the supra- and sub-intestinal ganglia which have been drawn in, in the general concentration, until they have reached a position close to the pleural ganglia (fig. 42, *Sup. int.* and *Sub. int.*).

The Pedal Ganglia are the largest ganglia in the whelk and are situated most anteriorly. They are oval in shape and lie upon the floor of the perivisceral cavity, in close contact. Consequently there is no pedal commissure (fig. 42, *ped. g.*). In the female these ganglia are symmetrical, but owing to the origin of the large penis nerve from the right ganglion, in the male, they become asymmetrical (fig. 43). The pedal ganglia are connected to the cerebral and pleural ganglia on each side by two very short connectives (fig. 42, *c.p.*, *pl. p.*), a small space, the "triangle lateral," being left between the ganglia and their connectives (fig. 42, *tri. lat.*).

A large number of nerves arise from the anterior end of each pedal ganglion and run forwards together for a short distance to plunge into the muscular foot. These are the pedal nerves (figs. 41, 42, *ped. n.*) and they innervate the entire foot. Other smaller nerves leave the pedal ganglia on both the dorsal and ventral surfaces. According to Bouvier there are two such dorsal (fig. 42, *do.*) and three ventral nerves (fig. 42, *ve.*) from each ganglion. The former pass to the head region whilst the latter innervate both the foot in the immediate vicinity, and the floor of the anterior body cavity.

The penis nerves leave the right pedal ganglion at the posterior lateral corner (fig. 43, *P.*) and consist of two trunks, one of which is extremely large and follows the vas deferens inside the penis to form a network from which delicate branches innervate the muscles of the organ.

The Cerebral Ganglia will be seen somewhat out of their normal position if the dissection is conducted as described above, for after the severing of the commissure and the removal of the alimentary canal, they will be turned back as indicated in fig. 42, *c.*

They are somewhat irregular in shape and are connected with each other by a commissure which passes over the alimentary canal. Owing, however, to the folding of the gut and the almost vertical position of the oesophagus at this point, the cerebral commissure lies rather posteriorly to the gut. Both the oesophagus and branches of the anterior aorta are encircled by the collar formed by the cerebral ganglia, cerebral commissure, and pedal ganglia.

It will be noticed that the cerebral ganglia in the whelk are by no means the most anteriorly placed. They lie some little distance behind the pedal ganglia and almost directly above the pleural centres. This position, which may give rise to a little confusion at first, is due to the course taken by the oesophagus between the proboscis and the gland of Leiblein. The cerebral centres are joined by very short connectives to the pedal and pleural ganglia, and at this point it may be observed that there is a slight asymmetry in the relative position of the right and left ganglia. Two other small ganglia, the buccal (fig. 42, *bucc.*) are in close contact with the cerebral and are themselves connected by a long and delicate commissure passing in front of the alimentary canal.

Three nerves innervating the sense organs leave the external face of each cerebral ganglion. The largest of these is the tentacular nerve (fig. 42, *tent.*). It can be followed quite easily in the tentacles, and bends at right angles when above the ganglia to reach them. A few twigs are sent to the head region from this nerve before it finally penetrates the tentacle. The other two nerves pass directly, the one to the eye, and the other to the otocyst (fig. 42, *op. n.*, and *n. ot.*). The two otocysts are situated immediately below the anterior ends of the pedal ganglia and just imbedded in the muscular floor. They are very easily overlooked, even when one examines the exact place where they occur. They are about two millimetres apart and 0·5 mm. in diameter.

In addition to these sensory nerves, there are two other groups which have their origin in the cerebral ganglia, i.e., the nerves of the proboscis and of the cephalic integument. The former arise just anterior to the cerebral commissure and form a compact bundle on each side, ascending with the salivary ducts and running along with them towards the proboscis. They innervate that organ and also the proboscis sheath. The cerebral nerves of the proboscis enter into close relation (forming anastomoses) with certain nerves from the small buccal ganglia, and all pass together into the proboscis. The buccal nerves innervate the oesophagus and radular apparatus, the cerebral nerves on the other hand appear entirely concerned with the walls of the proboscis itself. There are two other nerves innervating the integument of the head region and these arise from the cerebro-pedal connectives (Text-fig. 6, *ceph. n.*). They eventually branch, sending numerous twigs to the region immediately posterior to the tentacles.

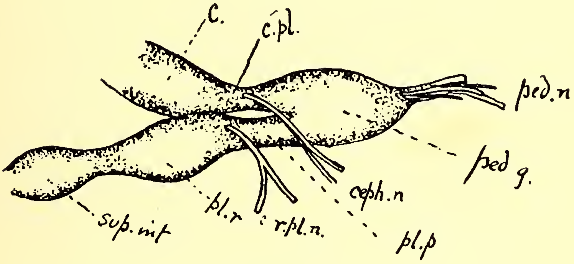


Fig. 6.

The Pleural Ganglia are asymmetrical owing to the positions taken by the supra- and sub-intestinal ganglia (fig. 42, *sup. int.* and *sub. int.*) in the general concentration of nerve centres. They are attached to the cerebral and pedal ganglia by short connectives, the cerebro-pleural (fig. 42, *c. pl.*) and the pleuro-pedal respectively (fig. 42, *pl. p.*). The pleural ganglia form part of another nerve collar owing to the position of the sub-intestinal ganglion. This, normally attached to the left pleural ganglion, is here in addition fused to the right pleural so that it comes to lie between the two.

The left pleural ganglion gives origin to the siphon nerves (fig. 42, *Siph. n.*), the columellar nerve, and several others which innervate the body wall (fig. 42). The two siphon nerves pass outwards along the floor of the perivisceral cavity until the body wall is reached. They plunge through this tough muscular wall and arrive at the siphonal region of the mantle. A number of branches are given off to the siphon, and certain fibres form important connections with the pallial nerve from the supra-intestinal ganglion, eventually taking part in an anastomosis in the mantle (fig. 41). A left *zygoneury* is thus formed (fig. 41, *zyg.*).

The columellar nerve leaves the ganglion posteriorly and crosses over the floor of the anterior cavity towards the right side. It is not a very large nerve and is easily overlooked. Eventually it reaches the columellar muscle.

The remaining nerves are small with the exception of one which arises on the pleuro-pedal connective, divides soon, and innervates the walls of the body cavity.

The right pleural ganglion has only one nerve of importance here, and this corresponds to the last nerve mentioned above, arising from the left pleural ganglion. It takes its origin on the pleuro-pedal connective (Text-fig. 6, *r. pl. n.*) and innervates the right lateral walls of the body cavity. The branches of this nerve are quite easily seen if the nerve collar *in situ* is pressed slightly over to the left side. The branches pass out directly to the right.

The Supra- and Sub-intestinal Ganglia. Three prominent nerves are easily seen crossing the floor of the anterior cavity and entering the wall on the right side. The most anterior of these is more delicate than the other two. All arise in the sub-intestinal ganglion (fig. 42, *sub. int.*). The two larger are the pallial nerves (figs. 41 and 42, *pall. n.*), and after plunging through the walls of the body cavity they reach and divide up on the mantle, the more anterior of the two forming an extensive network.

The branches of these pallial nerves of the right side come into contact with the branches of the left pallial nerves. This takes place in the mantle immediately above the pallial cavity. Thus a continuous network is formed running around the mantle edge.

A number of other small nerves (fig. 42) arise in the sub-intestinal ganglion and innervate the walls of the body cavity and the columellar muscle.

The largest nerve leaving the sub-intestinal ganglion arises from the left posterior corner. It is the Visceral Commissure itself (figs. 41 and 42, *Vis. com.*). This cord runs posteriorly almost in the middle line, in close contact with the floor of the body cavity, for some distance, and then passes underneath the most superficial muscle fibres. It is often very difficult to dissect out the visceral loop in the whelk, but if the specimens have been preserved in spirit, the track of the visceral commissure is visible as a delicate ridge on the floor of the body cavity running back from the point x in the figure.

The visceral ganglia are situated on the loop just posterior to the mantle cavity. They can be seen from the exterior, without any dissection, under the epithelium of the area between mantle, digestive gland and columellar muscle. The other part of the visceral loop connecting the visceral ganglia with the supra-intestinal ganglion is by no means easy to follow, for it lies under the superficial muscles of the left wall of the body cavity. It leaves the wall near the point of entrance of the two left pallial nerves (figs. 41 and 42, *pall n.″*), and runs along with them to the supra-intestinal ganglion. The three nerves have thus to cross over the alimentary canal and gland of Leiblein. Of the usual figure of eight formed by the visceral commissure, only the lower, posterior, loop is of any extent.

The two large left pallial nerves arise in the supra-intestinal ganglion, and passing over to the left side, plunge through the body wall. They are extremely close together at first, and form one thick band. On reaching the mantle they proceed to divide. The most anterior nerve innervates the osphradium. In addition to this, it gives rise to some twigs which, by means of their anastomosis with the siphonal nerve, set up the zygoneural connection already mentioned as existing on the left side. Both the anterior and posterior pallial nerves from the supra-intestinal ganglion take part in the innervation of the gills.

An important nerve arises from the sub-intestinal part of the commissure itself, just at the posterior end of the perivisceral cavity. It runs outwards, underneath the vas deferens in the male (fig. 41, *com. n.*) to the rectum and mucous gland.

The **Visceral Ganglia** are two in number. Of these the right is much larger than the left, and gives origin to most of the nerves. The principal nerves are the following:—The Visceral nerve (fig. 41, *visc.*) passes close to the left side of the vas deferens in the male and innervates the digestive gland and gonad. It is an extremely long nerve, in fact, the longest in the animal, and can be traced to the tip of the visceral mass. Two nerves, the recto-genital and rectal, (fig. 41, *rec.'* and *rec.*) pass out to the right, to the rectum and gonoducts. A larger nerve, the reno-cardiac (fig. 41, *r.c.*) passes out, breaking up very considerably on its way and sending a branch to the pericardium and heart. From the smaller ganglion a nerve arises which passes to the efferent branchial vessel (fig. 41, *eff.*).

THE SENSE ORGANS.

The sense organs may be divided into simple and compound, the former class including only the numerous sense cells which occur scattered amongst the ordinary epithelial cells, the latter the Eyes, Osphradium, and Otocysts.

The Eye.

The eyes are two in number and are situated at the base of the tentacles, on the dorsal surface of a small lateral protuberance.

They are visible as two round intense black spots, but when the tentacle is contracted and the body wall is thrown into folds, the eye, hidden in the angle between tentacles and head, is not easily seen. No metallic glitter so characteristic of the Pecten eye ever occurs, and, as will be seen below, the layer in the eye responsible for this feature is not present.

The lowest gastropoda possess eyes which are simply sac-like invaginations of the outer epithelium. At the bottom of the sac the epithelium is modified somewhat and forms the retina. The cavity remains open to the exterior.

In the higher gastropods the open pit is succeeded by a closed vesicle, and this ontogenetic sequence is probably an indication of the phylogeny. As we should expect therefore, the Buccinum eye is a closed vesicle cut off from the surface. The general epithelium extends over it, forming an outer cornea (fig. 47, *Cor.*). The wall of the vesicle is formed of a single layer of cells, once part of the bounding epithelium of the head. These cells are modified in various regions. The area immediately below the outer cornea, through which the light has to pass, is formed of cells free from pigment—the area itself is the inner cornea (fig. 47, *Ps. cor.*). The rest of the vesicle wall forms the retina and is made up of pigment-containing cells.

The cells of the outer cornea differ only from those of the epidermis in shape. As the optic vesicle is approached, the deep and narrow epidermal cells with slender nuclei become less deep and of greater thickness. There is a well-developed cuticular margin present. With this change there is an alteration in the form of the nucleus, a spherical shape taking the place of the slender compressed form. The optic vesicle is imbedded in a mass of connective tissue (fig. 47, *Con.*) and muscle fibres, in which numerous blood spaces occur irregularly. This tissue, which is usually more compact near the surface, is continued in so as to form a layer between the vesicle and the outer cornea.

The cells of the optic vesicle appear to be of two kinds, and only two kinds of cells make up the entire vesicle—retinal and corneal areas inclusive. In sections, the retina, or area directly opposite the cornea, is built up of very large cells, which can be distinctly seen extending from the connective tissue to the cavity of the eye (fig. 47. *Ret. c.*). They possess spherical nuclei in which may be seen a nucleolus and numerous granules, and their distal portions are lost in a mass of dense black pigment.

Between these large cells are to be found a number of compressed nuclei (fig. 47, *Nuc. int. C.*), which stain more darkly than those above mentioned, possess finer granules, and in short cannot be mistaken for the nuclei of the large cells. These nuclei belong to slender fusiform cells which are interpolated between the larger ones and whose boundaries are difficult to follow in sections. If the eyes are macerated in a 4 per cent. cocaine solution in sea-water, the true shape of the structures building up the retina becomes at once apparent. The large cells possess the extraordinary shapes indicated in fig. 48. It will be noticed that they are widest towards the base, and that the nucleus is in general situated not far from that region, in fact, somewhere near the centre of the cell. One of the most curious facts is the prolongation of the cell into processes, of which there may be several (fig. 48, *pr.*). The apex of the cell is rounded and contains a large quantity of black pigment (fig. 48, *Pig.*) in the form of minute granules closely crowded together. Very often, too, this rounded distal extremity bears a prominence which may be taken as the remains of the "Stiftchen" or hair-like processes seen in sections and mentioned below. The narrow cells also possess pigment, so that there is no differentiation here into pigmented and pigmentless cells.

The cavity of the optic vesicle is filled with a structureless gelatinous mass, which forms a lens (fig. 47, *Lens*). This lens does not possess a perfectly rounded contour where it abuts on the retinal cells, but is indented and in each indentation there is a delicate bundle of hair-like " Stiftchen " (fig. 47, *St. s.*), which appear to break away from the cells in macerations. Thus the eye of *Buccinum* agrees with the long series of eyes possessing Stiftchen-bearing cells. The presence of such processes is one of the most striking characters in the structure of visual organs.

There has been no small difference of opinion as to which are the visual cells in gastropod eyes. In many cases the difference between the cells which has struck the observer has been the presence or absence of pigment. Here both sets possess pigment. Could the actual nerve connections be demonstrated, the matter would be easily solved, but unfortunately the fibrous processes of both cells merge into the tangled mass of nerve fibres and connective tissue below the eye. Judging from structures in the eye of *Pecten,* and especially from the character of the nucleus, the author would say that the large cells are the visual cells notwithstanding the fact that the cell body of the slender cells is more in accordance with expectations.

This view is, however, supported further by two facts. The large cells appear to possess the " Stiftchen." Both kinds of cells occur laterally almost up to the inner cornea. There the large cells begin to disappear, whilst the nuclei of the others are very like, one might almost say the same as, those found in the cells of the inner cornea itself. According to this view, therefore, the slender cells are merely supporting cells, and they are continued across the eye to form the inner cornea.

The nuclei of the inner corneal cells are flat compressed structures (fig. 47, *Ps. cor.*), like the nuclei in the retina, but instead of being arranged at right angles to the wall of the cavity they have rotated, so that they now lie end to end and parallel with the plane of the cornea. The gelatinous lens is probably secreted by the supporting cells. The optic nerve breaks up underneath the optic vesicle, and a network of fibres extends below the retina.

So far as observations go, the whelk relies but little on its visual organs. It is difficult to understand how complicated organs of this kind could be produced in the mollusca, when one thinks of the feeble responses to experiments. Either our experimental methods have failed so far to demonstrate the utility of many of the molluscan eyes, or some of our conceptions of evolutionary processes require modification. The tendency to take anthropomorphic views, however, in work both structural and experimental, for invertebrate sense organs is perhaps the danger to be avoided.

THE OSPHRADIUM.

The sense organ known as the Osphradium, situated usually in close proximity to the respiratory organs, attains a degree of complexity in *Buccinum* which is probably never exceeded in the Mollusca. In the Lamellibranchs the osphradium is merely an area of somewhat thicker epithelium, whose presence is not even marked by pigment (except in *Arca*). It is, therefore, quite invisible to the naked eye.

The lower gastropods, the Diotocardia, possess an osphradium which seems to be somewhat of the same type so far as general structure is concerned. As one passes, however, towards the more highly developed Monotocardia, the osphradium takes the form of an axis bearing on each side a large number of leaflets. It becomes, in fact, bi-pectinate, and resembles superficially a gill.

The osphradium of *Buccinum* is usually obvious as soon as the shell is removed, for it can be seen through the mantle. There is no difficulty in finding it when the mantle cavity is opened and the roof examined. It stands out as a deep brown-black organ, situated right across the gutter of the pallial siphon and between this organ and the gill (fig. 8, *Osph.*). It lies, therefore, on the opposite side of the ctenidial axis, and by reason of its build was formerly known as the " false gill." It is long, and is made up of about 90-100 leaflets arranged on both sides of an axis, which is nothing but an elongated nerve ganglion covered by epithelium. These leaflets are largest in the centre and diminish in size towards the ends, giving the whole the appearance of an elongated oval. The leaflets are roughly triangular in shape, those of the right or ctenidial side being, however, larger than those of the left (fig. 44). Each leaflet has an inferior free edge (fig. 44, *Inf.*), a lateral edge (fig. 44, *Lat.*), and what must be termed the third side of the triangle—the internal edge—which is curved and fused to both mantle and nerve axis (fig. 44, *Pall* and *N. ax.*).

The entire surface of the lateral faces is pigmented, but the pigment is often free from the inferior edges of the leaflets, a condition the reverse of that described by Bernard for *Cassidaria*. For a further study of the organ reference must be made to sections.

Each Osphradial leaflet is a fold of the epithelial layer bounding the inner surface of the mantle, together with certain connective supporting tissues. Just as in the branchial leaflets, there is an external bounding epithelium resting upon supporting membranes and leaving a series of flat blood spaces, which are here occupied largely by branches of the osphradial nerves (fig. 45). The epithelium resembles that of the ctenidial leaflets further in being modified and specialised in different regions. These regions are (*a*) sensory, (*b*) glandular, (*c*) ciliated, the former being by far the largest in extent. The sensory region extends over the greater part of the free lateral surface of the leaflets. The glandular region is confined more or less to the edges, and in particular to the lateral edges (fig. 44, *Osp. gl.*). The ciliated area is a long narrow strip extending along both sides of the leaflet against the glandular edge and between it and the sensory area (fig. 44, *Osp. cil.*). Thus in a section taken through A-B (fig. 44), the glandular area is nearest B, that is where the free lateral edge meets the mantle, this is followed by the ciliated region, and then the remainder is sensory. The sensory area is characterised as in the lamellibranchiata by an absence of cilia, and a considerable thickening of the epithelium. This thickening is due to an increase in the length of the cells, which are further modified by the possession of a yellow granular pigment. Now the real structure of this important area is not easily investigated. Sections well preserved and fixed show that it is built up of a large number of pigment-bearing cells, whose nuclei are apparently arranged at different levels because one sees nuclei close to the basal membrane, and from here to near the free surface they are irregularly scattered (fig. 45, *Osp. so.*). There is, however, a stratum close to the free margin of the cells perfectly free from nuclei, and it is here that the pigment is situated.

Macerations of the osphradium explain the structure instantly. The pigment-bearing cells are of the type indicated in fig. 46, and all agree in possessing a terminal plateau in which the pigment lies. From this plateau the cell becomes constricted and fibre-like, with, however, one large swelling where the nucleus lies. The position of the nucleus varies considerably, and so it is possible to pack together many more cells than would be the case if the nuclei were all situated at the same level.

These cells are the indifferent cells of Bernard. One feature that he has overlooked is the well-defined cuticular margin (in sections), crossed by delicate striae arranged perpendicularly to the free surface of the epithelium.

Now, in addition to these cells, there are, according to Bernard, neuro-epithelial cells which are in connection with the nerve fibres. These neuro-epithelial cells are always fusiform and possess a rounded or oval nucleus. If the osphradium is an important sense organ (and one would assume so from the size of the nerves innervating each leaflet, as well as from the great central ganglion), and if the nerve endings are neuro-epithelial cells we should expect the latter to be numerous and fairly obvious. The contrary is, however, the case, and in ordinary sections it is hardly possible to make out many cells of a different type from the pigment cells already described.

Are the nerve endings different, then, from those described by Bernard? The osphradium of the gastropoda appears to be homologous with that of the lamellibranchiata, and so far as general structure is concerned there is perfect agreement. List has shown that in *Mytilus* there are free nerve endings in this organ, and the author of this memoir has seen and described the same structures in *Pholas* and *Pecten*. Furthermore, Gilchrist has described free nerve endings in *Aplysia*.

The most striking similarity in the microscopic structure of the organ in lamellibranchs and the whelk is evident, and the description of the lamellibranch osphradium might be used for that of the whelk. For example, List states that "the neurofibrillae split in the epithelium into several branches, form richly branched networks, and send some fibrillae through the cuticle to the outside. Since, however, every fibril does not pass beyond the cuticle, but often only goes as far as its outer edge, one can easily get the impression that the osphradial epithelium was ciliated with very delicate cilia which have partly fallen away in fixation." This pseudo-ciliated margin is, then, the cuticle with its numerous neurofibrillae.

Bernard merely states that there is an inter-epithelial network of nerve fibrils, and leaves one to assume that these are all connected with neuro-epithelial cells. The real case is as follows:—Below the epithelium runs the nerve, and with the nerve fibres are multipolar ganglion cells. From these multipolar cells delicate neurofibrillae pass out and enter the epithelial region. Here they branch in all directions and finally reach the surface. They run through the cuticular seam in a parallel manner perpendicular to the plane of the epithelium and appear, therefore, as striae in sections.

So far, Ranvier's gold methods have not been used, and Bernard's neuro-epithelial cells have not been actually re-investigated by the methods he used. The nerve network with the free nerve endings is, however, present and is without doubt the important sensory structure in the organ. By ordinary methods and macerations no obvious or numerous sense cells were found. The structure is, in my opinion, identical with that of the lamellibranch osphradium.

Little need be said about the non-sensory epithelium of the leaflets. The ciliated band (fig. 45, *Osp. cil.*) is about ten cells broad, the cells differ from those of the sensory area in being compact, more cylindrical, and with deeper-staining contents. Bernard is in error in saying they possess no pigment.

Underlying the epithelium of the osphradial leaflets is a delicate basement membrane and a connective tissue layer with prominent muscle fibres. The centre of the leaflet is occupied by irregular blood spaces, which communicate with a very definite sinus running down the external margin.

The nerves of the osphradial leaflets are derived from a central ganglion, situated along the axis of the organ. This ganglion consists of a central mass of fibrillae, the neuropil, with the usual cortex of ganglion cells. The ganglion cells occur, therefore, on all sides, but are, nevertheless, more concentrated laterally, except where nerves are given off to the leaflets.

To each leaflet a nerve is given off, and this leaves the side of the ganglion exactly halfway down. This principal leaflet nerve runs outwards across the leaflet, nearer the inferior border than the opposite and attached edge (fig. 44, *Os. n.*). It gives off numerous branches on both sides, but particularly on that towards the mantle. These latter branches are very regularly arranged, and from them arise the neuro-fibrillae which enter the epithelium to form the nerve-net already described.

THE OTOCYSTS.

The otocysts are spherical sacs formed of a delicate epithelium. The cells are low and irregular in shape with but little contents. Two types are present, sense cells and non-sensory cells.

The depth of cells is only $\frac{1}{22}$ of the diameter of the otocyst. The large cavity is filled with calcareous matter forming an otolith.

THE RENAL ORGAN.

The renal organ, the so-called "nephridium," is visible at a glance when the shell is removed. It occupies a position immediately behind the pallial cavity, on the right side of the pericardium above the digestive gland and rectum. The renal organ of *Buccinum* is not only one of the most highly developed in the Prosobranchiata, but one of the most complicated in the Mollusca. Fundamentally, it is a sac communicating with the pallial cavity and the pericardium. The wall of this sac performs a special function—that of renal excretion, but under no circumstances does the blood system open to the external world in this organ. Externally the sac is covered by the general integument of the body. The outer and inner walls of the renal organ, that is to say, the former underlying the integument and the latter resting upon the digestive gland, are entirely different in appearance. The epithelium of the outer wall is prolonged into filaments or processes of various shapes, which are held together in such a way as to form ridges projecting into and occluding the lumen of the organ (fig. 49). In addition to this epithelium, which is the true glandular layer, there is a supporting connective tissue layer. The other walls are merely a delicate transparent epithelium. The renal organ should be opened by making an incision along the right side close to the digestive gland. The internal surfaces can then be examined.

It will be noticed, however, without any dissection that another structure is present, lying close to the glandular renal organ proper and forming part of the walls of the sac. This forms a band about $\frac{1}{8}$ inch wide between the pericardium and the renal tissue. It differs from the latter in texture and also somewhat in colour. It is to a large extent quite independent of the renal organ and has been termed the Nephridial Gland (fig. 49, *neph. gl.*, fig. 50). Seen from the cavity of the renal organ, the nephridial gland differs altogether from the glandular wall of the former. Instead of ridges formed of numerous conical and other filaments, the surface appears as if it were made up of branched and anastomosing fibres, which generally run transversely to the long axis of the gland and renal organ.

If a solution of methylene green or säuresfuchsin is injected into the foot, one finds after a few hours that the renal organ is taking up the substance from the blood and is deeply coloured by the dye. The nephridial gland, however, is quite free from stain. A second feature of importance is that the nephridial gland is interpolated into the circulation between the renal organ and the auricle, and any injection mass forced into the efferent branchial vessel passes very easily into this gland after filling the auricle. In fact, the nephridial gland is a large spongy blood lacuna.

The Renal Aperture.—The external opening of the renal organ is situated on the anterior wall separating the gland from the pallial cavity. It lies slightly above and to the *left* of the rectum. It is a fairly conspicuous opening, slit-like, and of about 3 mm. in length. The long axis of the opening runs dorso-ventrally. The lips of the aperture are thickened owing to the development of muscle fibres, which form a sphincter muscle. The opening leads directly into the lumen of the renal organ, which is only separated from the pallial cavity by the membrane above mentioned.

The Reno-pericardial Aperture.—This opening is not situated at the most posterior part of the gland but laterally, on the inner wall of the pericardium, and some distance away from the main cavity of the renal organ. The opening is much smaller than the external renal aperture and often difficult to find, though it is rendered more conspicuous by the somewhat white lips standing out on the darker background of membrane. It is not easy to see what may be the use of the reno-pericardial canal and opening. In those molluscs in which a pericardial gland is present as an accessory excretory organ, the products, of course, would pass to the exterior by this canal. Pericardial glands are, however, not widely distributed in the gastropoda, and appear entirely absent in the whelk.

Structure of the Renal Organ.

In considering the vascular system of the whelk, reference has already been made to the large sinus which lies under the floor of the renal organ. From this sinus a number of vessels arise, which, after crossing the lumen of the nephridium, give rise to branches which pass to the filaments of the ridges (fig. 49, *ren. r.*). Each filament is an evagination of renal epithelium, and each contains a blood cavity. The cells of this epithelium are of two kinds, glandular and ciliated, but the former are by far the most numerous. The ciliated cells occur on the summits of the filaments (fig. 52, *ren. cil.*) and pass gradually into the gland cells. The gland cells are regular columnar cells, the height not greatly exceeding the width. The cytoplasm is very regularly vacuolated, and remains as a kind of fine network in the cells, staining reddish violet with methyl-blue-eosin. Very large vacuoles are not usually present. The nucleus is situated at the base of the cell. Underlying both kinds of cells is the continuous supporting membrane of connective tissue in which occur scattered muscle fibres (fig. 52). The blood spaces are extremely narrow but can be traced very easily after staining with methyl-blue-eosin (Mann). Every now and then one meets with sections of the vessels which occur on the ridges (see vascular system for further details of circulation in renal organ.) The ridges considered above belong to what has been termed by Perrier the "*principal system.*"

Running round the left side of the renal organ proper, between it and the nephridial gland, is a membranous flap ending in a smooth transparent edge (figs. 49 and 51, *ren. lam.*). It is continued, though very much smaller in size, along the posterior margin. From this lamella a number of secondary lamellae arise and run at right angles attached to the wall of the renal organ between the ridges already discussed. These little partitions (fig. 51, *lam. pr.*) are hidden by the ridges, but can be seen quite distinctly if the latter are just pulled aside. In order to examine the structures further it will be necessary to macerate the gland—and to remove the glandular filaments entirely.

It will then be seen that the secondary lamellae give off in their turn tertiary lateral lamellae, which finally divide up into very delicate branches (fig. 51, *lam. S.*). This secondary system does not appear to play any great part in the rôle of excretion. It seems to be confined to the highest prosobranchs, and Perrier regards the two systems as equivalent to the two lobes of the renal organ of the Volutidae. The histological structure of these lamellae is very different from that of the filaments. In section they are of considerable thickness. There is the same bounding layer of glandular cells, but they are more cubical than columnar. The greater part of the structure is filled by a mass of cells whose boundaries and nuclei are often quite difficult to make out (fig. 53). The reason is that the cells are filled with refringent granules (fig. 53, *C. gr.*), possessing great affinity for eosin stains. These granules when stained mask the nuclei. Under low powers of the microscope the substance of the lamellae looks therefore like a granular or even fibrous mass of connective tissue. In places, cells occur possessing none of these peculiar contents, and as a result cell boundaries and nuclei are easily determined, and the whole looks like an island of cells (fig. 53, *C. r.*) in the midst of the dense staining mass. In many cases it actually appears as if the granules were first developed *in* the nuclei.

Finally, one finds blood lacunae occurring amidst the mass of cells as in the filaments.

NEPHRIDIAL GLAND.

The structure of the nephridial gland is exceedingly interesting. It is composed of a somewhat compact lymphoid tissue, a fibrous groundwork with numerous lymph cells. Everywhere blood lacunae are to be seen. The most striking feature, however, is the presence of long canals, evaginations of the wall of the renal organ, which extend into the nephridial gland and end blindly. Sometimes the canals branch slightly before terminating. The canals are about $\frac{1}{12}$ mm. in diameter and are lined by ciliated cells. There is no trace of any opening between the nephridial gland and the lumen of the renal organ. The function of the nephridial gland does not appear to have been satisfactorily ascertained. This kind of statement recurs too frequently in descriptions of invertebrate structures. The injections made in the course of this work give only the negative result that the gland is not excretory like the renal organ. The experiments were, however, neither numerous nor detailed enough to allow of a really definite statement being made. On the other hand, the intimate relation between the nephridial gland and the vascular system implies some function connected with the composition of the blood. Perrier discusses two theories, the first that it may be an organ for reserve matter, the second that it is concerned in the formation of blood. The author of this memoir is inclined to believe that the gland is a lymph organ with some additional function: further work is being carried out on the subject.

The morphological value of this gland is another point of considerable interest, particularly in connection with the attempts made to discover a homologue in the Monotocardia of the second renal organ of the Diotocardia, or to determine which renal organ, if any, has gone from the Monotocardia. Originally it was supposed that the renal organ present in the whelk represented the right nephridium of the Diotocardia. Perrier took this view, and starting from the fact that in *Patella* both organs are present and both are situated to the right of the pericardium, he pointed out the resemblance in position of the nephridial gland and renal organ in such forms as *Buccinum*. His theory, in short, was that the two renal cavities of the lower gastropods had fused, and the left renal organ had passed to the right of the pericardium. Then the right organ had kept its true primary function of excretion, whilst the left became the nephridial gland by development in its walls of tissue with a new function. As further proof of this view, the intermediate forms—Haliotis, Turbo, and Trochus—are brought forward, in which, whilst both renal organs are still present, the left has almost lost its function of excretion.

Against this we have the fact that the renal aperture of the Monotocardia lies to the *left* side of the rectum, and embryological evidence supports strongly the view that the "kidney" of the whelk represents the *left* renal organ of the Diotocardia. This conclusion seems at present to be the most probable, and though in *Patella* it is the left kidney that is reduced, the Docoglossa can hardly be considered as on or near the line of evolution of the Monotocardia.

REPRODUCTIVE ORGANS.

Under this heading will be considered:—(1) the Gonads, (2) the Gonoducts, and (3) the organs of copulation. The sexes are separate in *Buccinum*, as in most prosobranchiate molluscs, and the difference is well marked externally owing to the male possessing a large penis which lies folded back in the mantle cavity. The gonoducts are well differentiated and quite separate from the renal organ, having their own openings to the exterior.

The Male Gonad (fig. 54, *Go.*), which resembles the female in shape, size and appearance generally, is situated upon the digestive gland and in close contact with it. Both are in fact covered by the same membrane forming the integument. The testis extends from the cleft marking the point of contact of the two lobes of the digestive gland, along the right side up to the very tip of the spire (fig. 54). By reason of its more or less bright yellow colour it stands out markedly against the dark coloured tissue of the digestive gland. Slightly ventral to the gonad on the right side, and on the surface of the so-called "liver," so that it is visible to the eye without any dissection whatever, runs the male duct, the vas deferens (fig. 54, *V. def.*). It is at first very narrow, but gradually increases in thickness as it approaches the region of the stomach. During all this length it receives branches from the gonad and is coiled and folded in a very characteristic manner. These convolutions become more complex as the vas deferens passes forwards, and finally it forms a tubular storing chamber in the region between gonad and renal organ (fig. 54, *V. def.'*). The actual length of the vas deferens is several times the distance from the tip of the spire to the end of that duct in a straight line. After the convolutions the vas deferens becomes again somewhat reduced in diameter and, with fewer folds, passes forwards towards the thickened body wall of the "neck" region. Just upon reaching the pallial cavity, it turns in a spiral manner—this part being again of somewhat greater diameter—and then runs directly to the base of the penis under the body wall, which forms the floor of the body cavity.

The Penis is a permanent organ of very considerable size, which arises somewhat on the right side of the neck (fig. 54, *Pen.*). It is spatula-shaped, flattened, and broadest at the distal extremity. Though capable of some contraction, this tough muscular extension of the body is so long that it would protrude from the shell were it not for the fact that normally it is bent back and lies hidden in the mantle cavity. A little distance from the end there is a small tentacle at the apex of which the vas deferens opens. The vas deferens, however, does not run directly through the penis. It winds on itself in a spiral fashion, running through a tunnel from the base of the organ to its aperture on the tentacle. The male organs, it will be seen, are comparatively simple, and no accessory structures are connected with the vas deferens. In some gastropods the penis has been found to undergo seasonal variation in size—no trace of this has been noticed in *Buccinum*.

Sections through the testis show a tubular structure, the tubes opening into one another until finally a small duct is formed which joins others and makes up the canal opening into the vas deferens. In the ripe testis the germinal epithelium, which forms the wall of these tubes, gives rise to spermatocytes, which break away and fill up the marginal area of the cavity (fig. 56). Nearer the centre of the cavity are numerous smaller cells, the products of division of the spermatocytes, and themselves the spermatids (fig. 56, *Sptd.*). Both spermatocytes and spermatids are characterised by the small quantity of cytoplasm and the densely-stained nuclei. Complete series of stages in spermatogenesis may thus be seen, but the bodies formed are not of such a size as to make observation easy. The nucleus of the spermatid gradually elongates and becomes more attenuated to form the head of the spermatozoon.

Retzius was the first to discover two kinds of spermatozoa in the whelk. The presence of two kinds of spermatozoa in the gastropoda was noticed so far back as 1875 by Schenk in *Murex*. Since then the double character has been recognised in several species of Prosobranchs. The two different forms have been designated by the names " hair-like " and " worm-like." The former are long fibres with an extremely long head, almost half the length of the sperm (fig. 57, *b.*). In ordinary stained preparations these will be probably the only sperms recognised, and the only differentiation will be into the long narrow head and tail. At the anterior end of the head is a small, clear, vesicular cap. From this point a central fibre is visible running down to the base of the head. Very often in fixation this contracts so as to throw the head into a spiral. A middle piece follows the head, but is of the same diameter. The tail is also of the same diameter and retains this until the pointed extremity is reached.

The "worm-like" spermatozoa (fig. 57, *c.*) are rather wider and shorter than the "hair-like," and the region of greatest diameter is near the anterior end. No differentiation can be made out except that the cytoplasm possesses a number of granules. Retzius states, however, that in macerated preparations a long fibre can be seen running down one side from end to end.

The vas deferens is lined by ciliated cells, and in the reproducing season is filled with spermatozoa, any cut causing a white milk-like fluid to ooze out.

The Female Gonad occupies the same position as that of the male, and running along its right and ventral side is the oviduct, which lies in very much the same position as the vas deferens in the male, and begins by being an extremely small canal. It is very different, however, from the male duct in being perfectly straight without the peculiar windings (fig. 55, *Ovd.′*), which seem to be characteristic of the male gonoducts. One meets with the same convoluted vas deferens in other groups of animals. It is probably due to the fact that development of the spermatozoa takes place after the spermatocytes have been cut off from the epithelium, and also to the absence of any large storing organ for the spermatozoa. The oviduct is a narrow tube with delicate walls. In fact, it resembles a large blood vessel, running along the right side of the digestive gland close to the surface (fig. 55, *Ovd.′*). At a point below the renal organ, it turns abruptly at right angles, and immediately takes on a very different structure (fig. 55, *Ovd.″*). The walls at once increase in thickness until the tube forms a cylinder about ½ an inch in diameter. The walls of this are, right and left, about ¼ inch thick, and the lumen in section is a long crescentic slit running dorso-ventrally. These walls are perfectly white and of a very peculiar cheese-like consistency. This posterior glandular portion of the oviduct, after its abrupt beginning, takes again the anterior direction, and runs along to the right of the rectum, the rectum, in fact, lying upon it (fig. 59). It eventually opens by a small orifice into the pallial cavity.

The ovary is also tubular in section, the wide tubules of which it is composed being arranged at right angles to the surface of the gonad. In a hand section the parallel arrangement of ovarian tubules may be distinguished quite easily with the naked eye. In transverse section they are five or six-sided (fig. 60), and are composed of a thin wall of germinal epithelium (fig. 60, *Ge. ep.*)—flattened cells—which here and there gives rise to large egg cells. These contain a conspicuous nucleus with nucleolus. One interesting fact is that the germinal epithelium gives rise to delicate follicles of flattened cells, which surround the developing eggs (fig. 60, *Foll. ep.*). This is seen again in the Cephalopoda, but does not seem to be the rule in the Lamellibranchiata. It is certainly not so in *Pecten* or *Cyclas*, where the stalked egg projects freely into the cavity, surrounded only by the egg membrane.

EMBRYOLOGY.

Fertilisation takes place internally, but details of the exact procedure have so far not been observed. The eggs, surrounded by a transparent viscous mass of albumen, are laid in capsules which are deposited in considerable numbers attached to each other, and often fixed to floating objects or to mollusc shells, rocks, crustacea, etc., on the sea bottom. Whelks' egg-capsules form one of the most familar objects of the flotsam and jetsam thrown up on our shores.

The individual capsules are flattened on the under side, and when seen from above they are oval in shape. A clearer idea of their appearance can be best obtained by reference to the figures. The wall is made of two layers of membrane, both of which are perfectly smooth on the ventral flattened side (fig. 61). The outer wall appears crinkled on the convex surface (fig. 65). This is due to the presence of delicate fibres, which, however, are of short length and often branch.

The outer walls of adjacent capsules are continuous, so as to join the yellow capsules together in masses.

The eggs of the gastropoda are not always laid in chitinous capsules of this kind, there being other modes, i.e. (*a*) free without any protecting capsule, (*b*) with calcified membrane, (*c*) deposited in ribbons (Opisthobranchs), and (*d*) in gelatinous masses. The capsules of the whelk have been supposed by most zoologists to be formed by the oviduct, and the most distal or uterine portion of that tube is extremely glandular. Cunningham, however, in 1899, in a letter to "Nature," announced that the egg capsules of *Buccinum* and *Murex* were formed by a secretion from the anterior groove of the foot. The eggs must therefore pass round from the pallial cavity, imbedded in a quantity of gelatinous material, to the under surface of the foot. Then in the groove they become surrounded by the chitinous capsule. Cunningham's discovery has apparently never been noticed, and no information on the subject appears in the textbooks. Not only does *Buccinum* form its egg capsules in this way, but the same thing applies to *Purpura*, and Pelseneer has actually found the capsules in the ventral pedal gland.

The exact number of eggs placed in the capsules also seems to have been overlooked by most workers. Koren and Danielssen, who give the largest numbers, say that variations from 6 to 800 occur in *Buccinum undatum*. Our counts have given from 49 up to 2,419! Moreover, the high numbers were by far the most common. Few capsules contained less than several hundred eggs. In what must be regarded as a very small clump of egg capsules (about 2 cub. inches) we calculated that there must be about 200,000 eggs.

It is a well-known fact that the number of young whelks leaving the capsules is very much smaller than the number of eggs placed therein. Here again, the figures vary, but the average is probably somewhere around the figure 10. Each capsule is penetrated by a small oval hole, which appears always in the same place, near one margin of the flat side (fig. 61).

The eggs are 0·25 mm. in diameter, the young shells at the time of leaving the capsules are 3 mm. from the tip of the spire to the end of the siphon, and three whorls are present of rapidly increasing size.

The embryology of the whelk must be left for a separate work, any consideration of it in a detailed manner would be beyond the usual limits of a memoir of this kind. Koren and Danielssen, in the "Fauna littoralis Norvegiae," were probably the first to describe the sequence of events taking place in the egg capsules. Their account is extremely interesting, though the treatment was naturally limited by lack of the methods now available for embryological research. The eggs when laid are imbedded in a perfectly transparent viscous mass. As development takes place, this albumen becomes less and less viscous, and the eggs become crowded together. Now, according to Koren and

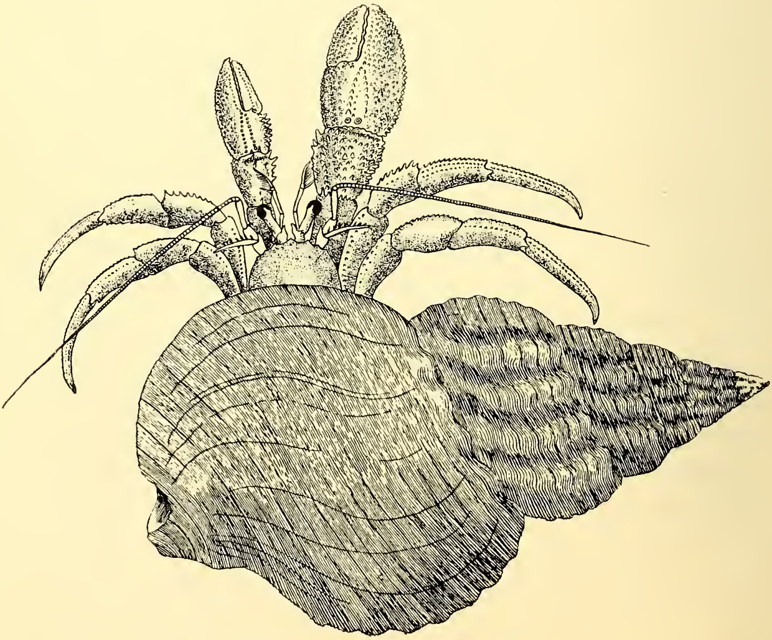
Danielssen, little groups of eggs, containing from 30-60, sometimes even 130 individuals, separate out, and around them a delicate granular mass appears—a supposed exudation from the eggs. Each little group of eggs becomes an embryo, and the granular mass takes on the form of a definite limiting membrane, which gives later the shape of the larva.

What really happens, however, is the much more probable sequence observed first by Carpenter in *Purpura lapillus*. According to this investigator, only a few of the eggs in a capsule are to be looked upon as true ova. The remainder are termed " yolk spherules." The distinction between the two is manifested at the time of the first segmentation; the yolk spherules dividing into two equal hemispheres, the real ova into a larger and smaller segment. Segmentation of both takes place, however, and it should be interesting to determine whether this is due to an actual difference in the eggs laid or to fertilisation by the different kinds of spermatozoa now known to exist. As the embryos develop they commence actually to *swallow* the segmented yolk spherules, and it is these carnivorous embryos which Koren and Danielssen took to be clusters of eggs with an exuded membrane.

Bobretzky describes in some greater detail the embryology of a gastropod supposed to be *Fusus* (sp. ?) Whilst, however, he gives in his account a description of the formation of blastula, gastrula, and early embryonic stages, he does not make any mention of the carnivorous act, and his egg capsules only contained 7-20 eggs! The egg divides into two similar halves, and then into four large cells by a second division. These four large cells cut off four small ones which lie close together. Four other small cells follow these, being cut off in a similar manner, and then by division of the first four small cells a total number of twelve is reached. By the segmentation of the small cells themselves, and by the addition of others a layer of cells (ectoderm) is formed which gradually grows round the egg until a space is left at the opposite pole. Here the four large cells remain visible and form part of the wall of what may be termed a blastula. The gastrula is formed by the depression or invagination (very slight) of the large cells, and the growth of the ectodern at the blastopore. The further details of this development do not actually apply to *Buccinum*. This, however, gives one a hint of the processes by which the early carnivorous stage is formed. As soon as stomach and oesophagus are developed, the embryo starts devouring the eggs in the capsule.

The ectodern is ciliated, and outlines of head and foot are soon to be observed. The otocysts are visible very early, and are closely followed by the eyes. At this stage the embryo is quite symmetrical. The stage shown in fig. 64 on Pl. VIII, represents a fully developed embryo some time before the shell and body attains the size which may be termed the "young whelk" stage, at which it leaves the capsule. At this period the head is well developed, and eyes and tentacles are obvious structures. The velum (fig. 64), in the form of a bilobed structure fringed with particularly large cilia, has reached its maximum development, and by that means the larva moves actively round in the capsule. The foot (fig. 64) is well developed—the pedal groove (*Ped. gl.*) being relatively large, and the otocysts can still be seen, though they have sunk away from the epithelium and lie quite deep in the body. The larval shell is also conspicuous. It is a very delicate chitin-like structure, not yet coiled in a spiral, and marked by delicate longitudinal ridges. One very curious organ must also be mentioned. Protruding slightly from the pallial cavity is a vesicle (fig. 64, *Pul.*), which is apparently an evagination from the floor of the cavity. This vesicle contracts rhythmically. It has been noticed in other larval gastropods and termed the "larval heart." It is not, however, to be regarded as an early stage in the development of the true heart, which is situated much further back.

Further development results in the absorption of the velum, increase in size, and spiral coiling of the now asymmetrical shell. Of the thousand eggs that might have been in the capsule, perhaps ten may eventually reach the stage, of which the shell is figured on Pl. VIII. This reduction is due in the first place to the small number of eggs that can develop into young embryos, and secondly to the cannibalism exhibited by those same embryos practically as soon as the first rudiments of an alimentary canal are developed.



Appendix

DISTRIBUTION AND ECONOMICS.

The genus *Buccinum* is widely distributed in Arctic, Antarctic and Temperate zones. The species *Buccinum undatum*, Linn., occurs all around our coasts, from low-water mark to 100 fathoms, and over a considerable area extending from the Atlantic coast of North America to the Siberian seas. The genus appeared first in the Jurassic rocks, the species *B. undatum* occurring in the Coralline Crag, since when it seems to have become increasingly abundant in our seas. The Common Whelk, *B. undatum*, is the most abundant species and the most convenient to examine as a type of the genus. It inhabits different kinds of ground, and several marked varieties are to be found from the littoral zone to considerable depths. There seems, however, to be little agreement in regard to, or scientific classification of, the varieties.

Whelks are used at many of the fishing ports along the coast as bait for the long lines. They are caught by the Manx fishermen from banks of a shelly nature, about 17 to 20 fathoms deep, often near beds of the scallop *Pecten opercularis*. The method employed is to sink wicker baskets (crab or whelk pots) of the kind used for capturing the edible crab, baiting them usually with the latter animal. The crabs are used fresh, and are strung on a piece of cane which is inserted in the basket. An average catch at Port Erin is about 20 to 25 whelks per two days.

The whelk is also used as food, and large quantities are usually exposed for sale in London. It does not appear to be eaten much in the North of England, but a few specimens are occasionally seen for sale in Liverpool. In the Isle of Man, and Scotland, the whelks are commonly termed "buckies"; in Heligoland "coxen," and in the days of British rule, the English fishermen who called there were known as "coxen clappers," from their habit of breaking up the shells to obtain the whelk for bait.

Joubin states* that *Buccinum undatum* is very common on the West Coast of France, and that in the Syndicat of Portbail a fisherman can collect as many as 200 at one low tide. These he can sell at 1d. to 3d. per dozen. They are consumed in the country, and not exported.

A considerable demand for whelks must, however, still exist in this country, and one finds quotations regularly in the *Fish Trades Gazette*, though, unfortunately, the quantities sold or brought in are not indicated. The prices at Billingsgate appear to vary from about 4s. to 10s. a bushel. Government reports give little information, whelks being tabulated with other edible animals as "unclassified shell-fish," in the statistics published by the Board of Agriculture and Fisheries; but Mr. C. E. Fryer, I.S.O., of the Fisheries Department of the Board, has very kindly supplied Prof. Herdman with the following particulars collected for last year:—

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* Bull. de L'Institut Oceanograph., Monaco. No. 213, July, 1911.

QUANTITY AND VALUE OF WHELKS RETURNED AS LANDED AT STATIONS IN ENGLAND AND WALES IN 1911.

Station.	Quantity cwts.	Value. £
East Coast—		
Grimsby	1,292	355
Lynn	5,293	1,039
Wells	12,758	2,218
Sheringham	8,074	1,131
Harwich	4,482	869
Brightlingsea	275	51
East Swale	360	144
Whitstable	10,022	2,256
Ramsgate	586	175
Total	43,142	8,238
South Coast—		
Eastbourne	497	149
Selsey	686	171
Portsmouth	774	115
Southampton	337	165
Total	2,294	600
Other Stations	1,014	272
TOTAL	46,450	9,110

The returns and remarks in trade journals with reference to Billingsgate are reflected in the statements made in the Annual Reports of the Inspectors of Fisheries for England and Wales. Thus one finds that practically the only ports where whelk-fishing is carried on are situated between Grimsby and Southampton. This probably means that the fishery is governed by the presence of a large market for the mollusc in the south-eastern area of England.

The following official statement shows the small extent of the fishery in the Lancashire and Western Sea Fisheries District:—

Landed at Liverpool—

	Wt. in cwts.	Value in £'s.
1906	nil.	nil.
1907	3 cwts.	nil.
1908	4 cwts.	1
1909	1 cwt.	nil.
1910	1 cwt.	nil.
1911	nil.	nil.

As a matter of fact, however, the real value of the fishery must be higher than is represented by these figures. It is known that four to five hundred whelks are landed weekly by small sailing boats, and these sell at 1s. to 1s. 3d. per hundred. In addition to these, others are apparently landed by longshore fishermen and find their way with illegal-sized flat fish into some of the smaller fish-shops.

In addition to whelk-catching by means of wicker pots, dredges are occasionally used; "trotting" is another method adopted in the south-eastern districts of England. A number of shore crabs are strung together with a needle and string, so as to make a bunch. These are sunk to the bottom and left for a time; they are afterwards drawn up and the whelks removed from them.

In England, some years back, the trade in whelks must have been of considerable importance, for one finds that the Lynn fishery alone supplied about 1,250 tons a year, for which about £10,000 was paid, and Grimsby exceeded this with a value of £22,000. These figures probably include *Fusus antiquus* (the "hard whelk"), which seems to have been more prized in some markets.

The name *Buccinum* comes from "buccina," a trumpet, but it is difficult to get evidence that *Buccinum undatum* was ever used as a musical instrument. Species of *Triton* seem to be most used for this purpose, and *Turbinella* (the Chank Shell) is used in Ceylon by the Buddhists. The Chinese use a species of *Fusus* for the same purpose. The shell of *Fusus antiquus* is also used occasionally in the Scottish Isles as a rude lamp, in which to burn the oil of sea-birds.

The two closely related families, the Muricidae and Buccinidae, contain various genera and species, which have figured, perhaps, more than most marine animals, in the histories and traditions of ancient peoples. They have played an important part in religion, mythology and war, in the production of ornaments, and in the preparation of the famous "Tyrian" purple dyes.

The whelk crawls about the sea-bottom by means of its muscular foot, and when kept in large aquarium tanks occasionally creeps above the level of the water. It seems to remain, however, about a foot or so above the surface, and never crawls further up. It was observed at Port Erin, on every occasion on which whelks were turned into a large tank into which a stream of water was running, that they found their way towards the entrance pipe. They then remained either just below or just above the level of the water, in the latter case bathed by the spray, although the water was well aerated in every part of the tank.

The whelk appears to be omnivorous so far as its diet is concerned, and dead (but fresh) or living organisms seem equally acceptable. The food, which is scraped away by its jaw apparatus, is taken into the stomach in a finely divided state, and little information as to its character can be gathered from an examination of the stomach contents.

The fishermen at the Isle of Man have found that the best bait for their whelk-pots is *Cancer pagurus*, the edible crab, used fresh. The whelk inserts the proboscis through the holes broken into the carapace of the crab. Whelks have been observed to attack living lamellibranchs, and on one occasion at Port Erin a large specimen of *Buccinum* was observed to prevent a *Pecten maximus* from closing its valves by inserting the anterior end of the shell between them. It then attacked the adductor muscle with its long proboscis, and so at the same time obtained food and disabled the closing mechanism of the scallop. The same process of disabling the prey has been observed by Colton in the American genera *Fulgur* and *Sycotypus*. Colton experimented with these animals, and found that when an oyster was given to a hungry *Sycotypus*, the latter crawled on the top of the oyster and waited until the valves were opened. It then rotated on the columella and inserted the end of its own shell between the valves. Forty minutes later it left an empty shell. *Fulgur* actually hammers the margin of lamellibranch shells by grasping with its foot and contracting the columellar muscle sharply. The proboscis is then inserted into the orifice so made. The impression one usually derives from the literature of the subject is that the whelk actively bores through lamellibranch shells by means of its odontophore. Colton states, however, that the radular teeth of *Fulgur*, *Nassa*, *Lunatia* and *Purpura* do not appear as if worn down against a hard substance, but broken off irregularly. To this list the whelk can be added, for the old teeth present a most ragged appearance (fig. 15).

On one occasion a whelk was observed attacking a dead *Nephrops* (the Norway lobster). It held the crustacean by means of the anterior part of the foot, using the latter to envelop the posterior part of the abdomen of its prey. The radula was then brought into action, and a hole was bored through the chitinous exoskeleton until the proboscis could reach the muscles. Here again the use of the foot as a grasping organ may be noticed. In its turn the whelk must fall a prey to many other inhabitants of the sea, and one often wonders what has happened to the former owners of the numerous whelk shells now found occupied by hermit crabs (see Text-fig. on p. 98).

The cod feeds to a certain extent upon the whelk, though this is by no means its chief food. Remains of the whelk have also been found in the stomach of the dog-fish. Curiously enough, in most cases these remains include only the fleshy part of the animal and the operculum. This implies that, contrary to expectation, the fish either bites off the protruding part of the whelk or otherwise achieves the apparently impossible in removing the animal from its shell.

Quite recently, Dr. C. G. Joh. Petersen has published a very interesting paper on the relations of the whelk to the fisheries of Denmark. In 1909 a committee was formed in that country to consider the harmful animals of the sea-fisheries; and five animals were black-listed—the sea scorpion, the stickleback, crabs, starfish, and whelks. Petersen suggested that before money was spent on efforts to exterminate these creatures, experiments should be made to determine the possibility of such a proceeding. The whelk was selected for the experiments, and the Board of Agriculture allotted funds for the work. The harm done by the whelks was known and had been investigated some time earlier (1895). It had been found that the whelk attacked the plaice entangled in fishing-nets. Although unable to seize actively-moving fish, they very soon found and attached themselves to the fish that had been caught. The whelk proceeds by boring a hole through the skin, inserting its snout, and then devouring all the muscular tissue, leaving nothing but skin and bones. The mollusc will not touch rotten fish, but experiments have shown that it will devour anything so long as it is fresh. Often enough, 10 to 20 whelks would be found attached to a plaice, and the fishermen estimated that one-third of the year's catch was lost in the region investigated (Thisted Bredning, in Denmark).

The experiments carried out by Petersen were of a two-fold nature—(1) to determine the number of whelks in a certain area, and (2) to find out whether these could be economically exterminated by capture. The first part of the work was carried out by using an instrument called the "bottom-sampler," and also by the employment of a diver. The latter caught from 106 square metres 100 whelks, 36 square metres 128 whelks, 106 square metres 70 whelks, 106 square metres 97 whelks. In the last two cases the man reckoned that he had only taken one-third of the whelks present. From the results it was calculated that 130 million whelks were present in the region (an area of 65 million square metres).

One motor boat, with 240 traps, was able to catch 3,845½ bushels (45 tons of whelks!) in the same district, between April 5th and November 8th.

On the whole, it was concluded that the extermination by catching would not be an economic method, especially since there did not seem to be any great use for the whelks caught in the district. Petersen also states that six or seven whelks' opercula may be found in one cod's stomach, and comments on the rarity of any remains of the shells.

PARASITES.

Two extremely interesting parasites have been found in the whelks from Port Erin. One of these is a Coccidian (*Merocystis kathae*, Dakin), and the other is an endoparasitic Turbellarian first found 14 years ago by Jameson, and re-discovered this year in whelks from the same district. The Turbellarian (*Graffilla buccinicola*) belongs to a genus of parasitic rhabdocoeles which occurs frequently in mollusca, but at the time of Jameson's discovery *Graffilla* had not been found in British waters. No further details of its anatomy will be given here, because it seems advisable that the species should undergo a thorough re-examination. One point, however, must be referred to. Jameson states that the parasite occurs in the kidney and "kidney duct" of *Buccinum undatum* and *Fusus antiquus*, and that almost all whelks examined were infected. My specimens were examined fresh, and considerable numbers were investigated. In *all* cases the parasites were found in the *stomach* and *rectum*, and there were as many as 14 seen in the stomach of one individual.

It is somewhat difficult to conjecture what the "kidney duct" referred to in Jameson's description can be, for the renal organ opens directly at one end into the mantle cavity. The minute reno-pericardial canal can hardly be called a kidney duct!

INDEX

EXPLANATION OF PLATES

Reference Letters

A. buc. = Buccal artery.
A. c. = Anterior aorta.
A. cut.' = Cutaneous artery.
A. col. = Columella artery.
A. g. = Gastric artery.
A. go. = Gonad vessels.
A. pall. = Pallial artery.
A. ped. = Pedal artery.
A. pen. = Penis artery.
A. vis. = Visceral artery.
Af. ct. = Afferent branchial vessel.
An. = Anus.
Ao. = Aorta.

Br. v. = Branchial vessels.
bucc. = Buccal ganglia.
c. = Cerebral ganglion.
C. c. = Occlusor muscle.
C. cav. = Blood spaces in oesophagus.
C. p. = Cerebro pedal connective.
c. d. m. = Centro dorsal muscle.
c. gr. = Granular cells of renal lamella.
Caec. = Oesophageal caecum.
cae. w. = Connective tissue of caec. wall.
cart. = Cartilage.
cer. com. = Cerebral commissure.
Col. mus. = Columella muscle.
Con. t. = Connect. tiss. gland of Leiblein.
Con. = Connective tissue.
Cor. = Cornea.
Ct. = Ctenidium.
ct. ax. = Ctenidial axis.
ct. con. = Connective tissue of gill leaflet.
ct. e.' = Epithelium of gill leaflet.
ct. ep. = Ctenidial epithelium.
ct. gl. = Connect. tissue of ctenidial axis.
ct. mus. = Ctenidial muscles.
ct. n. = Ctenidial nerve.

D. m. s. = Dorsal trans. muscle sheet.
D. pr. m. = Dorsal protractor muscles.
Dg.'' = Lobe of stomach.
Dg.c.'' Dg.c.' = Cells of digestive gland.
Dg. con. = Connective tissue of gland.
Dg.d. = Opening of post. digestive gland duct.
Dg.d.' = Opening of ant. dig. gland duct.
Dg. gl. = Digestive gland.
Dg. gr. = Granules of gland cells.
Dg. nuc. = Nucleus of gl. cell.

Eff. ct. = Efferent branchial vessel.

Foot = Foot.
Foll. ep. = Follicular epithelium.

Ge. ep. = Germinal epithelium.
Gl. c. = Gland cells.
Go. = Gonad.

l.r.r. = Dorsal retractor muscles.
L.t.b. = Lateral odontophoral bands.
Lam. pr. = Lamellae of secondary system.
Lam. v. = Vein of renal lamella.
Lens = Lens.
Ling. con. = Connective tissue of odontophore.
Ln. g. = Gland of Leiblein.

M. = Mouth.
m.v.r. = Median ventral muscles.
mem. = Membranous wall of larva.
Mu. gl. = Mucous gland.
Mus. circ. = Circular muscles.
Mus. col. = Transverse sections of mus. fibres.

N. ax. = Nerve of ctenidial axis.
n.ot. = Otocyst nerve.
neph. gl. = Nephridial gland.
Nuc. = Nucleus.
Nuc. Int. C. = Nuclei of interstitial cells.

O. cav. = Lumen of oesophagus.
oe. con. = Connective tissue with longitud. muscles.
oe. con.' = Connective tissue.
oes. = Oesophagus.
Op. = Operculum.
Op. n. = Optic nerve.

Os. n. = Osphradial nerve.
Osp. cil = Ciliated cell region of osphrad. leaflets.
Osp. gl. = Gland cell region of osphrad. leaflets.
Osp. so. = Sensory cell region of osphrad. leaflets.
Osph. = Osphradium.
Ot. = Otocyst.
ov. = Ovary (oviduct in figs. 38 and 37).
ova. = Eggs.
ovd. = Oviduct.
ovd.''' = Vaginal part of oviduct.

P. = Penis nerve.
Pall. = Mantle.
Pall. ep. = Mantle epithelium.
Pall. gl. = Mantle conn. tissue.
pall. n. & n.'' = Pallial nerves.
Ped. g. = Pedal ganglia.
Ped. gl. = Pedal gland.
ped. gr. = Pedal groove.
ped. mus. = Pedal muscles.
ped. n. = Pedal nerves.
Pen. = Penis.
Per. p. = Pericardial cavity.
Ph. = Pharynx.
Pig. = Pigment.
pl. l. = Left pleural ganglion.
pl. p. = Pleuro-pedal connective.
pl. r. = Right pleural ganglion.
pr. = Processes of retinal cells.
prob. = Proboscis.
prob. m. = Proboscis muscles.
Ps. cor. = Pseudo cornea.
Pul. = Larval heart.

r.' & r.'' = Retractor muscles (dorsal).
R. Sin. = Reno-mucous vessel.
Rect. = Rectum.
Ren. = Renal organ.
ren. cil. = Ciliated cells of renal epithelium.
ren. eff. = Vessels of renal organ.
ren. ep. = Renal epithelium.
ren. lam. = Renal lamella.
ren. r. = Renal ridges.
Ret. c. = Retinal cells.
rhyn. = Rhynchodoeum.
Rst. = Rhynchostome.

S. = Stomach.
S. gl. c. = Salivary gland cells.
Sal. d. = Salivary duct.
Sal. gl. = Salivary gland.
Siph. = Pallial siphon.
Siph. n. = Siphon nerves.
Sptd. = Spermatid.
Spte. = Spermatocyte.
Spz. = Spermatozoa.
St. = Stomach.
St. s. = Stiftchen.
sub. int. = Subintestinal ganglion.
sup. int. = Supraintestinal ganglion.
sup. m. = Supporting structure of ctenidial leaflets.

Tent. = Tentacle.
tent. = Tent. nerve (fig. 42).
tri. lat. = Triangle lateral.

V. def. = Vas deferens.
V. def.' = Coiled part of vas deferens
V. def.'' = Vas deferens in penis.
V. def. c. = Vas deferens canal.
V. e. m. = Ventral muscle sheet.
V. pr. m. = Ventral protractor muscles.
V. r. = Retractor muscles (dorsal).
v. r. m. = Ventral retractor muscles.
vas. d. = Vas deferens.
vel. = Velum.
vis. com. = Visceral commissure.

X. *con.* = Connect. tissue of mantle.

Zyg. = Zygoneuric connection.

PLATE I.

Fig. 1. Shell of *Buccinum undatum*. × $\frac{4}{5}$

Fig. 2. Section of Buccinum shell, showing septa at apex. × $\frac{5}{6}$

Fig. 3. View of part of columella of 5th whorl, showing attachment of columellar muscle. × $\frac{3}{2}$

Fig. 4. Surface view of periostracum.

Fig. 5. Superior surface of operculum. × 1.

Fig. 6. Longitudinal section of shell. × 40.

Fig. 7. General view of animal after removal of shell. × 1.

PLATE II.

Fig. 8. Roof of pallial cavity with organs of pallial complex. × slightly.

Fig. 9. Ventral surface of foot (expanded). × $\frac{1}{2}$.

Fig. 10. Transverse section of pedal groove and gland. × 17.

Fig. 11. Dissection showing cavity into which proboscis sheath is retracted and also rhynchocoel in which proboscis lies. × 1.

Fig. 12. Dissection of alimentary canal. Slightly reduced.

Fig. 13. Stomach as seen from digestive gland surface. Slightly reduced.

Fig. 14. Radula with teeth. × 48.

Fig. 15. Old teeth. × 64.

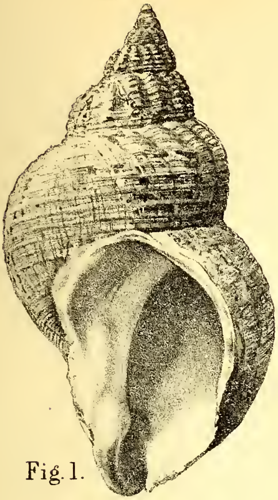
PLATE III.

Fig. 16. General view of odontophore, radula and muscles from above. Slightly magnified.

Fig. 17. Ventral end of radula with attached ventral retractors. Slightly magnified.

L.M.B.C. MEMOIR XX.

PLATE I.



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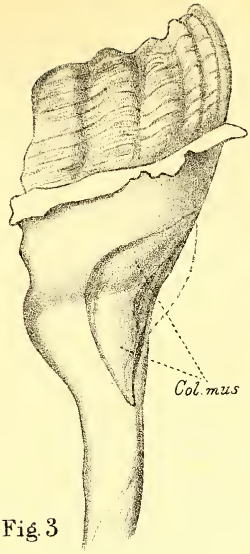

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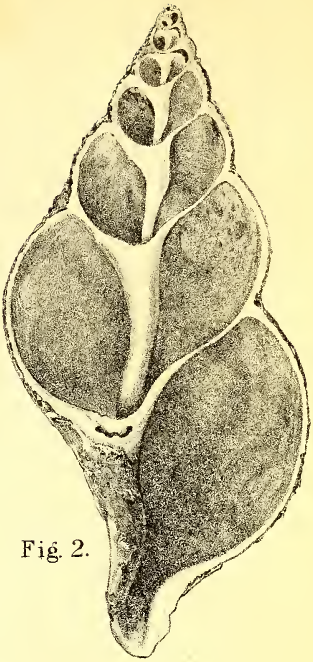

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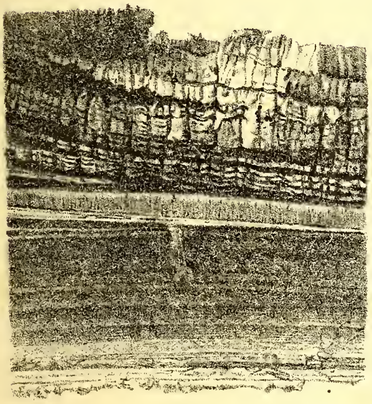

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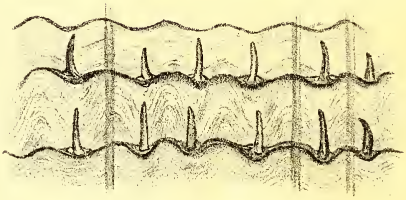

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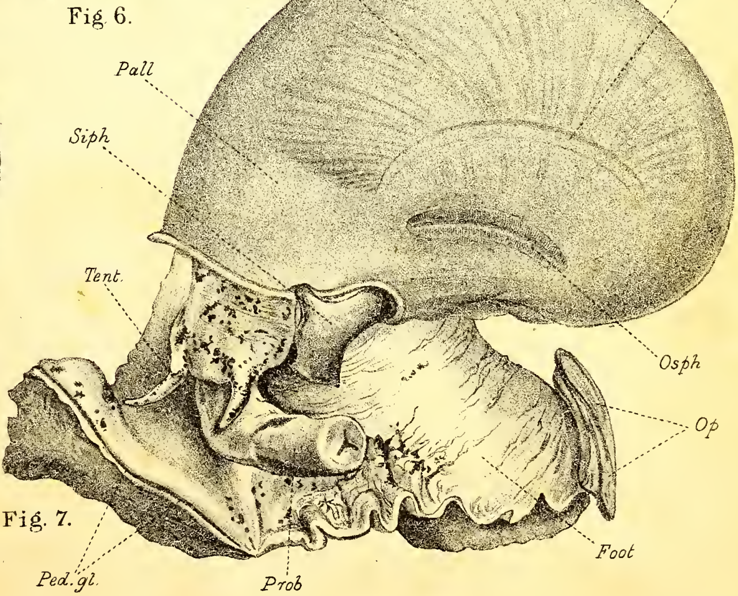

Fig. 7.

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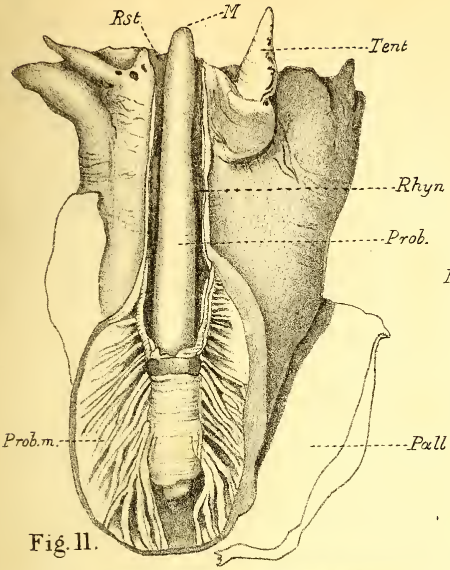

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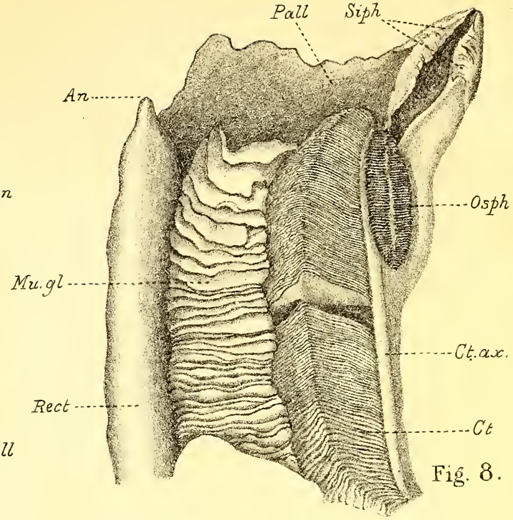

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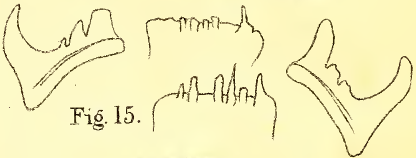

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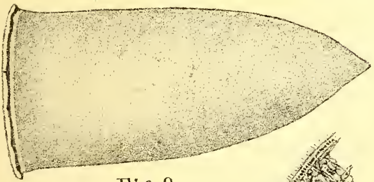

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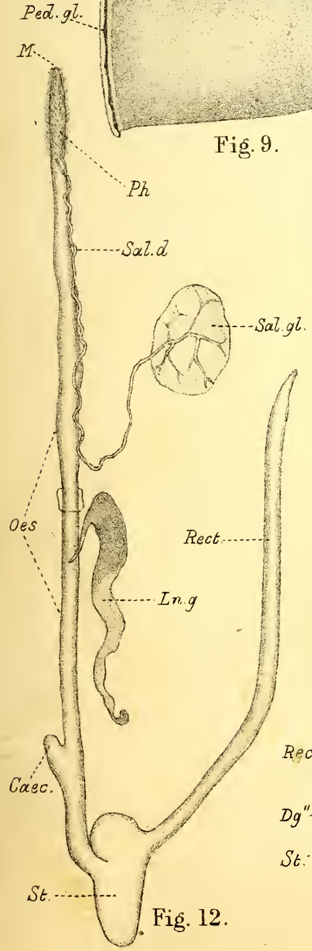

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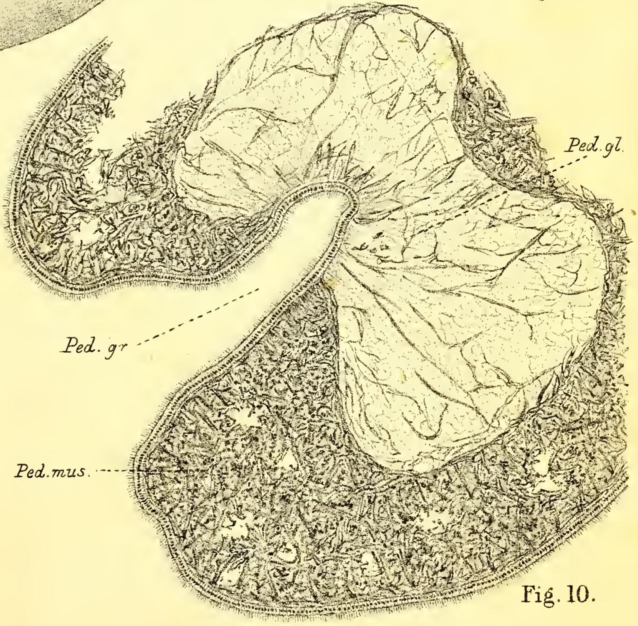

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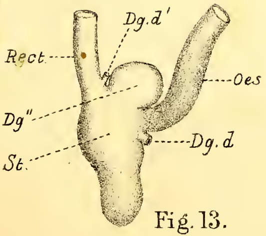

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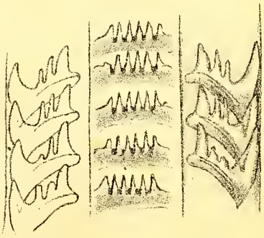

Fig. 14.

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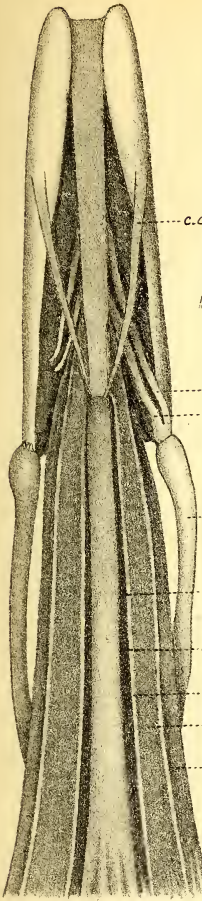

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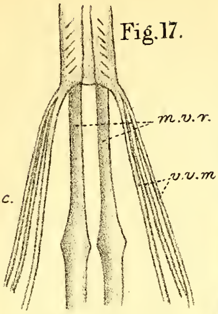

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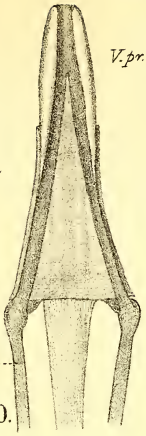

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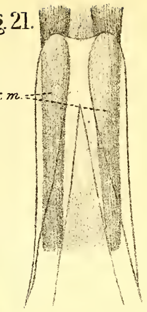

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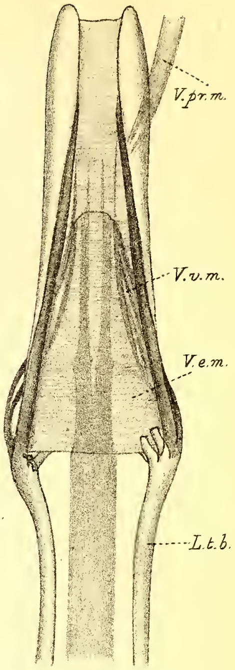

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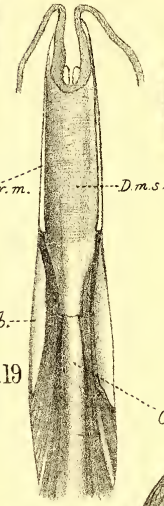

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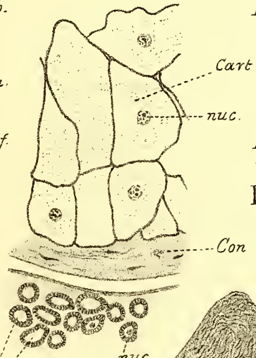

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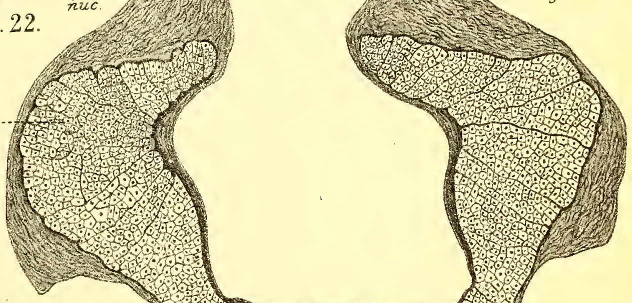

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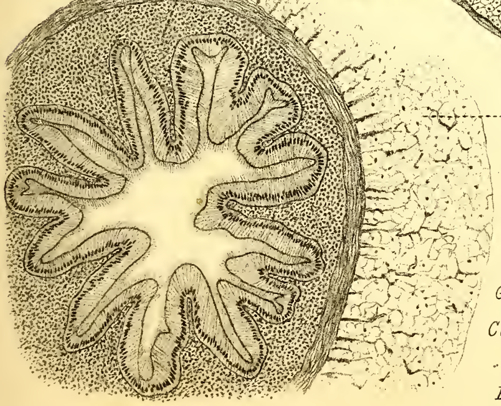

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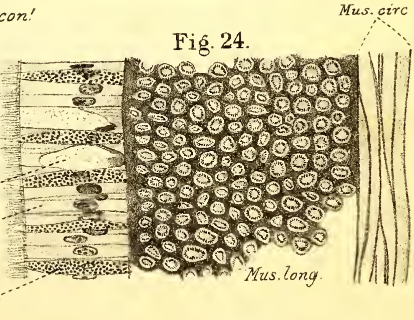

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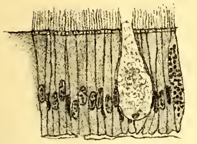

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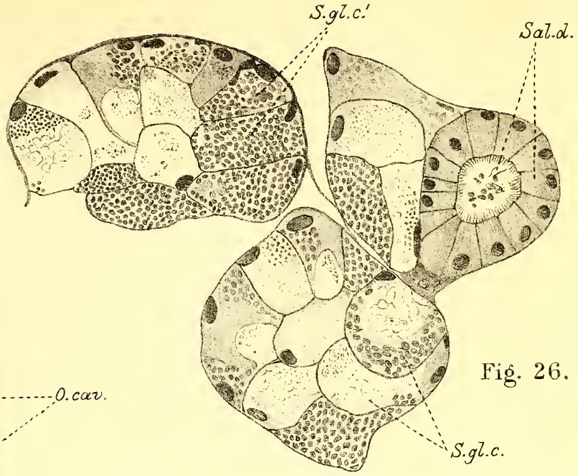

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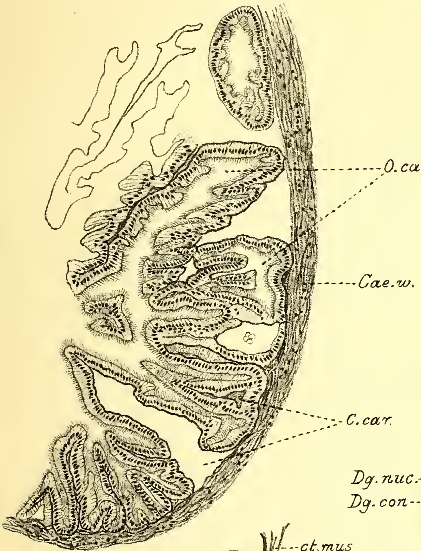

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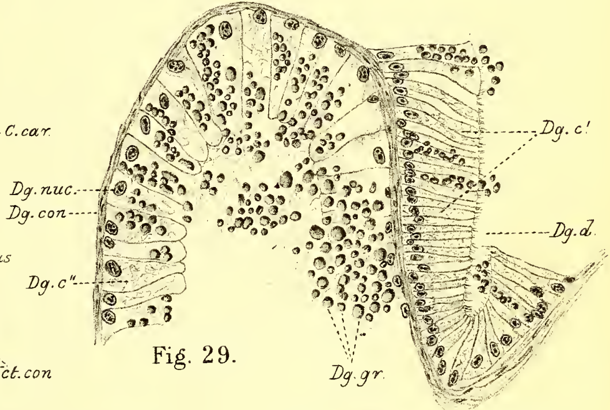

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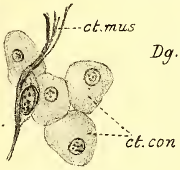

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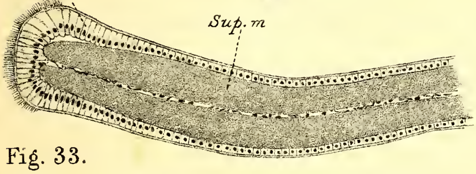

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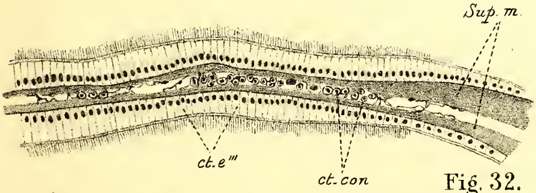

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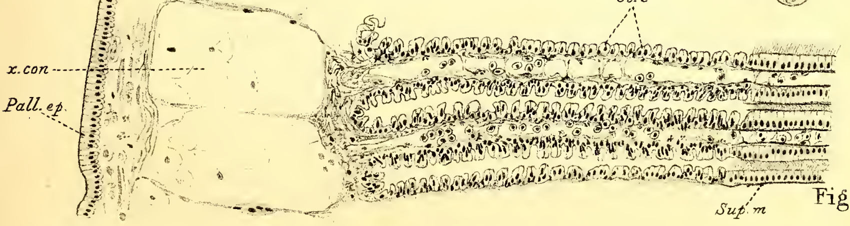

Fig. 31.

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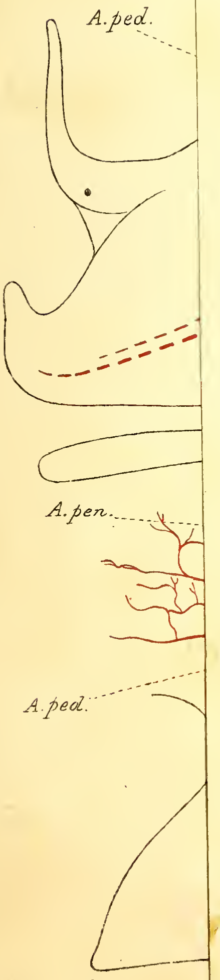
Fig. 38.



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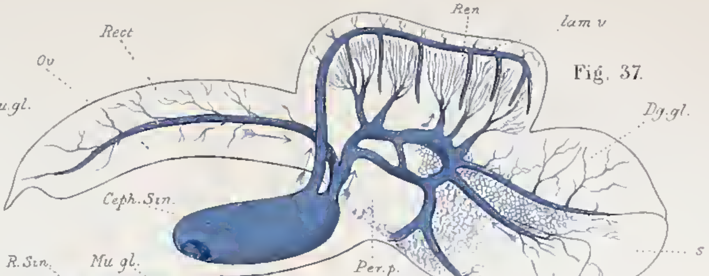

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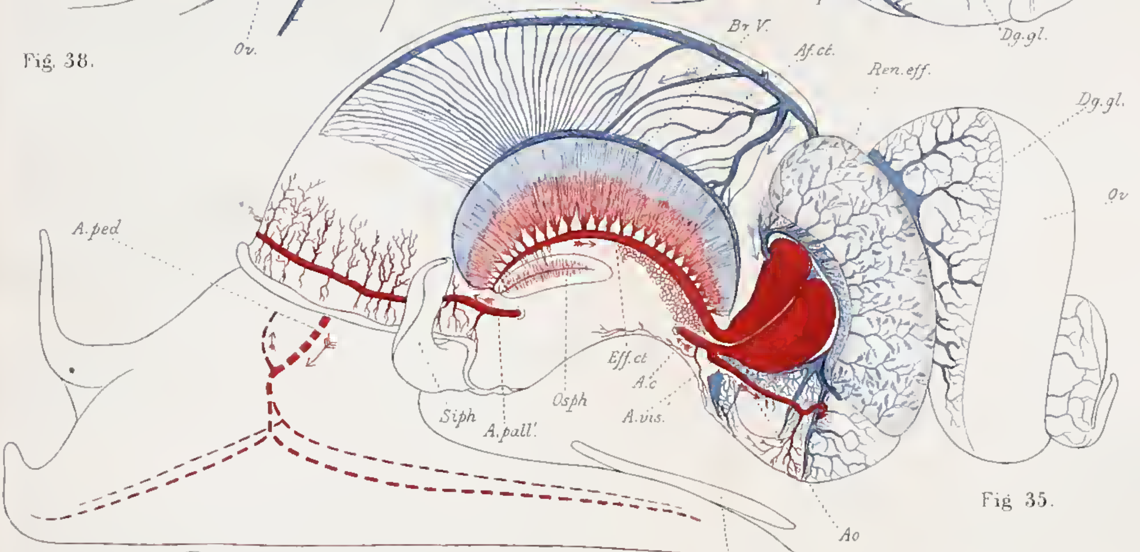

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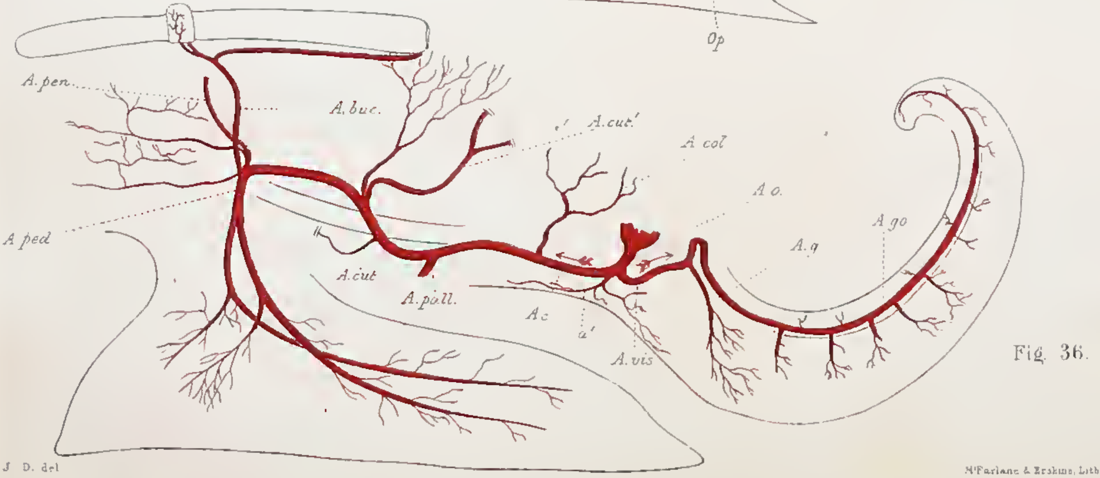

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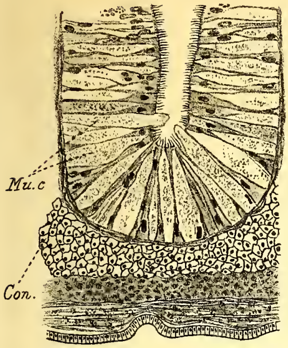

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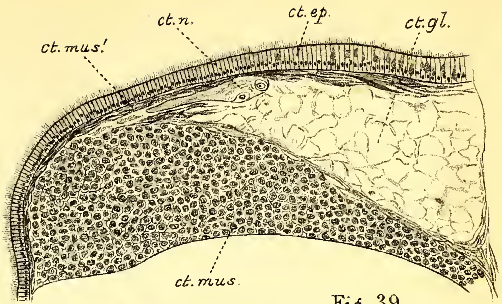

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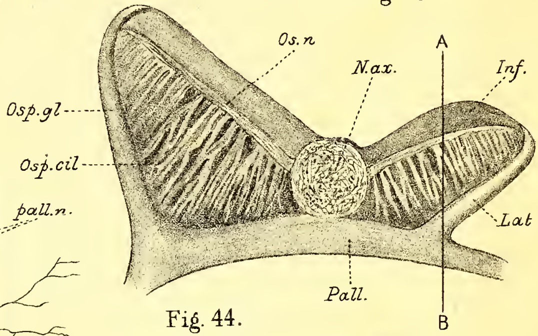

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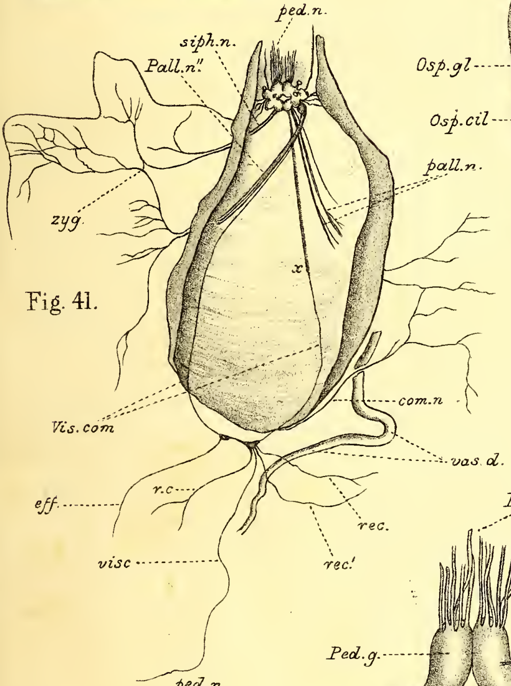

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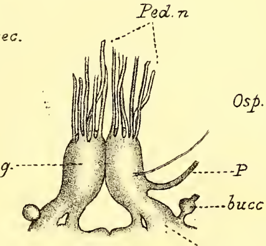

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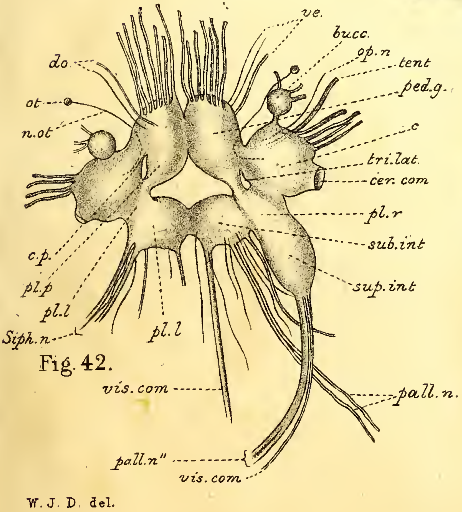

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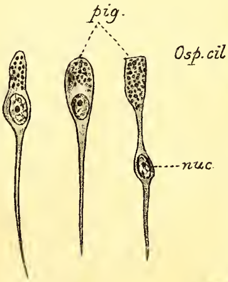

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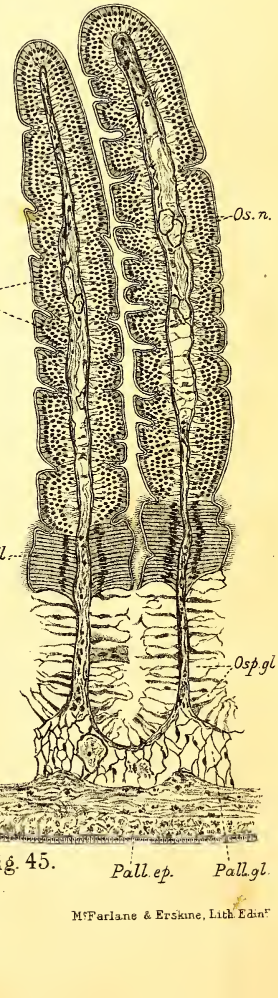

Fig. 45.

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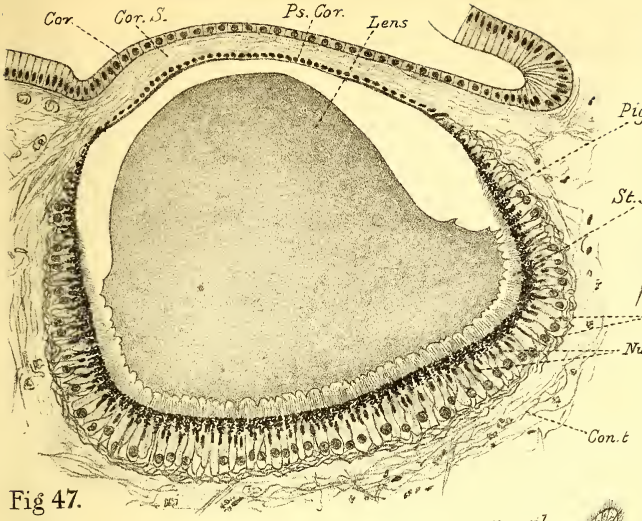

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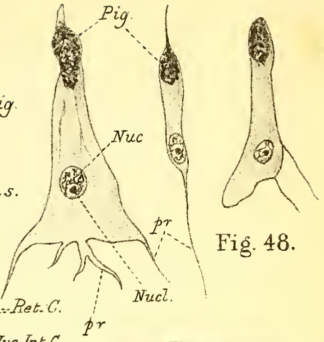

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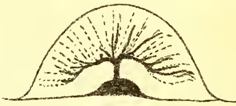

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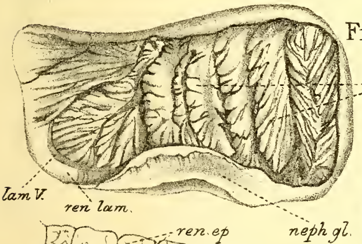

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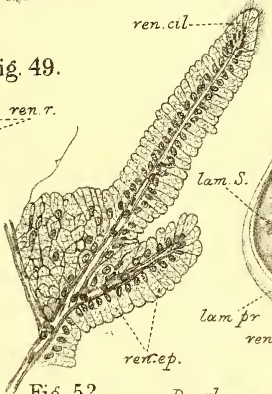

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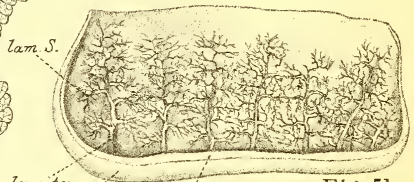

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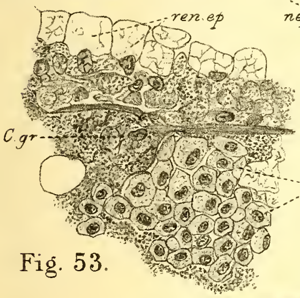

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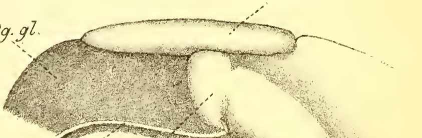

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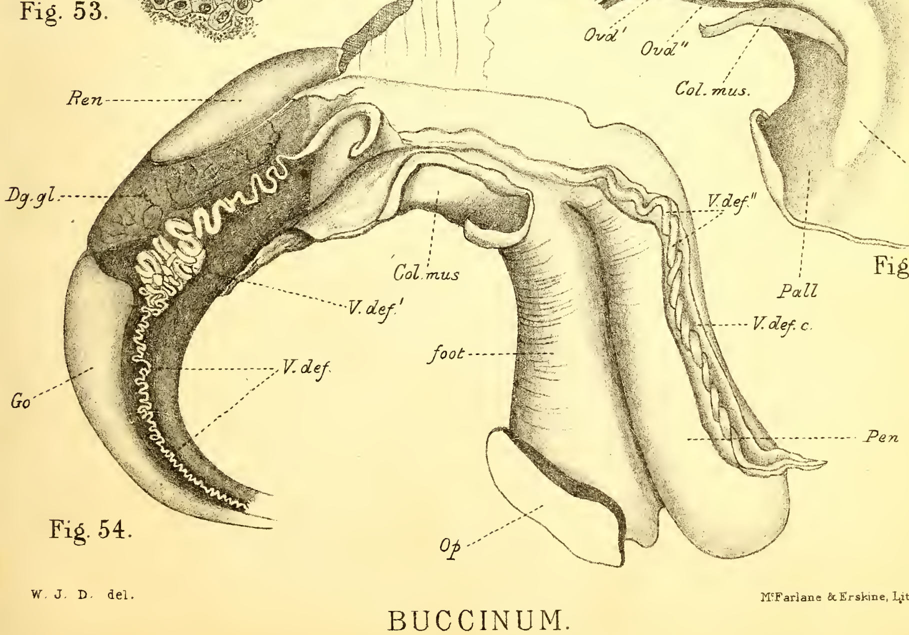

Fig. 54.

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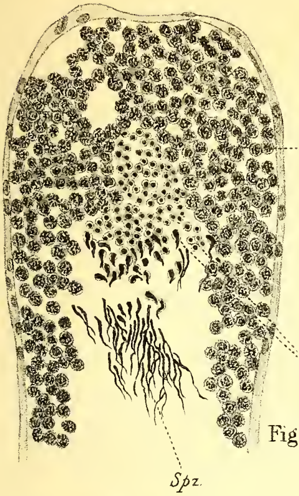

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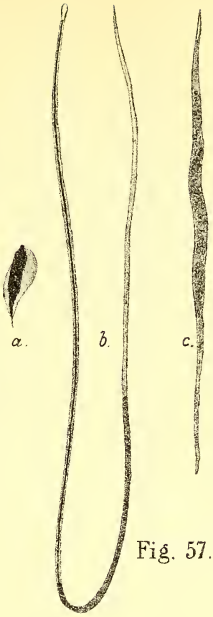

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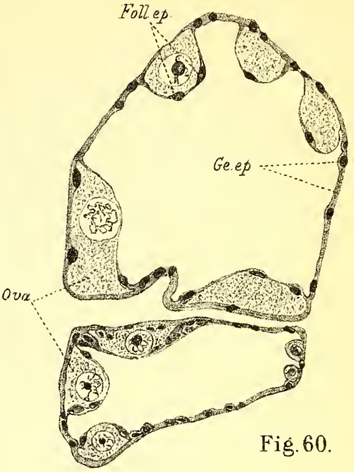

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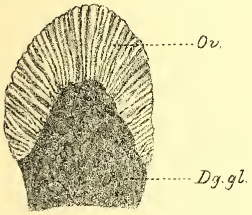

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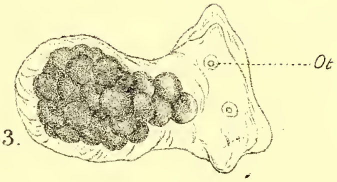
Fig. 61.



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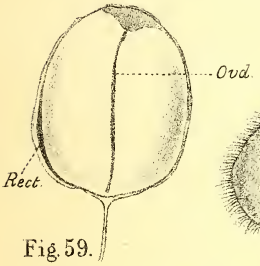

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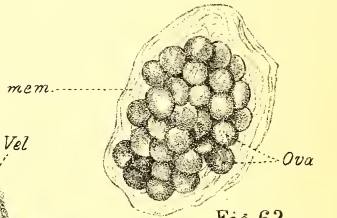

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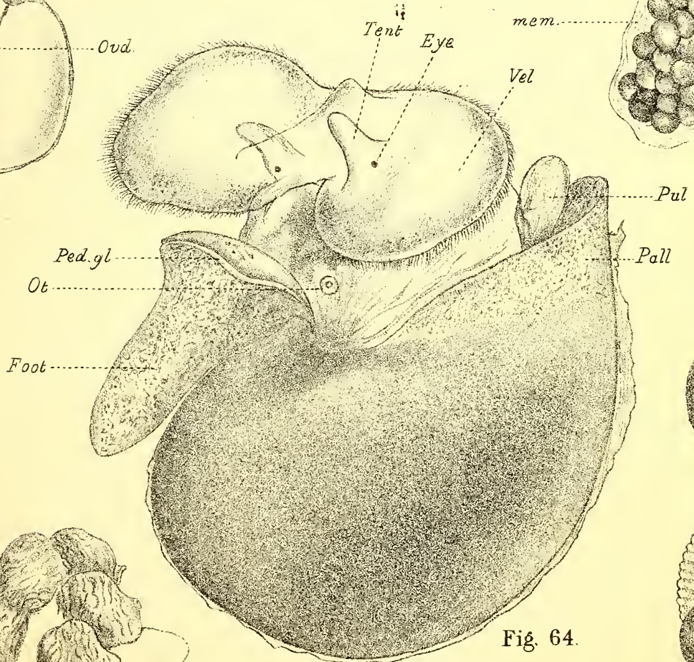

Fig. 64.

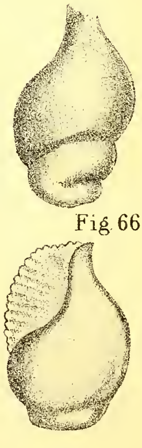

Fig. 66.

Fig. 65.

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BUCCINUM.

Fig. 18. Odontophoral cartilage (odontophoral tongue) with ventral muscles indicated through it. Slightly magnified.

Fig. 19. Odontophore from above before muscles are laid bare by cutting dorsal transverse sheath. Slightly magnified.

Fig. 20. Odontophoral tongue.

Fig. 21. Anterior end of odontophoral cartilage with ventral protractor muscles.

Fig. 22. Transverse section of cartilage and radula muscles. × 480.

Fig. 23. Transverse section near tip of odontophoral tongue.

Fig. 24. Transverse section of pharynx wall. × 200.

Fig. 25. Transverse section of oesophagus. × 30.

PLATE IV.

Fig. 26. Section through salivary gland and duct. × 450.

Fig. 27. Epithelium of oesophagus. × 800.

Fig. 28. Transverse section of oesophageal caecum. × 50.

Fig. 29. Transverse section of digestive gland. × 200.

Fig. 30. Section through wall of Gland of Leiblein. × 450.

Fig. 31. Transverse section through two gill leaflets.

Fig. 32. Transverse section through gill leaflet more distal to fig. 31.

Fig. 33. Transverse section through gill leaflet more distal to fig. 32.

(The three sections are consecutive and all × 100.)

Fig. 34. Cells from inner surface of wall of gill. × 800.

PLATE V.

Fig. 35. General view of superficial blood vessels. Slightly enlarged.

Fig. 36. General view of arterial system. Slightly enlarged.

Fig. 37. Venous System and especially circulation in Renal Organ. × 1.

Fig. 38. Veins on external surface of Oviduct, etc. × 1.

PLATE VI.

Fig. 39. Transverse section of Ctenidial axis. × 40.

Fig. 40. Transverse section of Mucous gland. × 50.

Fig. 41. Nervous system. × 1.

Fig. 42. Anterior Nerve centres, view from inside of nerve collar. × 6.

Fig. 43. Pedal Ganglia in male. × 6.

Fig. 44. Two leaflets of Osphradium. × 10.

Fig. 45. Transverse section of osphradial leaflets. × 70.

Fig. 46. Cells from osphradium (maceration preparation). × 400.

PLATE VII.

Fig. 47. Transverse section through eye. × 140.

Fig. 48. Cells from retina (maceration preparation). × 400.

Fig. 49. Outer wall of renal organ with renal filaments seen from the lumen. × 1.

Fig. 50. Nephridial Gland seen from inner surface (facing lumen of renal organ). × 1.

Fig. 51. Outer wall of renal organ after removal of renal filaments, showing secondary lamellae. × 1.

Fig. 51a. Diagram showing how blood passes to renal filaments by vessels crossing the lumen of the renal organ.
Fig. 52. T.S. Renal filaments. × 200.
Fig. 53. T.S. Secondary lamella. × 200.
Fig. 54. Male gonad and ducts with penis. × 1.
Fig. 55. Female gonoducts. × 1.

Plate VIII.

Fig. 56. Section of tubule of testis showing formation of spermatozoa. × 1.
Fig. 57a. Spermatid.
Fig. 57b. "Hair-like" spermatozoon }
Fig. 57c. "Worm-like" spermatozoon } after Retzius.
Fig. 58. Transverse section of ovary. Very slightly magnified.
Fig. 59. Transverse section of vaginal part of oviduct. Slightly magnified.
Fig. 60. Transverse section of ovary. × 150.
Fig. 61. Under surface of egg capsule showing pore of escape. × 1.
Fig. 62. Early stage in development of larva after cannibalism (after Koren and Daniellsen).
Fig. 63. Very early larval stage, otocysts present. (after K. and D).
Fig. 64. Late veliger larva (original). × 50.
Fig. 65. Egg capsules. Slightly reduced.
Fig. 66. Shells of young Buccinum at time of departure from egg capsules. × 10.

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