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.

## X.

# PATELLA

## (THE COMMON LIMPET)

BY

J. R. AINSWORTH DAVIS, M.A.,
*Professor of Zoology in the University College of Wales, Aberystwyth;*

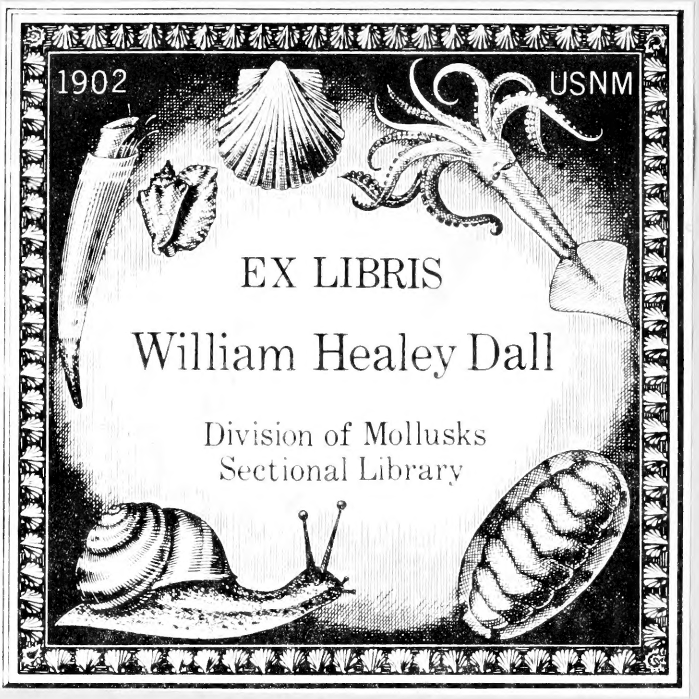
AND

H. J. FLEURE, B.Sc.,
*Fellow of the University of Wales.*

(With 4 Plates)

PRICE TWO SHILLINGS AND SIXPENCE

LONDON
WILLIAMS & NORGATE
MAY, 1903



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*L.M.B.C. MEMOIRS.*

X.

# PATELLA.

# NOTICE.

The Committee desire to intimate that no copies of these Memoirs will be presented or exchanged, as the prices have been fixed on such a scale that most of the copies will have to be sold to meet the cost of production.

The Memoirs may be obtained, post free at the nett prices stated, from Messrs. Williams and Norgate, 14, Henrietta Street, Covent Garden, London.

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# PATELLA

(THE COMMON LIMPET)

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James Richard
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# EDITOR'S PREFACE.

The Liverpool Marine Biology Committee was constituted in 1885, with the object of investigating the Fauna and Flora of the Irish Sea.

The dredging, trawling, and other collecting expeditions organised by the Committee have been carried on intermittently since that time, and a considerable amount of material, both published and unpublished, has been accumulated. Sixteen Annual Reports of the Committee and five volumes dealing with the "Fauna and Flora" have been issued. At an early stage of the investigations it became evident that a Biological Station or Laboratory on the sea-shore nearer the usual collecting grounds than Liverpool would be a material assistance in the work. Consequently the Committee, in 1887, established the Puffin Island Biological Station on the North Coast of Anglesey, and later on, in 1892, moved to the more commodious and accessible Station at Port Erin in the centre of the rich collecting grounds of the south end of the Isle of Man. A new and larger Biological Station and Fish Hatchery, on a more convenient site, has now been erected, and was opened for work last summer, in July, 1902.

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

The objects of the Committee and of the workers at the Biological Station have hitherto been chiefly faunistic and speciographic. The work must necessarily be so at first 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 greatly to the records of the Fauna and Flora. But the papers in the present series are quite distinct from these previous publications in name, in treatment, and in purpose. They are called the "L.M.B.C. Memoirs," each treats of one type, and they are issued separately as they are ready, and will be obtainable Memoir by Memoir as they appear, or later bound up in convenient volumes. It is hoped that such a series of special studies, written by those who are thoroughly familiar with the forms of which they treat, will be found of value by students of Biology in laboratories and in Marine Stations, and will be welcomed by many others working privately at Marine Natural History.

The forms selected are, as far as possible, common L.M.B.C. (Irish Sea) animals and plants of which no adequate account already exists in the text-books. Probably most of the specialists who have taken part in the L.M.B.C. work in the past will prepare accounts of one or more representatives of their groups. The following have performed or promised their services, and in many cases the Memoir is either issued or far advanced. The first Memoir appeared in October and the second in December, 1899, the third in February, and the fourth in April, 1900, the fifth in January, the sixth in March, the seventh in April, and the eighth in December, 1901, the ninth in July, 1902, while this tenth one will be ready in May, 1903, and an eleventh later in the summer; others will follow, it is hoped, in rapid succession. Probably Arenicola, Myxine, Gammarus, and the Oyster will be ready next.

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.
,, VI. Lepeophtheirus and Lernæa, Andrew Scott, 62 pp., 5 Pls., 2s.
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,, IX. Chondrus, O. V. Darbishire, 50 pp., 7 Pls., 2s. 6d.
,, X. Patella, J. R. A. Davis and H. J. Fleure, 84 pp., 4 Pls., 2s. 6d.
Arenicola, J. H. Ashworth.
Myxine, F. J. Cole.
Buccinum, W. B. Randles.
Bugula, Laura R. Thornely.
Oyster, W. A. Herdman and J. T. Jenkins.
Ostracod (Cythere), Andrew Scott.
Portunus, J. Pearson and W. Tattersall.
Cycloporus, F. F. Laidlaw.
Dendronotus, J. A. Clubb.

Peridinians, G. Murray and F. G. Whitting.
Zostera, R. J. Harvey Gibson.
Himanthalia, C. E. Jones.
Diatoms, F. E. Weiss.
Fucus, J. B. Farmer.
Antedon, H. C. Chadwick.
Gammarus, M. Cussans.
Botrylloides, W. A. Herdman.
Cuttle-Fish (Eledone), W. E. Hoyle.
Calanus, I. C. Thompson.
Actinia, J. A. Clubb.
Hydroid, E. T. Browne.
Calcareous Sponge, R. Hanitsch.

In addition to these, other Memoirs will be arranged for, on suitable types, such as *Sagitta* (by Mr. Cole), a Cestode (by Mr. Shipley), an Isopod, and a Pycnogonid.

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

W. A. Herdman.

University College, Liverpool,
*April*, 1903.

# L.M.B.C. MEMOIRS.

## No. X. PATELLA.

BY

Professor J. R. AINSWORTH DAVIS,

AND

H. J. FLEURE, B.Sc.

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## PREFACE.

THE chief objects of this Memoir are:—

(1) To provide a reliable account of the anatomy of *Patella vulgata*.

(2) To treat the subject matter so as to show the place among Gastropods which this type occupies.

The work has been carried out in the Zoological Laboratory of the University College of Wales; and no facts are included that we have been unable to personally verify, except those of the short résumé we have given from Patten with regard to the development.

It is unnecessary to refer to the many authors whose works we have had to consult, but we wish to acknowledge our special indebtedness to the researches and theories of Ray Lankester, J. W. Spengel, Pelseneer, Rémy Perrier, Bela Haller, Lacaze Duthiers, Boutan, Grobben, and Patten.

The matter which we believe to be new includes the following chief points:-

(1) A lateral glandular streak has been found along each side of the foot of young specimens, resembling that found in *Nacella* and its allies.

(2) A muscular zone (which we name the internal pallial muscle) has been found extending in the mantle between the tips of the shell muscle.

(3) The structure of the Crop, and inferences drawn therefrom as to special torsion of the viscera of Docoglossa during consolidation of the visceral hump.

(4) The respiratory function of the nuchal cavity as regards damp air.

(5) Discussion of the evolution of the present topographical relations of rectum, kidneys, pericardium, and heart.

(6) Details of mantle innervation and pallial tentacles.

Our best thanks are due to Professor W. A. Herdman, D.Sc., F.R.S., the Editor of this series, for his general advice and special suggestions, and to Prof. J. Travis Jenkins, D.Sc., Ph.D., late of Aberystwyth, for working out several intricate details of mantle innervation as well as other points. The greater number of the drawings are original, but a few are based on those given in Lankester's article "Mollusca," in the Encyclopædia Britannica (9th edition), and those of the development are after Patten.

# THE COMMON LIMPET (*Patella vulgata*).

## General Description.

The Limpet belongs to the asymmetrical class of Mollusca (*Gastropoda*), and, though it has lost both ctenidia, is referred to the order Prosobranchia, the members of which have the ctenidium (or ctenidia) anterior to the heart. Among the Prosobranchia its place is in the group of Docoglossa, while the absence of ctenidia and presence of a compensating circlet of pallial gills show that it belongs to the sub-group Cyclobranchiata.

Limpet shells are so simple and their few characters are so subject to variation, that it is not easy to classify the British forms into varieties and species. Of these, however, two are generally recognised:—

*P. vulgata* has its shell substance greyish or yellowish, but never white. The margin is fairly simple, and, though the radiating ribs vary a good deal, they are not usually very strongly developed. Aged shells have their vertices more central than those of young ones.

*P. athletica* has its shell substance white, and possesses numerous elevated ribs with regular series of projecting scales, the interstices being stained with brown. The shell is usually depressed. Forbes and Hanley state that Clark found the pallial tentacles shorter and thicker and the pallial gills longer than in *P. vulgata*. This species is fairly abundant but is locally distributed. It is usually found far down the intertidal zone, and its flesh is said to be tougher than *P. vulgata*. Jeffreys considers *P. athletica* to be merely a variety, and he enumerates three other varieties:—*P. elevata*—small, round, high; *P. picta*—small, thin, alternate ribs reddish and dark blue; *P. intermedia*—smaller, flatter, and oval, finer ribs, orange crown, inside of shell golden yellow or flesh-tint, fine ribs towards edges.

HABITAT.—*Patella* inhabits the intertidal zone, affixing itself to rocks with such force that it is dislodged only with some difficulty. The method of this adhesion is not known with absolute certainty. Limpets will hold on very tenaciously to a surface smaller than the foot, so it seems improbable that the latter acts like a sucker as has been suggested. Another view is that the animal is fixed to the rock by means of a glutinous substance secreted by its foot, but, from examination of specimens allowed to fix themselves to plate glass, it seems that this idea is also ill-founded. The most plausible explanation, and the one supported by our evidence, is that it is a case of adhesion of two very closely apposed surfaces, the foot being, so to speak, rolled out on the rock.

When the young limpet finds a suitable spot, it makes a home of it, returning thither even after wandering some distance in search of food. This " homing " faculty, noted by observers since the days of Aristotle, is one of the most remarkable endowments of the limpet, and it will be referred to further on, when the sense organs are described. One of us has studied this matter by observing animals, specially marked with enamel paint, which were moved and watched at suitable intervals.

As a result of continued residence on one spot an oval depression is formed in the rock-surface, at any rate on the softer and smoother rocks. This is called the limpet's scar. It has been suggested that the scar is made by the chemical action of an acid secretion of the foot, but there is no proof that any such secretion is produced, and well-marked scars are formed upon siliceous rocks. The distinctness of the scar appears to vary inversely as the hardness of the rocks, and its peripheral portion is deepest. Probably the excavation results from the mechanical action of the foot surface and of the bevelled edge of the shell. During life the animal constantly leaves and returns to its home, and even the comparatively soft foot must, therefore, bring about an appreciable amount of wear, especially as fixation is usually preceded by a certain amount of shuffling or twisting round on the scar. The deeper margin of the scar clearly indicates shell action.

An allied form, *Helcion pellucidum*, found at the top of the Laminarian zone, lives, when adult, in a sheltered "home" excavated in the bulb or, more rarely, in the frond of Laminaria, and possesses the same faculty of returning thereto after excursions. The depressions in the Laminaria surface are deeply eaten out, and have tracks leading from them. The shell is thinner than that of *Patella*.

FOOD AND ENEMIES.—The chief food of limpets consists of the minute Algæ covering the rocks, but they also eat the larger forms *Corallina, Melobesia, Fucus,* and *Laminaria.* With this food they must also take in a number of minute animals. The details of the feeding process are discussed later, in the description of the alimentary canal. They feed, at least partly, while the tide is low, returning to their scars with its advance to avoid danger from the tidal wash, but it seems likely that they also feed a good deal when covered by water; some, indeed, have actually been watched doing so, and, moreover, the finest limpets are often found low down on the shore where their uncovered period is necessarily very limited. Aquarium specimens also can be kept submerged for weeks, apparently without ill effect. On the other hand, tiny limpets and feeble scars occur in abundance high up the shore. The rock barnacles (Balanus) compete with the limpets for space, and in this, perhaps, lies the need of the development of the homing faculty, since a smooth surface is required for fixation. Limpets cannot, moreover, successfully invade an area already occupied by these competitors. Fixation is a protective measure against the wash of the tide and the attacks of enemies, and the normal adhesion can be largely increased when the shell is touched.

The limpet, with these habits, does not seem to have much to fear from active enemies when once the manifold dangers of youth are past; but it is to some extent eaten by seabirds, by the common starfish, and even by rats, while man is, in some districts, a serious enemy.

## External Characters.

I. Shell.—The shell is conical and its base has an elliptical outline, the anteroposterior diameter being greater than the transverse. The apex of the cone is in the sagittal plane and nearer the front end; its exact form varies greatly, being sometimes, especially in young limpets, bent over and pointing forwards. The external markings of the shell vary remarkably within the limits of the species, but there are always some lines radiating from the apex and other lines concentric about that point. The former are raised ribs running to the shell margin, but they vary considerably in number and in prominence; the latter are lines of growth. The edge of the shell is notched proportionately to the prominence of the radiating ribs, and its rim is roughly chisel-shaped, with the bevelled edge inside, and forming an efficient instrument for enlarging the scar and deepening its margin. There is considerable variation in the general shape of limpet shells, those of animals living far up the shore and on exposed flat surfaces being typically low and broad, while those of animals living nearer the low tide limits and in sheltered positions are often high and narrow, but these rules are not without exceptions. Plate I., fig. 1, shows extreme types of shell.

The larval shell shows the beginning of a spiral. This shell grows chiefly by additions to its posterior border and its mouth is thus lengthened and broadened until it has a cap-shape with the apex (the remains of the spiral) far forwards. This apex then breaks off and the hole is closed by secretion of nacreous material on the inside. In further growth the anterior border seems to have a larger share and older shells thus usually have the apex further back than young ones. This, however, depends largely on the precise form of the shell, the broad low cones above mentioned having the apex further back than the tall narrow ones. The transition from spiral to conical shell, with the correlated consolidation of the visceral hump and the broadening of the foot into an oval adhesive sole, are all adaptations to this animal's special mode of life. Limpets are peculiarly exposed to the wash of the tide and of storms, and it is an advantage to them to be able to adhere firmly to the rock and present as small an area as possible to the waves. Hence the thick, plate-like foot and the preparation of a smooth surface to which it can effectively cling. The shape of the shell offers a minimum amount of resistance to waves and tide; at the same time the shell is an effective protection against enemies, for it can be pulled down so as to completely cover the animal, while the deep margin of the scar increases the difficulty of detachment. The peripheral position of the shell-muscle, and its symmetrical disposition are adaptations to this protective arrangement.

The spiral-shelled Gastropods protect themselves by retreating far into the shell, the part of the animal nearest the opening being further protected in many cases by an operculum. When thus retracted, the animal can be knocked about without incurring serious risks. This form of protection is suited to an actively creeping animal. In a cap-shelled form the power of retraction is much less and the operculum has gone, so the animal draws down its cap and remains tightly affixed to the spot until the danger has passed.

Internally the shell shows markings, of which the most conspicuous is the horse-shoe shaped impression, with expanded front ends, of the shell muscle. This impression is divided into partially distinct areas corresponding to the component bundles or fasciculi making up this muscle. On the outer side of the horse-shoe muscle we see the pallial impression which is continuous across the front of the shell.

Sections of the shell show its structure to be as follows (Plate I., fig. 2):—

A.—A thin irregular external layer of brownish colour.

B.—A middle layer made up of very compact crystalline material the external part of which (*a*) is penetrated in every direction by branching minute canals while its inner part (*b*) is comparatively clear.

C.—An internal layer made up of numerous smaller layers extending for varying distances. Each such layer is, in its turn, made up of parallel but obliquely arranged lamellæ. This portion is thickest under the dome. It is the nacreous or pearly layer.

Accounts of the shell structure have been given by Gibson and by Boutan. Gibson noted the minute branching canals in the external part of the shell and ventured to suggest that they were due to boring Algæ, which our observations make us think highly probable.

Boutan speaks of an intermediate layer between the middle and internal, but, unless this corresponds with the inner and clearer portion (B, *b*) spoken of above, we have not found it.

II. SOFT PARTS OF EXTERIOR.—Before removal of the shell the prominent ventral foot, ill-defined head, and continuous mantle-skirt can be made out in ventral (fig. 3) and side view of the body.

(*a*) The oval muscular FOOT has a well-defined wavy edge which separates a smooth ventral surface from the smooth sides. Laterally and posteriorly the latter rise almost vertically to the insertion of the mantle, and anteriorly become continuous with the head.

(*b*) The HEAD, as seen from the side, is a prominent muscular projection overhanging the front end of the foot (fig. 5). In shape it may be compared to a truncated demi-cone with the cut end turned forwards, rounded off, and bent somewhat downwards to form a snout, the circular muscle in the wall of which is very well developed, and is practically a sphincter. The flat side of the demi-cone faces downwards, and is marked off by a distinct transverse groove from the snout. On either side of the groove is a well-marked retractor muscle band connecting the head with the side of the foot. The upwardly facing curved surface of the demi-cone is continued backwards till it passes into and becomes the floor of a cavity of which the wide opening can be seen above the head. This is the Nuchal cavity.

. The transversely oval mouth situated at the front end of the head is bounded by a continuous frilled lip, having a reniform outline resulting from an indentation of its ventral half. The lip is clearly divided into a long dorso-lateral portion and a short sharply incurved ventral portion. There is a depression at the junction of these two parts on either side. The mouth area faces downwards, and is placed on the end of the freely-projecting truncated end of the demi-cone, to which the term "snout" has been applied. The form of the mouth and lips is evidently adapted to the process of scraping forwards by which the animal feeds, and there is a marked contrast with the vertically elongated seizing mouth of a *Haliotis* or a *Pleurotomaria*. The snout is devoid of any power of introversion, and has no claim to be styled a "proboscis."

An elongated cephalic tentacle, swollen at its base, is attached on either side just behind the snout in line with the front end of the retractor muscle band, which runs back from the head to the foot. The eye is visible as a small black pigment spot on the posterior side of the thickened base of the tentacle.

(*c*) The MANTLE is a continuous flap or skirt, running completely round the body and lining the marginal part of the shell. The pallial impression is due to muscle fibres which take origin not far from the mantle edge and are inserted into the shell over a continuous band-like area a little above the margin. The mantle is of greatest extent in front, since here it roofs the nuchal cavity, the opening of which has already been seen. The edge of the mantle is pigmented and slightly thickened, and it bears numerous pallial tentacles each arising from the bottom of a pit into which it can be retracted. In a living animal, observed when covered with sea water, these organs can usually be seen projecting as a delicate fringe beyond the edge of the shell. The pallial tentacles are of two kinds, large and small, arranged in a regular manner, the latter being by far the more numerous. There may be over three hundred tentacles in a large specimen, and the number appears to increase with age. The mantle bounds externally a deep groove, the pallial cavity, the inner side of which, except in front, is formed by the side of the foot. Above the head a large transverse opening leads into the nuchal cavity already mentioned. This may be regarded as a local deepening of the pallial cavity, originally formed as a "branchial cavity" to shelter Ctenidia.

Projecting from the inner surface of the mantle are a large number of plate-like pallial gills, which are flattened in a direction perpendicular to the curve of the mantle outline. They form a continuous series right round the body, except at the left end of the nuchal opening (fig. 3); at this point the pallial vein, which completely encircles the gills, runs in to enter the heart. These pallial gills are secondary structures, which have replaced the primary gills, or ctenidia, just mentioned.

After removal of the shell the following points can be made out in dorsal view (fig. 4): —

(*a*) The shell muscle shaped like a horse-shoe with forwardly directed thickened ends. It is divided into a variable number (12-17) of fasciculi, separated by transverse fibrous septa.

(*b*) The mantle skirt running right round the body external to the shell muscle. In front it extends backwards for a short distance between the ends of this muscle to constitute the roof of the nuchal cavity. Just external to the shell muscle is seen the band of attachment of the pallial muscle to the shell. Just internal to the anterior part of this attachment band there is a very well marked second line of attachment running between the tips of the shell muscle and indicating the front boundary of the nuchal cavity. This is the internal pallial muscle. The mantle is pigmented dorsally near its edge, and so also is its band of muscular attachment, but the attachment zone of the internal pallial muscle is not pigmented.

(*c*) The low visceral hump occupies nearly the whole space within the shell muscle, and is therefore oval in outline, but the front end is truncated where it adjoins the back of the nuchal cavity. The hump is covered with a very thin layer of black pigmented epithelium which can be brushed off without difficulty; limpets are largely exposed to the baking action of the sun and this pigment may have been developed as a protective measure. After its removal the following organs are seen by transparency (fig. 4):—

(*d*) The dorsal surface of the digestive gland occupying the central region.

(*e*) A superficial loop of intestine dividing off an obliquely oval patch in the centre. The two limbs of this loop run out to the edge of the mass near its right anterior corner.

(*f*) More or less of the coiled stomach, external to the left limb of the loop (*e*) above and concentric with it.

(*g*) The rectum running transversely a little way in front of the stomach, and bending forward on the right to reach the nuchal cavity.

(*h*) The somewhat triangular pericardium occupying the left front of the visceral mass. One side of it abuts against the left end of the shell muscle, a second side runs obliquely inwards from the shell muscle on the left to the nuchal cavity on the right, while the third side abuts upon the nuchal cavity. The second side is approximately parallel to the rectum which is a little way from it. The left front corner of the triangle is continued along the rounded left end of the shell muscle as far as the attachment of the internal pallial muscle.

(*i*) The kidneys, two in number, (1) a small left kidney between the rectum and the right side of the pericardium; (2) a very large right kidney, of which two diverging lobes almost completely encircle the visceral hump except at the extreme left front. The visible parts of the kidneys lie very superficially, closely bound to the visceral integument, and their boundaries can, as a rule, only be clearly seen in injected specimens, since, in uninjected ones, the digestive gland often shows through by transparency. As the renal waste is dark coloured, the kidney is fairly often naturally tinted so as to make its outline clear.

III. NUCHAL CAVITY AND RELATED APERTURES.—The continuous mantle cavity which lodges the pallial gills deepens in front to form a fair sized nuchal cavity, so-called because it lies above what may be called the neck region of the animal. It opens by a wide slit between the anterior ends of the shell muscle. Its roof is formed by a backward extension of the mantle, and its floor by the muscular body wall of the neck region. With the exception of the mouth, all the apertures of the body open into it, *i.e.*, the anus, the left renal opening, and the right renal opening (figs. 4 and 5). When the cavity is opened by careful removal of its roof the following structures can be made out:—

(*a*) The anal papilla opening into the back of the cavity upon the animal's right shoulder.

(*b*) On either side of this a renal papilla, the right being rather more conspicuous than the left.

(*c*) The pericardium, which bulges into the cavity along a line from the left tip of the shell muscle nearly to the left renal papilla.

(*d*) The pallial vein (also visible from outside before opening the nuchal cavity) at the left side of the cavity, running into the pericardium.

(*e*) The small "pulmonary veins" running in from the roof of the nuchal cavity (visible before opening) and piercing the pericardial wall to the right of *d*.

(*f*) The pair of sensory patches or osphradia, which probably cover the vestiges of the ancestral pair of ctenidia. Each structure is a minute orange or reddish coloured elevation on the floor of the nuchal cavity close against the shell muscle on either side. It is nearer the back of the nuchal cavity than the tip of the shell muscle. These structures prove that the nuchal cavity is really a branchial cavity of which the ctenidia have degenerated.

## BODY WALL, MUSCULAR SYSTEM, AND MANTLE.

The body of Patella is covered by a layer of columnar epithelium which in most parts possesses a well-developed cuticle. That covering the visceral hump is mostly black-pigmented as already mentioned; that covering the regions of muscular attachment is, as might be expected, much flattened. A great deal of the epithelium is ciliated in young animals. Unicellular glands are not common in the epidermis, but a few occur in the foot and mantle; they are of the usual goblet type. The covering tissues will be discussed in greater detail in connection with the various organs.

MUSCULAR SYSTEM.—Though muscle fibres are found in almost every part of the animal, there are special aggregations of them which need separate mention. These are the body-wall muscles of the head and neck, the foot, the shell muscle, the pallial muscles, and the muscles of the odontophore. The last of these will be described in treating of the odontophore.

The muscles of the dorsal body-wall in the head region comprise the following layers:—

(*a*) An outer transverse layer, (*b*) a layer of longitudinal and obliquely arranged fibres which are head retractors. There are also some fibres running transversely internal to (*b*).

The ventral body-wall in the head region is thicker, but possesses almost solely transverse and oblique fibres. The muscle of this region is continuous with that of the foot and shell muscle.

The general appearance of the foot has already been described. It is essentially a thickening of the ventral body wall made up, for the most part, of bundles of muscle fibres bound together by connective tissue. In the ventral part the fibres run in all directions, while in the dorsal part they are mostly horizontal and oblique. The fibres in the outer portion of the foot are steeply oblique, and these, together with some of the dorsal fibres, are continuous with the shell muscle. The absence of a horizontal circular muscle, and the many differences between the disposition of fibres here and in the suckers of various animals, tell against the hypothesis of a sucker-like action of the foot, which, as was said above, is also not supported by observation. The spaces between the bundles of muscle fibres contain blood and, when full, make the foot swell far beyond its usual size. Two of the blood spaces above mentioned are of special importance, they run along in the vicinity of the pedal nerve-cords, and it is from them that blood spreads to the remainder of the organ (fig. 8*a*).

In very young specimens (about $\frac{1}{4}$ in. long) there is a distinct glandular outgrowth from either side of the foot, which disappears more or less completely when the animal gets older. The outgrowth is, from its position and histological characters, the homologue of the "lateral streak" in *Nacella*, etc. There is also a rudimentary flap covering the glandular tissue in the anterior region, where also the whole structure is best developed. The persistence of this glandular tissue is possibly connected with the protection of the young animal against desiccation, to which it is specially liable in its habitat far up the tidal zone, and because of the greater ratio of surface to volume in smaller than in larger forms.

The foot (fig. 8*a*) is covered externally by a layer of columnar epithelium, which possesses more or less of a cuticle, with goblet cells here and there. The cells on the side of the foot are small, but increase in height towards the ventral surface, where they are fairly long and regular, with nuclei usually near the base. The ventral covering, as might be expected from the amount of wear to which it is subjected, seems to be shed frequently. The epithelium of the sides of the foot is thrown into a number of small ridges, which, in very young specimens, are found nearly up to the mantle attachment, but in older animals are mainly restricted to the part near the ventral edge. Internal to the epithelium of the sides of the foot is a deeply staining layer with nuclei, which is apparently a sub-epithelial nerve plexus, and from it there proceed outwards narrow deeply staining cells which are probably sensory. Beneath this covering tissue is a dermis, an irregular network of connective tissue with blood spaces which are more numerous internally. The dermis is thin at the sides of the foot. Along the anterior border of the foot there occur several small glands opening near the edge of this organ.

Internal to the dermis are found the muscle bundles which make up the main mass of the foot. Most of these bundles are continuous with those of the shell muscle, and, in fact, the horse-shoe impression might be spoken of as the area of attachment of the muscle fibres of the foot. Of these bundles the outer ones proceed downwards in a steeply oblique direction, while the inner ones curve in and become the slightly oblique bundles which form the dorsal part of the foot. Between these bundles are numerous blood spaces, the most important pair of which have already been mentioned. It is the quantity of blood in these spaces that governs the turgidity of the foot and therefore its functional activity. Besides the above muscle fibres there are others which run horizontally and obliquely especially in the ventral part. The muscle bundles are wrapped in connective tissue.

The lateral glandular streak is a much larger projection than the puckerings of the side surface of the foot and it occurs amongst these just below the ventral limit of the mantle cavity, extending backwards a variable distance on each side. It consists mainly of tubular gland tissue, the upper surface of which is covered by small columnar epithelium as also is the under surface except where the glands open. There is very little connective tissue between the glandular tubes. The epidermal and subepidermal tissue just ventral to the projection is to some extent vacuolated. A variable number of muscle fibres go out to the projection, and dorsal to it, in the anterior region, is found a vestige of a flap formed by muscle fibres and connective tissue covered by epithelium.

The muscles are composed of smooth fibres. These may be scattered, when they are seen to be each an elongated cell with lateral nucleus, or aggregated into bundles, as in the shell muscle. None of the fibres of this muscular tissue show striation.

The SHELL MUSCLE.—The bundles of oblique fibres forming the dorsal part of the foot are continued around its dorsal rim into the shell muscle, so called because its fibres are attached to the shell (by means of a compressed epidermis). This muscle encircles the visceral hump except at the anterior end where it is wanting across the neck region, it is therefore of a horse-shoe shape and the anteriorly placed ends of the horse-shoe are enlarged.

The fibres of this muscle are closely packed and aggregated into 12-17 bundles, each surrounded by connective tissue. Through this connective tissue run the afferent blood spaces of the mantle, gills and mantle skirt. Embryological evidence, derived from *Acmaea*, shows us that this type of muscle has arisen by enlargement backwards of a pair of lateral muscles. Such a paired condition exists only in *Haliotis* and *Scissurella* among recent Gastropods, and in the former the left member of the pair is almost vestigial. The columellar muscle of the typical Prosobranch is the modified right member of the ancestral pair. The outer more steeply oblique fibres of the shell-muscle in *Patella* pull down the edge of the shell by their contraction, while the medianly running inner ones exert downward and inward traction which must greatly strengthen resistance to lateral blows. The latter fibres are more numerous in Patella than in more primitive Docoglossa (*e.g.*, *Acmaea virginea*).

The PALLIAL MUSCLES attach the mantle skirt to the shell all round and will be described in the account of the mantle which follows. Their insertion into the shell has already been mentioned.

The MANTLE SKIRT is covered dorsally by a layer of columnar epithelium which passes gradually into the flat pigmented epithelium covering the visceral hump. Peripherally it is thrown into a large number of folds (fig. 8) parallel to the free edge, the cells on the crests of these folds being very much elongated. Near the extreme edge of the mantle on the dorsal side the epithelium is not folded in this way. There is a broad pigmented band outside and concentric with the shell muscle and a narrower and less continuous band of the same character a few cells from the free edge of the mantle, the mantle edge itself is also pigmented (fig. 8*a*). The epithelium covering the attachment of the pallial muscle is compressed and pigmented, and that covering the internal pallial muscle between the tips of the shell muscle is compressed but not pigmented. The epithelium clothing the under side of the mantle skirt is also columnar, folded to a less extent, and not pigmented. The ventral epithelium of the nuchal roof is shortly columnar. Many of the epithelial cells of both the dorsal and the ventral epithelium, are clear and glandular, and near the edge of the mantle skirt a great deal of sub-epithelial glandular tissue is present, one set of glands opening at the extreme edge of the mantle and the others further ventrally. These glands secrete the material for the outer shell layers. Many sense cells are present in the epithelium of the mantle and of its tentacles, which are best described in a separate paragraph. These are particularly abundant in the epithelium of the dorsal side just near the free edge which, as has been stated, is not folded.

The substance of the mantle, including the roof of the nuchal cavity, is made up of a basis of connective tissue containing numerous blood spaces and traversed by muscles and nerves The blood spaces in the roof of the nuchal cavity are specially large and are traversed by distinct trabeculæ of connective tissue. This fact, combined with the comparative thinness of the epithelium, is in itself adequate evidence of the respiratory function of the nuchal roof. The other more regular blood spaces are best considered along with the remainder of the circulatory system and with the pallial gills.

The chief aggregates of muscle fibres are those forming the pallial muscle and the transverse band which we have called the internal pallial muscle.

The fibres of the pallial muscle take origin in the pallial impression of the shell and then travel outwards, radiating into the mantle edge which they serve to retract and into the sub-epithelial tissue of which they are inserted. They also furnish the retractor muscle slips which run into the pallial tentacles. The fibres of the internal pallial muscle take origin in the corresponding transverse impression, and form a definite layer of radiating fibres, which are also inserted into the mantle skirt nearer the edge than the level of origin of the other pallial muscles. A continuous ring-nerve runs round in the tissues of the mantle skirt. It is formed in front by the anastomosis of the anterior branches of the pallial nerves, and behind by the fusion of the posterior branches of the same nerves (fig. 24). From the outer side of this ring-nerve numerous twigs are given off, which break up into a network from which branches pass into the pallial tentacles.

## DIGESTIVE ORGANS (figs. 4, 6, 10, 11-22).

These consist of a very long and complex Gut and some important Glands which open into it. The mouth opens into a buccal mass (containing the Odontophore), which is succeeded by gullet, crop, stomach and long intestine, the last part of which is the rectum. There are buccal ("salivary") glands opening into the buccal mass and a large digestive gland or hepato-pancreas ("liver") opening into the stomach.

I. THE GUT.—This complicated tube is formed of many coils arranged in a characteristic manner. We now proceed to the detailed description of its various parts.

The *Buccal Mass* (fig. 6).—This is best exposed by lateral incisions of the anterior part of the body wall. Connect these by a transverse incision near the tentacle bases and carefully peel off the dorsal body wall from before backwards, noting that the gullet is very liable to be damaged in the process on account of its intimate connection, by means of fibres, with the body wall.

The buccal mass, as seen in dorsal view (fig. 12), is roughly rectangular in outline with the broad sides lateral. The anterior quarter of the rectangle contains the buccal cavity and the remainder constitutes the broadened anterior end of the radular sac, the rest of which will be seen later. The gullet is a thin-walled tube which opens at the junction of these two regions, and then runs backwards covering and concealing from view the radular sac. The four buccal ducts (fig. 16) are seen running forwards with a somewhat wavy course, the two outer lie freely at the sides of the gullet, the inner run above the dorsal wall of the gullet to which they are closely attached. All four ducts open at about the level of the beginning of the gullet by piercing two thickened dorso-lateral areas, which will be discussed later on in connection with the glands. The gut cavity is wider at this level than further back, and these thickenings have been homologised with the dorso-lateral buccal pouches of *Haliotis*.

The *Buccal Cavity* is best studied by comparing the results of median dorsal incision, lateral incision, longitudinal median section, and transverse section in a few specimens (figs. 6 and 12). The following points are to be noted:—

(*a*) The situation of the cavity.—As the mouth is ventral, the morphologically front and back ends of the cavity are topographically ventral and dorsal, while the morphological roof and floor are respectively anterior and posterior. In describing the cavity we shall refer to the parts in their morphological relations. The main or palatal buccal cavity has a posterior extension, which we shall call the post-palatal buccal cavity, situated on the dorsal side of the odontophore under the commencement of the gullet (fig. 12). This cavity narrows behind into the radular sac.

(*b*) Within the dorsal and ventral outer lips an inner lip is present on either side as an upwardly growing fold (fig. 6). Boutan refers to this pair of lips as "*une lèvre en forme de fer à cheval.*" These two lips can be approximated so as to close the mouth almost entirely. A median papilla, or "licker," belonging to the odontophore, projects between the lips so as to completely fill the chink between them when the mouth is closed.

(*c*) The dorsal palatal plate is a chitinous sub-epithelial thickening forming an arch over the region of the inner lips. It imparts firmness to the lip and also serves to lift the tissues connected with it out of reach of the rasping radula. It is prolonged into two pairs of expansions, one pair dorso-lateral and one pair ventro-lateral (fig. 11). This plate is most probably a pair of jaws united by a median dorsal piece.

(*d*) The front end of the odontophore or rasping organ projects into the palatal section of the buccal cavity from its postero-ventral wall, and the front end of the radula, a horny tooth-studded ribbon, occupies a narrow median strip on this projection (fig. 12), extending backwards on the posterior part of the odontophore cushion, which is placed beneath the floor of the post-palatal section of the buccal cavity (*a* above) underlying the gullet. The epithelium covering the tip of the odontophore, anterior to the radula, has grown out into a transversely ribbed projection, which is the papilla, or "licker."

(*e*) The sub-lingual pouch is a recess below the front end of the odontophore (fig. 6). It is found in *Chiton* and many other forms. In *Patella* it is lined by yellowish epithelium and contains mucus-secreting cells in its roof.

(*f*) The floor of the buccal cavity is muscular with a slight sub-epithelial median development of chitin.

(*g*) The odontophore and its muscles are described later on.

The *Gullet* (figs. 6, 10, 15, 16, 22) runs back as a thin-walled tube from its point of junction with the buccal mass, overlying the central part of the posterior two-thirds of this. Immediately behind the buccal mass it shifts slightly to the left of the median line and merges into the thick-walled crop, dilating into two ventro-lateral œsophageal pouches just before the point of junction (fig. 10). The œsophageal pouches are in part spare tissue for the purpose of avoiding strain when the buccal mass is extruded for feeding. They are probably homologous with the lateral œsophageal pouches of *Pleurotomaria* and *Haliotis*, though their functions cannot be quite the same, as in these two forms they are lined by ridged glandular epithelium, while in *Patella* they are comparatively smooth, and not markedly glandular. The gullet has various folds (figs. 15 and 22), as follows:—

(*a*) A transverse section taken near the posterior end of the buccal mass, shows the gullet as a dorso-ventrally flattened structure, the central portion of which is marked off from the sides by two long folds projecting downwards from the dorsal wall.

(*b*) There are a pair of longitudinal ventral folds starting slightly behind the junction of the gullet and the post-palatal section of the buccal cavity. These folds converge as they run back, and the triangular space between their front ends is marked by slight transverse ribs. It seems to correspond with the much better developed "ventral valve" of this region in most primitive Prosobranchs.

(*c*) A number of small oblique folds lie external to each ventral fold.

The great width of a posterior section through the gullet is due to its ventro-lateral extension into the œsophageal pouches. These occupy part of the space at the back of the buccal mass and are not sharply marked off, being, as it were, mere bulgings of the gullet. The lumen of each pouch is continued forwards into that part of the gullet cavity lateral to the dorsal fold of its side. The gullet is, to some extent, asymmetrical on account of the shift to the left where it merges into the crop.

The *Crop* (figs. 10 and 18).—On passing into the visceral mass the food tube shifts further to the left of the median line and its walls become very much thickened. This thick-walled region is called the crop. It is imbedded in the visceral mass and care is needed to expose without damaging it. The buccal and digestive glands adhere to its walls, and various gut coils also hide it from view. In this imbedded position it runs back some distance, becomes much narrower, and then passes to the right and runs forward.

The lining of the crop projects internally to form the following folds:—

(*a*) The continuations of the longitudinal dorsal folds of the gullet. These folds pass down the left side of the gut-wall and become mid-ventral, thus indicating that the crop has been subjected to a torsion of 180° relative to the head. Further back, these folds run up the right side showing an additional torsion of 90° or more (fig. 22).

(*b*) The continuations of the ventral longitudinal folds of the gullet. These have fused basally, so we find a single outgrowth branching distally into two. This keeps at a uniform space of 180° from the dorsal folds and so is twisted round through the same angular distance (fig. 22).

(*c*) Obliquely transverse folds running across the wall space from the single divided fold (*b*) almost to the pair of folds (*a*) (fig. 18).

Where the crop narrows down posteriorly the transverse folds of its walls cease, but the longitudinal ones are continued until the gut begins to run forward on the right side. At a certain level all folding ceases, and this point should probably be taken as the termination of the crop.

The *Stomach* (figs. 4, 6, 10, 19, 20).—Beyond the crop, the now thin-walled gut runs forward for a short distance and then bends over on itself and becomes a large coil which encircles the dorsal surface of the digestive gland. The whole of this region may be called stomach. At the point where the stomach bends over on itself the duct of the digestive gland opens into it on the left (fig. 19). This opening is fairly conspicuous, and the wall of the duct has a groove with thickened projecting sides (figs. 19 and 20). This groove is continued along the inner wall of the stomach throughout the whole of the superficial coil, and becomes indistinct where the stomach narrows down and passes into the intestine at the right side of the visceral mass. At the point of bending, near the opening of the duct, there is an inward flap-like projection of the posterior wall (fig. 19).

*Intestine.*—Numerous coils of intestine (figs. 4, 6, 10, 21) form the remainder of the gut.

(*a*) A coil following the stomach, running back along the right side, then round just ventral to the crop, returning finally to the right anterior corner of the visceral mass. This coil has a relatively wide cavity (fig. 10, *Int.* 1).

(*b*) A coil on the dorsal surface of the visceral mass within the stomach coil (fig. 10, *Int.* 2). The anterior limb of this coil communicates with the end of *a*, and the posterior limb with the posterior limb of *c*.

(*c*) A small coil ventral to (*a*) (fig. 10, *Int.* 3). Its anterior limb passes, at the right anterior corner of the visceral mass, into

(*d*) a long coil (fig. 10, *Int.* 4) which first passes over the right anterior corner of the visceral mass and then proceeds beneath the pericardium and around the external border of the stomach to about the middle of the right side, when it turns back and forms

(*e*) the last coil (fig. 10, *Int.* 5), which is in close contact with (*d*) until it reaches the pericardium, when it proceeds along the posterior edge of this to the animal's right shoulder and opens on the anal papilla. The last part of this coil (*e*) is the rectum. Its ventro-lateral wall has two inwardly projecting ridges with a gutter between them. The anus opens at the tip of the anal papilla which projects into the nuchal cavity on the right shoulder (fig. 4). The walls of this projection are much thickened, and its lining is papillated. The ventro-lateral ridges of the rectal wall become more strongly marked as the walls thicken towards the anus (fig. 21). Judging from the condition in other Gastropods it would seem probable that the rectum once ran forward in or near the median plane traversing the pericardium. The shifting of the anus to the right side, and of the pericardium to the left, has made the rectum lie across the body, and has pulled out the whole of the last coil of the gut so that it now lies on the extreme outside of the hump around the left side of the latter.

II. THE LARGE GLANDS OF THE GUT.—The *Buccal Glands* (figs. 6, 15, 16) are four compound orange-coloured tubular glands occupying the front of the visceral hump below the pericardium and rectum. They are usually united practically into one mass, but occasional specimens show, anteriorly, more or less division into four (fig. 16). The two inner ducts run in the grooves formed externally by those inward projections into the gullet cavity, called above the dorsal longitudinal folds. Free at first, they become, towards the front end, involved in the gullet wall (fig. 15), but they run along in it and only open at about the same level as the outer pair. The two outer ducts run freely at the sides of the gullet, and open into slight lateral pouches in the buccal cavity behind the palate; they often have ampullæ placed at irregular intervals along them (fig. 16). Cuvier noticed small patches of yellowish tissue near the openings of the buccal ducts, and named them "salivary glands." It is interesting to note that similar yellowish glandular masses occur in the pharyngeal wall of *Fissurella* near the opening of its (one pair of) buccal ducts; these Boutan has unhesitatingly called traces of another pair of buccal glands.

The *Digestive gland*, or Hepato-pancreas ("liver"), is a large racemose gland, occupying the centre of the visceral mass (figs. 4 and 6). The bilobed condition, which is primitive for Mollusca, may have disappeared long before the differentiation of the Docoglossa, or may be obscured by the consolidation and compression which the viscera have undergone in this group. The ducts of this gland converge into two main ducts, which unite just before they open into the stomach, as described above. The ridge-bounded groove on the internal wall of the stomach is continued on the floor of the main duct and even of its first branches.

## Histology of the Gut and Glands.

The digestive tube is lined throughout by columnar epithelium, many of the cells being ciliated, others glandular, and a cuticle being developed in some parts. Beneath the epithelium the wall consists of connective tissue and elongated muscle fibres. The size of the lumen of the gut varies considerably in different parts, as also does the thickness of the walls. The cavity of the gullet is extensive (fig. 15), while its walls are very delicate and closely bound dorsally, by strands of connective tissue, to the outer body wall covering the head. The crop has thick walls and a correspondingly reduced cavity (fig. 22), while the stomach has a very wide cavity with rather thin walls; the succeeding coil of the gut is narrower and thin-walled, and the remaining coils are still narrower; the rectum is thicker walled (fig. 21).

The sub-lingual pouch, like the rest of the gut, is lined by columnar epithelium, which here has a distinct yellow colour, is largely glandular, and probably mucus-secreting. The region of the buccal cavity, into which the buccal glands open, has its walls yellow tinged and somewhat thickened, the thickening being due to the presence of the small tubular glands previously mentioned. Their cells resemble those of the buccal glands. The crop has a greater development of sub-epithelial tissue than is possessed by other parts of the gut, but the major part of the thickening is due to the epithelial folds projecting into its cavity.

The longitudinal folds are covered by high columnar epithelium, which includes a large number of glandular cells. Many of the cells contain rounded granular highly refractive bodies. Under the epithelium of each fold is a distinct, mainly fibrous, band which can be traced outwards through the thickness of the crop wall. The transverse folds are infoldings of the side walls between the longitudinal folds just mentioned. They connect with the single divided longitudinal fold, but not with the pair of longitudinal folds. Each of these folds has secondary foldings on itself, and these run approximately along lines radiating from the centre of the crop. Near the inner and free edge of the fold are smaller papilla-like outgrowths (fig. 18).

The stomach is lined by columnar epithelium, with subjacent connective tissue which is not very abundant. The epithelium is fairly even all round except along a line on the internal wall where we find a groove formed by the upgrowth of two ridges. The height of these ridges is due mainly to the unusual height of the epithelium along them, while the cells lining the groove are very short (fig. 20). This description is correct for a young limpet, but as the animal grows older the groove deepens.

Much of the intestine has ridged walls. The rectum shows two ventro-lateral folds, which are covered by fairly high columnar epithelium, growing into its cavity and forming a gutter between them. These folds become much more distinct on the anal papilla (fig. 21), and here they branch into secondary foldings. Fæces seem to be extruded only from the upper section of the rectum, dorsal to the "gutter" and folds.

The buccal glands are made up of much branched tubes which are imbedded in connective tissue, and the glands, for this reason, have the appearance of one large mass. The cells lining the gland tubules are large and contain numerous granules, they are fairly equal in size and have large and distinct basal nuclei. The cells near the apices of the tubules appear not to be ciliated, but those further towards the ducts possess cilia and have smaller nuclei.

The digestive gland is similarly a great mass of branching tubules imbedded in connective tissue. The cells lining these tubules vary a good deal in size and shape but are very distinctly glandular, and usually so gorged with droplets of a yellowish-green secretion and fine granules that they burst while being prepared for microscopic examination (fig. 17). The ducts of the digestive gland are lined by ciliated columnar epithelium resembling that of the general gut lining. Miss Newbigin finds that, in sections of specimens hardened in formalin, the epithelium lining the intestine has a band of brownish green pigment near the inner margin of the cells. When examined under a higher power the pigment is seen to occur in minute closely packed granules, brownish green in mass, green when viewed singly. The cells of the digestive gland vary in size, the large cells near their inner surface contain several of the characteristically molluscan pigmented vesicles, usually of a brownish yellow colour, while scattered through the protoplasm occur numerous oil drops. The presence of varying amounts of a pigment, called enterochlorophyll, causes great variations in the colour of the digestive gland. The same pigment also occurs in the fæces.

III. THE ODONTOPHORE (figs. 6, 12, 13, 14).—The Odontophore, or rasping organ, characteristic of all cephalous Molluscs, arises in development as a ventral pouch of the fore gut, the ectoderm of which, together with the underlying mesoderm, ultimately gives rise to:—

(*a*) A projection on the floor of the buccal cavity—the Cushion (Mesodermic).

(*b*) A pouch—the Radular Sac, formed of ectodermic epithelium, with a little subjacent connective tissue.

(*c*) A horny tooth-studded ribbon, the Radula, of which the part in use rests on the surface of the cushion, while the parts in reserve and in course of formation are lodged in the radular sac.

The *Cushion* is the projection on which the radula rests, and whose movements enable that organ to perform its scraping function. It consists essentially of muscles and four pairs of cartilages, and is covered above by the fore gut epithelium and that of its diverticulum, the radular sac. The radula is placed in a median groove on the dorsal surface between the paired cartilages (fig. 12).

The cartilages are best named Anterior, Antero-lateral, Ventro-lateral and Posterior. Their shapes and relations are most suitably explained by diagrams (fig. 13). Each anterior cartilage has a ridge towards its front end, acting as a lateral pad for the radula. The cartilage is of the type called spongy, as it consists of fairly large, clear, nucleated cells, separated by a comparatively small amount of structureless intercellular substance. The antero-lateral are placed at the sides of the anterior cartilages near their front ends, and give the cushion its characteristic broad front. The ventro-lateral cartilages, first noticed by Amaudrut, are very small, and on the ventral surface of the cushion. The posterior cartilages are well developed, and not so ventral as in some Rhipidoglossa.

The muscles of the Odontophore include (1) Extrinsic Muscles, connecting the odontophore with the walls of the buccal chamber, (2) Intrinsic Muscles, connecting the cartilages with one another and with the sub-radular membrane.

The chief Extrinsic Muscles are:—

(*a*) The large ventral protractor muscles attached posteriorly to the ventral part of the posterior cartilages and spreading out towards their anterior origin behind and at the base of the inner lips.

(*b*) Dorso-lateral protractor muscles attached at the front end around the expansions of the dorsal palatal plate, and, behind, to the sides of the posterior cartilage.

(*c*) Antero-lateral retractor muscles going from the sides of the anterior cartilages to the floor of the neck cavity. These may be divaricators of the cartilages.

(*d*) Numerous fibres, more or less irregularly arranged, and including some posterior ventral retractors going from the odontophore to the floor of the neck cavity. The protractor muscles seem to be by far the most important, and probably, therefore, the act of retraction is mainly a natural relapse to normal conditions from a state of strain.

The chief Intrinsic Muscles (fig. 13*b*) are:—

(*a*) Two transverse layer-like bands connecting the ventral sides of the anterior and lateral cartilages together. These are separated by (*b*).

(*b*) A pair of muscle bands going forwards from the posterior cartilages to the epithelium beneath the front end of the radula.

(*c*) Muscle bands connecting the anterior and antero-lateral cartilages dorsally, and

(*d*) Muscle bands connecting these cartilages ventrally.

Besides the above muscles, various bands of connective tissue bind the antero-lateral and the posterior cartilages to the anterior, and some further minute details are shown in the figures (figs. 13*a*, *b*, *c*).

The *Radular Sac* (figs. 6, 12) is a long cylindroidal diverticulum of the post-palatal section of the buccal cavity. Arising at the upper limit of the back of the cushion, it first runs downwards close to this, and then, after a swerve to the left, bends back along about two-thirds of the under surface of the visceral mass in the median plane. It then curves well round to the right side, taking a forward course to about the middle of the visceral mass, after which it bends sharply upon itself and retraverses the greater part of its former course. This second part is closely applied to the right side of the first, and its caecal tip extends forwards almost as far as the back of the cushion. The anterior part, at least, of the radular sac and the odontophore, are surrounded by a large blood space, whence blood travels both to the visceral hump and to the foot.

The *Radula* is altogether about twice the length of the animal, and is a narrow belt-like structure with rows of teeth, having at its anterior end a flat plate-like expansion on either side. This plate is bent over the front end of the cushion where the covering epithelium has secreted it. Behind this the radula sinks into a groove along the middle of the odontophore and runs back into its sheath.

The teeth of the radula are arranged in convexly curved transverse rows, the convexity being forwards on the dorsal surface of the cushion. There are twelve members to each row (fig. 14). Of these twelve the four central ones are similar, although the middle two are slightly smaller than the others. Each consists of a yellow stalk and a black-tipped brown "claw," the claw having its concavity directed backwards. Next to these four and behind their level is another tooth of the same kind but larger and with three claws. Lateral to these again we have three pairs of teeth without claws, these have their ends curved slightly backwards. They are at the same level as the four central teeth.

The absence of one definitely differentiated median tooth characterises all the Docoglossa except the Lepetidæ, and other special features are the fewness of teeth in each row, and the high degree of specialisation of the individual tooth. These characters sharply differentiate the Docoglossa from other Gastropods, for the specialisation of their radula is certainly along a line diverging absolutely from that adopted by the Tænioglossa, where the fewness of teeth per row is due to several having fused to form compound ones.

To this account of the alimentary canal we may add a short description of the relations of the various parts of the fore-gut to the feeding process. The generalised diagram of a median longitudinal section of *Patella*, given in fig. 6, is intended to illustrate these relations.

By contraction of its strong ventral protractor muscles the tip of the odontophore is extruded from between the lips, and the radula is rubbed along the rock surface from behind forwards to scrape off minute Algæ. The outer lips, aided by the "licker," seize and hold any fragments torn from the rock, the dorsal palatal plate greatly strengthening the dorsal outer lip for this purpose, besides lifting the roof of the buccal cavity out of reach of the rasping radula. The food, consisting of small Algæ and tiny organisms of various kinds, with an admixture of rock substance, is then passed into the buccal cavity from which its exit is barred by the closure of the inner lips. The mouth parts are almost always examined when both they and the head are in a retracted condition, and it may be that the œsophageal pouches are, in part, spare folds of tissue allowing the protrusion of the odontophore without breakage of any of the gut lining. Specimens paralysed by a dilute solution of chloral hydrate in sea water often die with the head partly expanded, and they certainly seem to show less folding in the region of the œsophageal pouches.

*Patella* also feeds in another way by gripping a piece of seaweed with its outer lips (aided by the palate) and then scraping off fragments from it by the rasping action of the radula. The mechanism for retracting the odontophore is not as manifest as that for its extrusion, and this process is probably in part a return to normal conditions from a strained state of expansion. The slightly developed retractor fibres, the cessation of contraction of the protractors, and the antero-lateral muscles probably all help, and assistance must also be given by the contraction of the muscular snout.

While the tip of the radula is scraping food from the rock, another part of it is, by the same motion, working against the jaw, or palatal plate, and thus helping to grind the food already obtained. This working of the radula against the jaws continues after actual feeding has ceased, and the œsophageal pouches seem to retain the food fragments temporarily till this function has been completed, and till they can be passed on into the crop. This passing on is necessarily slow on account of the many folds projecting into the cavity of the crop. Meanwhile, also, the food becomes mixed with the secretion of the buccal glands.

It is noteworthy that the œsophageal pouches of Patella do not show the development of folds and papillæ which characterises presumably homologous structures in the primitive Rhipidoglossa, and another feature is that the dorsal and ventral valves, which in the latter, and even in *Acmæa* (dorsal valve), prevent passage of the food from the pouches back into the buccal cavity, are very much reduced or absent. The pouches are therefore probably, in part, spare tissue and, in part, temporary stores, and not highly specialised secretory regions, as in *Haliotis*, and other Rhipidoglossa. The corresponding secretory function is performed by the crop, which is extremely specialised among the Cyclobranch Docoglossa, and thereby gives evidence of the difficulty of digesting the tough vegetable food; the high development of folds must also enable this region of the gut to act as a strainer, preventing the further transport of large fragments into the thin walled regions which follow. The great length and size of the stomach, which is the region where the secretion of the great digestive gland becomes mixed with the food is a further testimony to the slowness and difficulty of the digestive process.

## NERVOUS SYSTEM AND SENSE ORGANS.

The nervous system of *Patella vulgata* (fig. 23) may be considered under three headings.

(*a*) The Circumœsophageal ring with its cerebral, pleural and pedal ganglia, and the principal nerves thence given off except—

(*b*) The Buccal and Labial nervous systems, connected to the ring at the cerebral ganglia.

(*c*) The Visceral Loop and nerves thence given off, connected to the ring at the pleural ganglia.

The Circumœsophageal Ring.—This is seen, after exposure of the dorsal surface of the gullet, on pressing apart the gut tissues and body wall in the region of the head and neck. When completely exposed it is observed to be roughly four-sided, the plane of the quadrilateral sloping downwards and backwards, while its upper and lower sides are curved outwards. The quadrangular form of the ring is due to its having accommodated itself to the outlines of the buccal mass. Though certain swellings on the ring are referred to as ganglia, it must not be supposed that nerve cells are not found in other parts, the concentration of these being by no means complete. The two upper corners of the quadrilateral are set near the tentacle bases and are swollen to form the well-marked cerebral ganglia. These are connected by the cerebral commissure (forming the upper side of the quadrilateral) which runs across very far forward just beneath the dorsal outer lip.

The right and left sides of the quadrilateral (continuous above with the respective cerebral ganglia) have become double by separation of the connectives going to the pleural from those going to the pedal ganglia.

The lower side of the quadrilateral is a very short pedal commissure thickening at either end into the commencement of the great pedal nerve cord, which is ganglionic for a considerable portion of its length. The outer side of this anterior end of the pedal nerve cord is continuous with a short stout pleuro-pedal connective, and this latter thickens at the side and a little to the front into a pleural ganglion. From the ganglionic centres a number of nerves are given off, as follows (see fig. 23):

(*a*) From each cerebral ganglion:

(1) The cerebral commissure, the cerebro-labial connective, and the cerebro-pedal and cerebro-pleural connectives.

(2) The branching tentacular nerve.

(3) The fine optic nerve supplying the eye which is placed on the posterior side of the base of the tentacle.

(4) Fine nerves (3 in number) going to the snout.

(5) A nerve which, for some distance, runs along with the cerebro-pedal connective, but which diverges from this at about the level of the pleural ganglia, going thence to the dorsal body wall.

(6) A nerve which is at first fused with the cerebro-pleural connective but soon becomes distinct from it and supplies the otocyst which lies at the base of the pleural ganglion against the pleuro-pedal connective.

(*b*) From each pedal cord, the anterior end of which may be called an ill-defined pedal ganglion:—

(1) From the anterior end, a nerve going forwards to the foot and ventral body wall.

(2) Nerves to the dorsal layers of the foot and to the shell muscle.

(3) Stout nerves to the ventral part (sole) of the foot.

(4) Fine nerves, those from one cord going towards those from the other. These nerves from the two cords unite in two cases forming anastomoses, of which one is close behind the pedal commissure, and the other quite posterior. It is probable that these nerves and anastomoses are vestiges of an ancestral ladder-like condition of the pedal cords and their interconnections.

(*c*) From each pleural ganglion:—

(1) Two small nerves (one more strictly from the cerebro-pleural connective and one from the ganglion itself) arising close together and supplying the dorsal body wall.

(2) A distinct nerve which seems to supply the anterior end of the shell muscle.

(3) A small nerve arising near the lateral extremity of the ganglion close to the origin of (4).

(4) The great pallial nerve, which soon divides into two:—(*a*) The anterior branch—this again divides usually into two; and (*b*) The stouter posterior branch—this runs outwards with the anterior branch and then turns backwards. At this point it may be seen just beneath the tissue covering the foot when the visceral hump is lifted off. This branch gives off, from its outer side, several nerves which run outwards to the mantle. Dr. J. Travis Jenkins has shown by minute dissection that an anastomosis does exist between the anterior and the posterior branches of the pallial nerve (fig. 24). It is,

however, hardly as direct as in the more primitive Docoglossa (*e.g.*, *Acmæa*). From the pleural centres are also given off the nerve bands which together form the visceral loop.

A first examination seemed to show a slender nerve connecting the two pleural centres together, and running just in front of the pedal commissure. Microscopic investigation, however, shows that this slender cord is a fibrous band connecting the two otocysts and extending beyond them to end in the dorsal surface of the foot.

The Labial and Buccal Nervous System.—A fairly thick connective arises from the inner border of each cerebral ganglion, and goes along the floor of the snout, very soon swelling into what may be called a labial ganglion. The commissure between the labial ganglia is thin and markedly curved, with the concavity forwards, the curve being underneath the sub-lingual pouch. The labial ganglia give rise to nerves going forwards to the lips, and, at the back, to a few supplying the snout muscles, &c. (see fig. 23). From each of these ganglia also arises a fine sinuous labio-buccal connective, which enters the tissue of the odontophoral cushion. When it reaches the dorsal surface of this organ it swells into an elongated buccal ganglion. The two buccal ganglia converge to some extent posteriorly, and are connected with one another by a well-marked commissure entering their posterior extremities. The buccal nervous system is easily seen on removal of the gullet and the radular sac, but the connection with the labial centres is difficult to trace. The labio-buccal connective gives off a nerve to the anterior parts of the odontophore. Each buccal ganglion gives rise, at its anterior end, to a nerve supplying the lateral muscles of the odontophore, and several small nerves arise from its inner border. A well-marked nerve arises from the posterior border of the ganglion and supplies the posterior muscles of the odontophore; it gives off a branch to the radular sac.

The Visceral Loop.—Tracing this loop from the right pleural ganglion, which is easily exposed, we find that it takes an upward course somewhat towards the left, and soon enters the visceral region, wherein it travels backwards and towards the left, through the salivary glands for a short distance till it reaches the supra-intestinal ganglion (so-called for phylogenetic reasons, because it is on the connective which, in pre-Docoglossan forms, ran across above the gut). This ganglion varies very much in size and distinctness, but from it is always given off a long and slender connective which runs across to the left side above the crop and terminates in a ganglion just beneath the left osphradium. This osphradial ganglion supplies the sense organs near it, and Bouvier has also found a slender nerve arising from it which loses itself near the anterior wall of the pericardium. This, he says, is the vestigial ctenidial nerve, and it has no connection with the osphradium. From this, and from histological considerations, he seems disposed to argue that the osphradium, so-called, is entirely such, and not, as is commonly believed, both osphradium and ctenidial vestige. Resuming our consideration of the visceral loop we find that, from the supra-œsophageal ganglion, it goes backwards and towards the right for a short distance and then runs into the visceral ganglion. This visceral ganglion gives rise to the following chief nerves:

(*a*) The great visceral nerve which is richly branched and supplies the heart, left kidney, rectum and various viscera.

(*b*) A nerve to the right kidney.

(*c*) Smaller nerves with doubtful distribution.

From the visceral ganglion the loop goes on towards the animal's right side, attaining its extreme position in this direction near where it emerges in front from the visceral mass, thence it goes across beneath the other part of the loop and above the pedal cords to the left pleural ganglion. At the extreme right point a few ganglion cells can be found, and from this point arises a thin and short nerve going to the right osphradium, beneath which there is a small osphradial ganglion. This extreme point would be the proper place for the usual sub-intestinal ganglion, which, therefore, may be represented by the few ganglion cells found there. It is possible that the vanished ganglion is now included in the left pleural ganglion, which is much elongated and partly divided into two. The "sub-intestinal" part of the visceral loop, that is the part next the left pleural ganglion, gives off a couple of slender nerves, one near the pleural ganglion and one further along (fig. 23).

It is characteristic of the Docoglossa that the visceral loop lies entirely to the right of the fore gut, instead of over it and near the right side, as in many other Gastropods. This is in relation to the extra torsion of the fore gut which has taken place in the group.

SENSE ORGANS (figs. 25, 26, 27, 28).—A sub-epidermal plexus of primitive type, with connected sensory cells, still remains in some parts of the body, notably in the sides of the foot of the young animal, but we also have concentrations to form specialised sense organs. These are the cephalic tentacles, the eyes, the otocysts, the osphradia, and the pallial tentacles.

The *Cephalic Tentacles* are a pair of specialised sensory out-growths, situated at the sides of the snout (figs. 4 and 5). They are extremely extensible, and their surface appears corrugated; the apical part is pigmented. At the base of the outer side is a small pit (the eye) lined by deeply pigmented epithelium; this is discussed below.

The tentacle (fig. 25) is covered by a layer of columnar epithelium, the cells of which are long and narrow, with elongated nuclei, and they do not appear to be closely packed when the tentacle is moderately extended. They have a cuticle, which stains yellow with picric acid. There are ordinary epithelial cells, sensory cells and goblet cells. The sub-epithelial layer is a very compact felt-work of fibres, many of which are undoubtedly nervous. Beneath this is a mass of muscle fibres of the usual type, arranged in bundles surrounded by connective tissue. Most of them go from base to tip, and so are longitudinal tentacle-retractors; there are also a few oblique fibres, but no circular muscle occurs. The tentacle nerve goes down the centre, receiving its fibres from the sub-epithelial region, and finally entering the cerebral ganglion, which is at the base of the tentacle. There is a good deal of loose tissue in the tentacle, as might be expected in an organ with such a high degree of contractility.

The animal waves its tentacles as it moves along, the lateral surface near the tip just barely grazing the rock surface over which it is creeping. This lateral surface near the tip is the region of maximum sensitiveness. The tentacles are undoubtedly tactile, and Professor Lloyd Morgan considers them as the organs of the well-known "homing" sense, but, though they may assist in that function, his conclusion seems more than is warranted by evidence. Limpets with the tentacles cut short have "homed" successfully in several cases, and two animals were observed at Granton doing the same, though the entire tentacles had been removed. The pigment on the tentacles is probably of use as a protection, like that on the visceral hump.

The *Eyes* are a pair of organs situated on the outer sides of the swollen bases of the tentacles (figs. 4 and 25), but their shape and position does not seem to be affected by the expansion, contraction and motion of these organs. The eye is really a simple pit, lined by a continuation of the general surface epithelium, part of which has become modified in connection with the sense of light-perception. This modified epithelium is found over a shell-like area, which approaches nearer to the opening of the pit on the lower and outer than on the tentacular and central side (fig. 25). In this modified epithelium we find two kinds of cells (fig. 26):—(1) Elongated sensory cells, with swollen bases, and long clear processes directed towards the surface; and (2) long Pigment cells surrounding and filling up the interspaces between the sensory cells. Each cell consists of (*a*) an internal tapering region, fairly clear, and containing a nucleus in its outer part; (*b*) a broader middle region crowded with minute pigment-granules, and (*c*) a clear outer region. The Pigment is black and resembles that of the mantle.

Nerve fibres, going to the optic nerve, are found beneath this sensory epithelium. The cuticle is well developed over the epithelium of the sensory region. The eye of the Monobranch Docoglossa is more highly developed, its cavity is filled with a jelly-like substance, and the opening is a narrow slit. It is, therefore, almost certain that the eye of *Patella* is degenerate, and this is what might be expected from the conditions of life, since the head remains under the shade of the conical shell.

The *Otocyst*, like the eye, first appears as a depression in the epidermis at the side of the head. With further development it comes to lie far in, and its connection with the exterior is lost. It is found finally just posterior to the pleuro-pedal connective on either side (fig. 23).

The otocysts of the two sides are bound to one another by a fibrous band passing ventral to the pleuro-pedal connectives, and just in front of the pedal ganglia. This band is continued a short distance beyond the otocysts and terminates in the dorsal surface of the foot. It is probably related to the equilibrating function of the otocysts.

The otocyst nerve passes ventral to the pleuro-pedal connective and goes forward between the cerebro-pedal and cerebro-pleural connectives, fusing with the latter not far from the middle of its length. Its fibres enter the cerebral ganglion. The otocyst itself is a cavity lined by ciliated epithelium, the cells of which are in intimate communication with the underlying nerve fibres. The nucleus of these cells is more voluminous than in epithelial cells, and in both *Patella* and *Haliotis* the cells are smaller and longer than in many other forms. The otoliths are small, usually rounded and numerous; the otocyst nerve is hollow, and the otoliths may be found in its cavity some distance away from the main cavity of the otocyst (fig. 27).

The *Osphradia* are patches of brown-pigmented epithelium, situated at the sides of the posterior part of the nuchal cavity, as already stated.

The component cells (fig. 28) are elongated and ciliated, and, beneath them, we find a group of multipolar ganglion cells (osphradial ganglion). In the immediate neighbourhood of the osphradia, and covered by a continuation of this epithelium, are projections, supposed by some to be the last vestiges of the ctenidia of the limpet's ancestors. Their lacunæ are encumbered with corpuscles, and Boutan thinks they have some special glandular function connected with the blood.

The *Pallial Tentacles* round the mantle edge have already been mentioned in general terms, and it has been said that they are of two kinds, large and small, of similar structure. A large tentacle can extend as much as $\frac{1}{8}$ of an inch beyond the mantle edge. The surface of a tentacle presents a number of fine encircling ridges, and, by the action of muscle strands, it can be retracted into a pit, when its surface is thrown into prominent circular folds. The pits for the large tentacles are situated further ventral than those for the small ones (figs. 8 and 24). The tentacle (fig. 8) is covered by columnar epithelium made up of two kinds of cells resting on a basement membrane:—(*a*) Relatively broad goblet cells with a basal nucleus; and (*b*) Sensory cells which are slender, and narrowest in the middle where the nucleus is situated. The outer end bears a number of stiff sensory processes, so that the cell is of the brush type (*pinselzelle*) described by Flemming.

Underneath the basement membrane scattered ganglion cells and nerve fibres can be made out; the latter converge to the axis of the tentacle, where they form a nerve which is connected with the peripheral part of the nervous network of the mantle. At the points of fusion of the tentacle nerves with this network a few ganglion cells are found. Where a tentacle is retracted its nerve is thrown into a coil.

Beneath the epithelium of the tentacle is a fairly continuous sheath of longitudinal muscle fibres, the majority of which are inserted into the tip, though some end at the basement membrane. Most of them collect at the base into two bands which run into the mantle in different directions, those of a laterally placed tentacle being relatively more or less anterior and posterior, though not necessarily in the same horizontal plane. The core of the tentacle is a loose network of connective tissue, muscle fibre, and nerve, and contains large blood spaces.

The above described arrangement of the muscle fibres of the pallial tentacles accords well with our supposition as to their nature, for, better than any other arrangement, it allows of their sweeping over the rock surface, thus enabling the animal to recognise it in some way, and so subserve the "homing" faculty. When the animal "shuffles" round on the scar on returning from an excursion they are in active use.

## CIRCULATORY ORGANS AND CŒLOM.

BLOOD SYSTEM.—As in Molluscs generally, this is to a large extent lacunar, and is greatly developed at the expense of the cœlom, which is reduced to small dimensions. The so-called body-cavity is a hæmocœle, consisting of blood spaces, and the cœlom is reduced to the pericardial cavity, which is, therefore, not a blood space. The blood is a colourless fluid in which float amœboid corpuscles. The parts concerned in blood circulation are the Heart, the Arteries, and the irregular Blood Spaces.

The Heart may be described as a specialised portion of the hæmocœle, which has projected itself into the cœlomic space called the pericardium.

In the primitive *Chiton*, therefore, the feebly differentiated heart is surrounded by cœlomic epithelium, which goes up on either side to the dorsal wall of the pericardium, *i.e.*, the heart is, as it were, suspended from the dorsal wall of the cœlom in an infolding of the lining of that cavity. In *Patella* the heart (ventricle) is also connected with the pericardial roof, but the connection is not so regular and complete as in *Chiton*. In most Gastropods, this connection has disappeared, and it is even possible that it is a secondary consequence of the special reduction of the pericardium in *Patella*.

The *Heart.*—To expose the heart of Patella, carefully make a transverse incision in the front part of the roof of the pericardium. Then remove this roof, first cutting the fibres connecting it with the heart. The heart, thus exposed, will be seen to consist of a thin-walled auricle in front, and a thicker walled ventricle behind (fig. 29).

The auricle receives blood from the pallial gills and related mantle skirt, from the roof of the nuchal cavity, and, perhaps, is directly connected with the reduced left kidney. Blood from the pallial gills and mantle skirt is returned by the great pallial vein into the left front of the auricle, while that from the nuchal cavity is conveyed by a number of small channels opening into the right front part of the auricle. Perhaps among these small channels, which can be very distinctly seen in a fresh uninjured specimen, some bring blood from the left kidney; at any rate, when the auricle is filled by coloured injection the colour is communicated to this kidney.

On opening the auricle by a transverse incision, the large orifice of the pallial vein can be noted, and, to the right of this, a linear series of small apertures from the little channels just mentioned. At the back is the auriculo-ventricular septum, pierced by a transversely oval opening, the edge of which is thickened. The junction of auricle and ventricle is shown by a well-marked constriction, which corresponds to the thickened margin of the auriculo-ventricular septum.

The ventricle stretches right across the pericardium, and its antero-dorsal wall is thicker than the postero-ventral. As has already been said, its dorsal wall is connected by fibres with the roof of the pericardium, along a line going obliquely from right to left (*i.e.*, the long axis of the ventricle), and representing what was the main or antero-posterior axis of the ventricle in ancestral Molluscs.

On opening this chamber of the heart, the interwoven muscle fibres, which form much of its wall, are seen radiating from the thickened margin of the auriculo-ventricular aperture, which is situated near the middle of its antero-dorsal side. The aperture is guarded by two valvular flaps which project into the ventricle cavity.

The main aorta and its posterior branch, the visceral artery, diverge in opposite directions right from the origin, and as they run parallel to, and in close connection with, the ventricle wall, we get an appearance as of a third chamber of the heart. This appearance is emphasised by the fact that the beginnings of the aorta and visceral artery are swollen, and that this pseudo-chamber resembles the ventricle in general characters. The heart of *Patella* was described as three-chambered by Wegmann, who gave the name "Intermediate Chamber" to that which is here called "Ventricle," and the name "Ventricle" to the pseudo-chamber or aortic bulb formed by the swollen arterial bases. Wegmann's determination of parts would make the limpet's heart practically *sui generis*, and would remove the genus very far from the Rhipidoglossa, and even from its nearer allies. The present account, on the other hand, shows the essential similarity between *Patella* and the other Docoglossa in this respect, and agrees with the conclusions of Haller and of Boutan. The aperture between the ventricle and the aortic bulb is guarded by a valvular flap which projects into the cavity of the latter.

*Arteries.*—The Aorta, of which the origin has just been described, runs to the right end of the pericardium, and then goes on in front of the rectum, soon curving downwards and forwards until it becomes continuous with an anterior sinus, surrounding at least the front part of the radular sac, and enlarging forwards so as to enclose the cushion of the odontophore.

The movements of the odontophore must affect this sinus, especially as it connects with the pedal sinuses and other blood channels. It is in this way that these latter sinuses probably got blood pumped into them. This opinion is greatly strengthened by the observation of the head of living specimens, in which the odontophore can sometimes be seen moving forwards and backwards almost rhythmically. It is interesting to note that a similar and similarly connected sinus exists in *Chiton*, and the pumping work thus done outside the heart may be correlated with the feeble muscularity of the ventricle in so many of the lower Molluscan forms. The existence of arterial branches of the aorta, other than the posterior or visceral artery, is doubtful, though possibly one goes into the salivary glands.

The Visceral Artery seems to branch almost immediately after leaving the left posterior corner of the pericardium, one branch certainly goes to the gonad region and the other also seems to enter the visceral hump.

The course of the arteries cannot be traced far from the pericardium, the greater part of the blood system being lucunar, *i.e.*, consists of spaces which have not a definite epithelial lining.

*Lacunæ and Sinuses (Blood Spaces).*—Blood from the Anterior Aorta goes into the great anterior sinus surrounding the radular sac and odontophore cushion. Thence it proceeds into

(*a*) The Pedal Sinuses (fig. 8*a*).—These are fairly distinct spaces running back through the foot on either side just internal to the nerve cord. The anterior sinus opens into these near the pedal ganglia.

(*b*) Spaces in the visceral hump, from that part of the sinus which surrounds the radula.

The foot is, therefore, supplied from the anterior aorta *viâ* the anterior sinus, while the visceral hump is supplied partly in the same way and partly by the posterior artery. The shell muscle seems to be furnished with blood from the pedal sinuses. The impure blood from the foot and that from the visceral hump goes to the perivisceral sinus which, as its name implies, surrounds the viscera. From this sinus some of the blood goes to the blood spaces in the trabeculæ, etc., of the large right kidney, and, more doubtfully, to those of the left kidney. For this reason the perivisceral sinus and large kidney are about co-extensive. Practically the whole of the blood from the perivisceral sinus, including that which has traversed the kidney trabeculæ, etc., ultimately finds its way out to the mantle. Some of it goes to the nuchal mantle, while the remainder reaches the mantle skirt by way of channels running between the fasciculi of the shell muscle.

Before describing the oxygenation of the blood, it is convenient to describe the circulation in the head, in the nuchal mantle, and in the left kidney. The main channels in the head region are the parts and ramifications of the anterior sinus, *i.e.*, spaces below the lining epithelium of the gut, and particularly of the odontophore. From this space, blood seems to go all over the head around the body wall. The inner lips, which are puckerings of this gut epithelium and subjacent tissue, contain each a blood space so that their opening and closing may be brought about in part by changes in blood pressure. It is impossible to say whether the circulation in the head is a loop system, or whether it is merely an enlargement of the great blood space around the odontophore—probably both interpretations are to some extent correct, and, if so, the foot is partly supplied with blood that has already been around the head. Possibly, however, the blood in the head becomes re-purified where it runs near the surface in places covered by delicate skin (*e.g.*, tentacles, etc.).

From the anterior end of the perivisceral sinus some blood goes into a network of spaces in the nuchal mantle, and these lead off ultimately into the auricle through the linear series of small apertures seen on opening the latter. This blood must be partly oxygenated. Blood channels from the mantle, in more primitive forms, probably opened, as they do in the Rhipidoglossa, into the efferent ctenidial veins, but as these latter disappeared they have become directly connected with the auricle, and have undergone compensating development.

The blood reaching the left kidney, in a more primitive form, would have gone out to the corresponding ctenidium for oxygenation, returning thence by the left branchial vein to the left auricle. A change has necessarily had to follow the disappearance of the left ctenidium, and now in *Patella* there is some doubt as to the circulatory arrangements of the left kidney. Possibly it receives blood from the perivisceral sinus and passes it on almost direct to the auricle. If this is not the case, this organ must be in direct dependence on the auricle for its blood supply—a condition which its homologue in *Haliotis* seems to have attained. The circulatory arrangements of the left kidney, even of the primitive *Patella*, show how far this organ has departed from the ordinary condition of a kidney among the lower Gastropods.

The blood which does not reach the heart through the minute channels of the nuchal mantle, or *viâ* the left kidney, goes out to the mantle skirt and pallial gills through channels running between the fasciculi of the shell muscle, and, afterwards, in the substance of the mantle skirt. After oxygenation in the pallial gills and mantle edge, blood is returned to the large pallial vein by small veinlets projecting on the ventral surface of the mantle skirt (fig. 7). Those from the edge (Vl. fig. 7) unite with those from the gills (G.V. fig. 7), and the channels thus formed turn outwards to open into the large pallial vein. The veinlets from the mantle edge can, therefore, be seen at intervals crossing over the ventral surface of this large pallial vein, which runs completely round the mantle skirt just external to the attachment of the pallial gills (fig. 3). The completeness of the circle is broken at one point directly anterior to the left front end of the shell muscle; here the two sides of the vein bend inwards and fuse into one trunk which runs along the inner side of the shell muscle to the left front corner of the pericardium.

It must be remembered that, though the name "vein" is applied to them, none of the blood channels in the mantle are true vessels, even the great pallial vein being of the nature of a lacuna.

Cœlomic System.—The extensive development of the blood system has entailed a corresponding reduction of the cœlom, of which there remains practically nothing except the pericardium. The form and position of the pericardium have already been described, and it only remains to say now that the pericardial gland seems to be absent. The pericardium communicates with the large right kidney, and, as we can positively state, with the small left one as well, but this matter will be discussed later in dealing with the excretory organs.

Haller described a pair of cœlomic cavities between the visceral hump and the foot, but Pelseneer does not confirm this, and our results tend to the conclusion that the only epithelium-lined cavity in this region is that of the large kidney.

The cavity of the gonad, visible only in a very young specimen in which the sex products have not yet been much differentiated, is necessarily a remnant of the cœlom. It becomes practically obliterated at a later stage.

## RESPIRATORY ORGANS.

With the specialisation of the right side of the branchial chamber as an excurrent channel for waste products, the right ctenidium, we may suppose, disappeared at an early stage in the descent of the Docoglossa. In the less modified members of this group, *Acmœa*, etc., the work of respiration is, therefore, performed mainly by the surviving left gill, but in part also by the mantle skirt, which has increased in importance as the shell became more cup-like, and its projecting edge spread farther out. The mantle skirt in these Monobranch forms already shows a tendency to the formation of a series of transverse ridges, constituting incipient secondary or mantle gills (*Lottia* and *Scurria*). In *Patella* both primary gills are reduced, being represented only by vestiges (fig. 4). The nuchal chamber, in which these vestiges are contained, is equivalent to the branchial chamber of a *Pleurotomaria*, *Fissurella*, or *Acmœa* in a reduced condition. This chamber, however, still plays a subordinate part in respiration, although that function is mainly effected by the circlet of pallial gills, which have now attained a high degree of development.

It will be convenient to give details under three headings:—Nuchal Roof, Vestigial Ctenidia, Pallial Gills.

The *Roof of the Nuchal Chamber* has already been mentioned, and it has been stated to be permeated by a network of blood channels; its histological structure has also been discussed. The abundance of blood channels, the general structure, and the fact that blood goes direct from it to the auricle makes it probable that this tissue acts as a respiratory organ. Probably the movements of the head, nuchal floor, etc., enable the cavity to function as an imperfect sort of lung when the animal is left uncovered by the tide. Individuals living far up the shore are uncovered for the greater part of the time, and such a specialisation would undoubtedly be advantageous.

The supposed *Ctenidial Vestiges* are probably entirely functionless, but there is a large osphradium, with underlying osphradial ganglion, in connection with each. It is generally thought that the function of an osphradium is the qualitative testing of the respiratory medium, and the retention of these organs in *Patella* is an argument in favour of the respiratory activity of the nuchal chamber. The osphradium has been described in the account of the sense organs, where it is also stated that Bouvier does not accept as such what are here described as ctenidial vestiges. The vestige is a mass of connective tissue containing blood spaces, and situated near the osphradium; these blood spaces contain numerous corpuscles, and Boutan remarks that the mass resembles a lymph gland.

The *Secondary* or *Pallial Gills* have already been mentioned. Each gill is triangular in form, with the base attached to the mantle. The inner side is curved and runs from the mantle to the outwardly projecting apex, and, from this apex, the third side runs straight up to the mantle (fig. 8*a*). A pallial gill is merely a downgrowth from the mantle skirt, and both, therefore, have an essentially similar structure. It is covered by epithelium, with many cells ciliated, some glandular, and some sensory (fig. 9*b*); beneath this is a nerve plexus, with a few multipolar ganglion cells (fig. 9*b*). Within this we find a comparatively small amount of muscle fibre and other tissue enclosing a large blood space subdivided by fibrous trabeculæ (fig. 9*a*). Blood enters the inner border of the gill and leaves from its outer border, and in these two positions we, therefore, find rather large and distinct blood spaces.

We may now shortly summarise what has been said concerning respiration and the circulation of the blood in the mantle.

Blood comes in from lacunæ running between the fasciculi of the shell muscle; it is then distributed both to the pallial gills (through a blood channel running ventrally and reaching the inner border of the gill) and to the mantle proper (through lacunæ running further dorsally). In the latter set of lacunæ, the blood seems mostly to reach the mantle edge whence it returns through channels which project like veinlets on the ventral surface of the mantle. In the former set of lacunæ it is distributed over the gills and is then collected into ventrally placed efferent lacunæ (fig. 7), which leave the outer border of the gill and join the veinlets from the mantle edge. The united sinus opens into the inner side of the great pallial vein (fig. 7). Though the pallial gills and the nuchal roof are the only distinctly respiratory organs, it must not be supposed that they are the only places in which blood is oxygenated. The skin in several parts seems to be sufficiently delicate to allow the necessary diffusion to proceed; such places, for example, are the surface of the tentacles, of the inner lips, etc.

## EXCRETORY ORGANS.

Two kidneys are present, of which the right is much the larger.

The much-reduced *Left Kidney* (see figs. 4, 5, 8, 31) is a small compact sac with only a limited excretory activity. The wall of this kidney is thin where it abuts on the rectum. but is much thickened where it adjoins the pericardium. It possesses renal epithelium like that of the right kidney, and the amount of excretory matter visible is fairly large. The concensus of opinion is in favour of its possessing a reno-pericardial pore, a conclusion which our preparations confirm. The thickened wall between the left kidney and the pericardium is a heterogeneous mass made up of a few muscle fibres and connective tissue, with occasional granular cells of lymphatic function. In this mass are numerous cavities which are blood lacunæ.

The *Right Kidney*, which seems to be the main excretory organ throughout the Gastropod series, has, in *Patella*, been flattened out and spread around the visceral hump, in correlation and connection with the great perivisceral blood sinus. It is a large structure made up of several lobes (figs. 4, 5, 8, 31):—

(*a*) An anterior dorsal lobe, extending superficially over the front of the visceral hump behind the pericardium and rectum.

(*b*) A posterior or perivisceral lobe, extending around the visceral hump backwards along the right side, and then a fair distance forwards along the left. In very old limpets (*a*) and (*b*) are united distally.

(*c*) A ventral lobe, extending on the ventral surface of about the right half of the visceral hump and connected laterally with (*b*).

(*d*) A sub-rectal lobe stretching beneath the rectum and the back part of the left kidney, and with its apical portion contiguous to the pericardium.

When coloured by excretory matter or by injection, the outlines of the dorsal parts of the kidney become visible, making it appear to be a much branched arborescent gland. On opening, this impression is corrected, for we find the structure characteristic of the excretory organs of Mollusca. It is essentially a sac lined by renal epithelium, but the space is much obstructed by the growth across it of subjacent tissue, forming pillars over which the renal epithelium is, of course, continued. These pillars or trabeculæ contain extensions of the part of the perivisceral sinus in contact with the kidney (see fig. 32*a*). They increase the excretory surface, and in this way add to the efficiency of the organ. It was long supposed that the blood channels actually opened into the kidney, and that the blood, in this way, received water; but this idea is now quite discredited, and we know that the renal epithelium forms a boundary everywhere between the blood sinus and the kidney cavity. This renal epithelium consists of a single layer of cells of variable size. Many of them are ciliated, especially when young. As they grow older, these cells amass concretions, some developing a number of small ones, other a few larger ones (fig. 32*b*). These concretions contain, mainly, nitrogenous waste, and are dark brownish green in colour. The relation of the kidney to the perivisceral blood sinus is that typical for Molluscan kidneys generally, the renal epithelium forming a much complicated partition between a blood space on the one hand, and, on the other, a cavity opening to the exterior. The excretory papillæ of the kidneys have a small central canal lined by ciliated epithelium, outside which is a fairly strong ring of circular muscle. The blood supply of the kidneys has already been spoken of in the account of the circulation, to which reference should be made.

The pericardial communication of this right kidney has often been discussed, the difficulty of observation having led to the enunciation of conflicting opinions by different workers. It is generally admitted that the reno-pericardial canal opens into the sub-rectal lobe of the kidney, but the exact position of this opening, and the length of the canal, are subjects of dispute. Cunningham makes the canal open into the dorsal surface of the sub-rectal lobe some distance to the left of the rectum, while Goodrich and Pelseneer find the opening on the ventral surface of that lobe practically ventral to the rectum. Our results (fig. 31) support the latter view, and we find that the long canal opens into the extreme right end of the pericardium. Most of our sections differ somewhat from those of Pelseneer and Goodrich as regards the space relations of kidneys, pericardium and nuchal cavity, but we think these relations vary a good deal in different specimens, and also change somewhat with the age of the individual.

## REPRODUCTIVE ORGANS.

The gonad occupies the ventral face of the left side of the visceral mass (figs. 6, 8) in both sexes. It varies very much in size at different seasons. In a very young form it is practically a pouch, the cavity of which is cœlomic. This cavity is lined by germinal epithelium, which, with its underlying tissue, grows in as folds, some of which unite into trabeculæ (fig. 33*a*), thus converting the pouch into a mass of sex cells covering the connective basis. As the gland grows in each season towards maturity it pushes forwards, sometimes as far as the level of the œsophageal pouches, and often extends across the median line towards the right side (fig. 8). At the time of complete maturity the ova are surrounded by a tough coat, which possesses a micropylar opening. The ovum contains numerous yolk spherules (fig. 33*b*). The sperms (figs. 34) are very minute and consist of head and tail as usual.

The gonad expels its products by rupture into the cavity of the right kidney, and they thus make their way to the exterior. The gland seems peculiarly liable to overgrowth, and, among specimens collected in autumn on the Welsh coast, various ruptures can frequently be noticed, sometimes between the shell muscle and the foot, sometimes above the shell muscle, though this latter does not seem to be of any advantage for the expulsion of sex products. The season of sexual maturity is the autumn; Boutan finds it to be about September at Roscoff; at Aberystwyth we think it is somewhat later. A few limpets have been found by Gemmill with male and female regions in the gonad, and he also notes that the percentage of the two sexes do not depend on tidal level.

Though the gonad is situated on the animal's left side it must not, therefore, be supposed to be the (post-torsional) left member of an ancestral pair, for there have been such changes in connection with the consolidation of the hump that the present position cannot be taken as a guide. The evidence rather points to the view that we have here the (post-torsional) right member of the ancestral pair, for:—

(1) In all other classes of Gastropods the (post-torsional) right gonad, and, in Cephalopods, the one corresponding to this (*i.e.*, the left), is the one which survives.

(2) The blood supply of the gonad (from the posterior artery) is identical with that of the gonad of other primitive Gastropods, in which that organ distinctly belongs to the post-torsional right side. Possibly, however, the other member of the ancestral pre-torsional pair of gonads has fused with it.

(3) The sex products are expelled into the right kidney, and, perhaps, the extension of this organ on the ventral surface of the hump is, in part, an attempt to preserve its ancient connection with the gonad, an attempt which, as we have seen, is partially unsuccessful.

It is, however, not impossible that the apparently single gonad has arisen from the fusion of the primitively distinct pair.

## DEVELOPMENT.

(See figs. 35 to 42).

The ovum has already been described as a small globular body covered by a tough coat, which is incomplete at one spot—the micropyle. The sex products are extruded into the surrounding sea water and fertilization occurs in a haphazard fashion, the sperms entering *viâ* the micropyle. Sperms seem to make their way occasionally into the females, as ciliated embryos are occasionally found which have not yet been extruded. It is not impossible that hermaphroditism, to a very small extent, may be rather more common than is supposed, and this kind of variation would seem to be advantageous to the animal, though self-fertilization has its drawbacks. Fertilization may be obtained artificially by injecting the sex products of one kind into the nuchal cavity of a mature member of the other sex, or by mixing both kinds of sex products in a small volume of sea water. By observation of artificially fertilized ova, Patten has been able to follow the early stages of development.

The fertilized ovum segments into two, and then into four fairly equal cells. Subsequent divisions are markedly unequal, giving rise to numerous small cells (future ectoderm), and, less rapidly, to a few larger cells (future endoderm and mesoderm). The "Gastrula" stage is initiated by growth of the smaller (ectoderm) cells over the large cells, *i.e.*, by epiboly. The blastopore is the spot over which the small cells do not spread. By differential growth a blastocœle is now formed, into which the inner ends of the large cells grow. These cells bud off smaller ones towards the blastocœle, and from one of these are developed the two primary mesoderm cells.

The ectoderm is mostly ciliated at first, but two adjacent transverse rows of cells soon develop larger and more conspicuous cilia, thus forming two (pre-blastoporal) ciliated rings around the embryo. These together form the "Prototroch," the first rudiment of the "Velum." The apical cells of the embryo also develop very long cilia, and those around them shorter but still conspicuous ones. These ciliated cells lengthen and sink, forming a fairly flat apical plate. At the opposite pole of the embryo two ectoderm cells increase in size and also bear cilia. These are called the anal ciliated cells. Another group of ectoderm cells, posterior to the Prototroch and on the dorsal side, become depressed and lengthened. These form the shell gland which increases in extent especially at the back, making this part of the surface of the embryo convex, and shifting the ventrally-placed blastopore relatively forwards. Meanwhile the blastopore changes its relative position, becoming U-shaped and then slit-like. In the position of its most anterior portion, there occurs an insinking of ectoderm, which pushes this part of the blastopore inwards, and its ultimate destiny is to form the opening from the (ectodermic) stomodœum into the (endodermic) mesenteron. The remainder of the blastopore has closed. On either side of the blastopore in its slit-like stage we find one of the mesoderm cells, which divides and gives rise to a pair of rounded elevations. These two elevations are the rudiments of the foot.

At this stage the larva is practically a trochosphere. Its præoral region is large and possesses a well-developed prototroch and an apical plate. Near the apical plate there appear two small ciliated elevations each consisting of a single cell with cilia. The shell gland secretes a shell which becomes more and more convex outwards, attaining a rounded cup-shape. The originally solid mass of endoderm becomes hollowed out and arranges itself as the lining of the midgut. It gives off a diverticulum postero-ventrally, which ultimately opens to the exterior forming the rectum. The fore-gut gives off a diverticulum ventrally, which is the rudiment of the radular sac.

The ectoderm thickens and projects along a band just external to the shell margin, and this is the first trace of the mantle skirt. The anal diverticulum reaches the ectoderm ventral to this, and between anus and mouth we now find the well-marked pair of foot rudiments. A pair of depressions occur at the sides of the mouth and grow inwards along the sides of the foot, becoming closed sacs and forming the otocysts.

As the shell and foot continue to grow, the anal diverticulum and the rudiment of the branchial cavity become confined between them; and we then observe their migration from the postero-ventral position, along the animal's right side, ventral to the mantle skirt, up to an antero-dorsal position behind the prototroch, which has now grown out and become the "Velum," the differentiated locomotor organ of the larva. The larva is bound to its cap-shaped shell at first by a strand of tissue inserted into the apex of the cap. Later on, Boutan has observed in *Acmæa* the development of a pair of antero-lateral muscular strands inserted near the shell margin and functionally replacing the apical strand. This pair of muscles spreads backwards, and ultimately form the horse-shoe shell muscle of the adult.

The shell now grows chiefly by additions to its posterior border so that its mouth is much widened and the apex comes to lie relatively far forwards. The apical portion, which may show the beginnings of development of a symmetrical spire, breaks off and the hole is closed by a secretion of nacreous material. The next stage known has the foot broadened into the adhesive sole of the adult, the shell muscle horse-shoe shaped, and the shell conical. This stage possesses a glandular streak on each side of the foot, homologous with that found in the adult of *Nacella* and its allies; it disappears later.

In further growth of the shell, the anterior margin seems to share more largely, so the apex subsequently undergoes relative motion towards the back. This is more marked in limpets which live in positions much exposed to the action of the waves, such limpet-shells being lower cones than those in which the growth is more equal.

## CONCLUSIONS.

Of the features which have now been described in *Patella*, the following characterise the Cyclobranchs, the specialised group of the Docoglossa to which our type belongs:—

(1) The highly differentiated crop placed so as to form a

curve with concavity towards the right anterior corner of the visceral mass.

(2) The intestinal coil (Int. 2) placed on the dorsal surface of the visceral mass. Its position varies in different forms, being often much further to the left than it is in the limpet.

(3) The presence of three uncini and nearly always, at any rate, three lateral teeth on each side of each row of teeth in the radula.

(4) The strong odontophore with its squarish front, its highly differentiated transverse muscles, and its numerous cartilages (more than the usual two pairs).

(5) The large development of buccal glandular tissue.

(6) The pseudo-chamber (or aortic bulb) formed by the varying amount of swelling of the basis of the aorta and posterior artery.

(7) The practically transverse posterior boundary of the triangular pericardium.

(8) The absence of a ctenidium, the smallness of the branchial (nuchal) cavity, and the occurrence of a circle of pallial gills. This circle is incomplete above the head in some Cyclobranchs (*Helcion*), and in others the gills in that position are small (*Nacella*).

(9) The presence of a lateral or epipodial streak. It has not been found in *Helcion* and its allies, and it disappears in the adult *Patella*, but persists throughout life in *Nacella*. It is not known in any of the more primitive Docoglossa (Monobranchs and Lepetidæ).

(10) The specially degenerate eye.

(11) The numerous differentiated large and small pallial tentacles.

The following features characterise the whole group of the Docoglossa :—

(12) The apex of the simple conical shell is typically bent

over so that it points forwards and is usually placed in front of the middle of the shell. In adult Cyclobranchs growth of the front edge of the shell often makes these features less distinctly marked.

(13) The long raking radula with a limited number of specialised clawed teeth. The median tooth is not specially differentiated (except in some Lepetidæ), and is typically reduced and often absent.

(14) The disposition of the parts of the gut shown in Fig. 10*a*, except as regards details mentioned in (1) above. This is not quite constant throughout the group, but is found in several types and the disposition of the stomach-coil is quite characteristic.

(15) The position of the visceral loop of the nervous system well to the right of the median line.

(16) The practically triangular pericardium completely filled by the heart and situated at the left anterior corner of the dorsal surface of the visceral hump.

(17) The superficial extension of the right kidney (almost characteristic) and the retention of a certain amount functional excretory tissue by the tiny left kidney.

The following features show that *Patella* and the Docoglossa rank among the lower Gastropods :—

(19) The presence of a horse-shoe muscle derived, as the development of *Acmæa* shows, from the backward extension of a pair of laterally placed muscles.

(20) The retention of external symmetry throughout the development, as far as is known.

(21) The feeble concentration of ganglia in the nervous system and the anastomosing commissures between the pedal cords.

(22) The presence of a complete labial commissure and the form both of this and of the buccal nervous system.

(23) The possession of a pair of osphradia placed right and left in the nuchal cavity.

(24) The possession of two kidneys right and left, the left still possessing some excretory tissue.

(25) The extrusion of the sexual products through the right kidney and the absence of all accessory sexual organs.

Of those characters which are peculiar to the Docoglossa amongst Gastropods—

No. (12) is an adaptation to the adhesive habit, while (14), (15), and (17) are consequences of the consolidation of the visceral hump involved in the development of (12).

No. (16) is due to the disappearance of the right ctenidium and the subsequent shifting of the heart to the left side so that it might lie behind the remaining ctenidium (which has also disappeared in *Patella*).

No. (13) is a specialisation enabling the animal to gather its food by scraping the rock or other surface over which it creeps.

Among the Cyclobranchs:—

Nos. (1) and (5) are specialisations to overcome the difficulty of digestion of the tough food.

Nos. (2) and (7) are special consequences of the further compression of the parts of the visceral hump among these forms.

No. (3) is an undoubted characteristic, but is not easy to understand.

No. (4) is an adaptation to the habit of extruding the tip of the odontophore for raking purposes and to the consequent need of a flat dorsal surface, a broad front, and facilities for adjustment.

The reduction of the pericardium has led to the development of No. (6), this arrangement promoting the regular and unimpeded circulation of the blood.

No. (8) is the feature which gives the group of "Cyclobranchiata" its name. The ctenidium in a fairly deep branchial cavity could not be kept well rinsed among sluggish forms often left uncovered by the tide. The ctenidium, therefore, became inefficient and has disappeared, the pallial gills being a new and compensating development.

No. (9) is an interesting feature not easy to account for. Perhaps the glandular secretion improves the animal's power of holding on and helps it to withstand desiccation in the exposed spots which these forms typically inhabit.

No. (10) is a consequence of having the head always under the shadow of the shell.

No. (11) is a specialisation which helps the animal to obtain a topographical acquaintance with its immediate neighbourhood.

It will thus be seen that the Docoglossa, though undoubtedly correctly included among the lower Gastropods, are yet specialised on lines of their own in connection with their adoption of the habit of adhering to exposed surfaces and making limited excursions for the purpose of raking up food.

They cannot be said to be directly and closely related to any of the other primitive Prosobranchs, the connection in each case being due to descent from a not very remote common ancestor. *Pleurotomaria* and the Trochidæ have specialised on quite other lines as regards the shell, foot, and shell muscle, and this is true also of *Haliotis*, which has adapted itself to creeping about in chinks and confined spaces. The great contrasts in the respiratory systems and in the general disposition of organs show the distance that separates these forms phylogenetically. The Fissurellidæ have also evolved on quite other lines though they have a shell muscle and visceral hump closely resembling that of the Docoglossa externally. The most striking contrasts are the presence of a pair of ctenidia in the Fissurellidæ and the shortening of the path of the excurrent stream of the branchial cavity in these forms by the deepening of the slit or its conversion into a hole at or near the apex of the conical shell.

*Scissurella* is certainly one of the most primitive Prosobranchs known and may be more nearly related to the Docoglossa than are the other groups named, but even in this form the left kidney is specialised in the same way as in *Pleurotomaria*, etc.

The fossil Bellerophontidæ were very primitive Gastropods, though we cannot know enough about them to say much of their relationships. It is, however, possible to conceive of the evolution of the Docoglossa from forms something like them, the symmetrical spire undergoing relative reduction as the posterior margin of the peristome grew out.

## EXPLANATION OF THE PLATES.

### Reference Letters used in the Plates.

*Note.*—The letters d—n in Figs. 13*b* and 13*c* refer to the minute muscles of the odontophore, and are not included here.

*A.* = Thin brown external layer of shell.
*A.C.* = Anterior cartilage of odontophore.
*A.-D. Lobe* = Antero-dorsal lobe of right kidney.
*A.-L.C.* = Antero-lateral cartilage of odontophore.
*An. C.* = Anal cells.
*Ant. Ao.* = Anterior aorta.
*Ap. D.* = Apical disc.
*B.* = Thick middle layer of shell.
  (*a*) Outer part traversed by branching canals.
  (*b*) Clear inner part.
*B.C.* = Buccal cavity.
*Bp.* = Blastopore.
*Buc.* = Buccal commissure.
*Buc.D.* = Duct of buccal gland.
*Buc.G.* = Buccal ganglion.
*Buc.Gl.* = Buccal glands.
*C.* = Internal laminated layer of shell.
*Cer.* = Cerebral ganglion.
*Cer.C.* = Cerebral commissure.
*Cil.R.* = Pre-blastoporal ciliated ring which becomes prototroch.
*C.-Ped.* = Cerebro-pedal connective.
*C.-Pl.* = Cerebro-pleural connective.
*D.F.G.* = Dorsal fold of gullet wall.
*D.H.P.* = Duct of hepato-pancreas.
*D.P.* = Dorsal palatal plate.
*D.Pal.Gl.* = Dorsal pallial gland-tissue.
*Ect.* = Ectoderm.
*E.-M.* = Endo-mesoderm.
*Ep. F.* = Epithelial fold.
*Fl.* = Flap of lateral ("epipodial") streak.
*F.R.* = Foot rudiments (mesoblastic).
*G.-l.* = Gland tubules of lateral ("epipodial") streak.
*G.M.T.* = Greater pallial tentacle.
*G.M.V.* = Great pallial vein.
*Go.* = Gonad.
*G.V.* = Veinlet from pallial gill.
*H.* = Head.
*H.-P.* = Hepato-pancreas.

*Int.* = Intestine (the coils are numbered in Figs. 10*a* and *b*).
*I.L.* = Inner lip (only a line is shewn as neither lip comes in median section).
*K.C.* = Kidney cavity.
*Lab.* = Labial commissure.
*Lat.St.* = Lateral ("epipodial") streak.
*L. Au.* = (Morphologically left) auricle.
*L.K.* = Left kidney.
*L.K.Ap.* = External aperture of left kidney.
*L.M.T.* = Lesser mantle tentacle.
*L.Osph.G.* = Left osphradial ganglion.
*M.* = Mantle or pallium.
*Mcp.* = Micropyle.
*Mesen* = Mesenteron (endodermic).
*Meso.* = Foot rudiments (mesodermic).
*M.Gang.C.* = Multipolar ganglion cell.
*M.T.* = Pallial tentacle.
*Mth.* = Mouth.
*M.T.N.* = Nerve of pallial tentacle.
*N.C.* = Nuchal cavity.
*N.R.* = Nuchal roof.
*N.R.V.* = Veinlets from nuchal roof.
*Odont.C.* = Odontophore cushion.
*Oes.P.* = Oesophageal pouch.
*O.L.* = Outer lip.
*Op.N.* = Optic nerve.
*Os.* = Osphradium.
*Os.E.* = Osphradial epithelium.
*Osph. G.* = Osphradial ganglion.
*Ot.* = Otocyst.
*Ot.N.* = Nerve of otocyst.
*P.* = Pericardium.
*Pal.Gl.* = Pallial gland-tissue.
*Pal.M.* = Pallial muscle.
*Pal.N.* = Nerve in mantle tissue.
*Pap.* = Ridged papella or "licker."
*Pap.Cr.F.* = Papillæ of internal edge of transverse crop folds.
*P.C.* = Posterior cartilage of odontophore.
*P.Cell.* = Pigment cell of eye.
*Ped.* = Pedal nerve cord.
*Ped.Anas.* = Pedal anastomosis.
*Ped.S.* = Pedal sinus.
*Pig.Bd.* = Pigment band.
*Pl.* = Pleural ganglion.
*Pl.Ped.* = Pleuro-pedal connective.
*Post.A.* = Posterior artery.
*P.Pal.N.* = Posterior pallial nerve.
*P.p.b.c.* = Post palatal buccal cavity.
*Pr.Tr.* = Prototroch.
*P.-V.Lobe.* = Perivisceral lobe of right kidney.
*P.Z.* = Pigment zone of pigment cell of eye.
*R.* = Rectum.
*Rad.* = Radula.
*Rect.* = Rectal evagination of mid-gut.
*R.G.* = Rudimentary gill (ctenidium).
*R.K.* = Right kidney.
*R.K.Ap.* = External aperture of right kidney.
*R.Osph.G.* = Right osphradial ganglion.

*R.R.P.* = Renal aperture of renopericardial canal of right kidney.
*R.S.* = Radular sac.
*S.C.* = Sense cell of eye.
*Sec.F.Cr.* = Radial secondary folds on the transverse crop folds.
*Sec.G.* = Secondary or pallial gills.
*S.L.P.* = Sub-lingual pouch.
*S.M.* = Shell muscle.
*S.-R. Lobe.* = Sub-rectal lobe of right kidney.
*S.R.M.* = Sub-radular membrane.
*St.* = Stomach.
*St.Gr.* = Groove in stomach-wall.
*Sub-Ep.N.L.* = Sub-epithelial nervous layer.
*Sub-Oes.C.* = Sub-oesophageal connective of visceral loop.
*Sup.-Int.* = Supra-intestinal ganglion of visceral loop.
*S.Z.* = Sensory zone of mantle epithelium.
*T.* = Tentacle.
*T.N.* = Tentacular nerve.
*V.* Visceral loop.
*Vac.E.* = Vacuolated epithelium beneath lateral streak.
*V.F.G.* = Ventral fold of gullet.
*V.G.* = Visceral ganglion.
*V.H.* = Visceral hump.
*V.L.C.* = Ventro-lateral cartilage of the odontophore.
*V.-l.F.* = Ventro-lateral folds of wall of rectum.
*Vl.* = Veinlet from mantle edge.
*V.-Lobe.* = Ventral lobe of right kidney.
*Vn.* = Ventricle.
*V.St.* = Valve hindering flow of secretion of hepato-pancreas into anterior part of gut.
*X* is the point of connection between Int. 1 (Fig. 10*a*) and Int. 2 (Fig. 10*b*).
*Y.* is the point at which the stomach folds on itself (Fig. 10*a*).
*Z.* is the anastomosis between the posterior pallial nerves of the two sides.

The terms *right* and *left* are always used to signify post-torsional relations unless otherwise specified.

## PLATE I.

Fig. 1. Extreme forms of shell of *Patella vulgata.* From specimens collected in the Gouliot Caves, Sark.

Fig. 2. Section through the shell. *A* Thin brown external layer. *B* Thick middle layer: (*a*) outer part traversed by branching canals; (*b*) clear inner part. *C* Internal laminated layer. × 15.

Fig. 3. The animal in its shell—Ventral surface. *H.* = Head.

Fig. 4. Dorsal view to show positions of organs. The pigment layer of the mantle has been rubbed off

and the nuchal roof removed. *M.T.* = Pallial tentacle. *Os.* = Osphradium. × $1\frac{1}{4}$.

Fig. 5. The animal seen from the left anterior point of view (diagrammatic and based upon published figures). The nuchal roof has been removed. × $2\frac{1}{2}$.

Fig. 6. Diagrammatic sagittal section—most of the blood sinuses, also the kidneys and nerves are omitted for the sake of clearness. *B.C.* = Buccal cavity. *D.P.* = Dorsal palatal plate. *I.L.* = Inner lip (not in median section). *O.L.* = Outer lip. *N.R.* = Nuchal roof. *Oes.P.* = Tissue of oesophageal pouch. *Pap.* = Ridged papilla. *S.L.P.* = Sublingual pouch. × $2\frac{1}{2}$.

Fig. 7. A small portion of the ventral surface of the mantle showing the circulatory arrangements. *Vl.* = Veinlet from mantle edge. *G.V.* = Veinlet from pallial gill. × 10.

## PLATE II.

Fig. 8*a*. Diagrammatic transverse section of a very young specimen to show the lateral streak, the arrangement of fibres in the foot, the relations of the kidney cavity, the structure of the mantle skirt, × 35. *D.Pal.Gl.* = Dorsal pallial gland-tissue. *Ep.F.* = Epithelial fold. *Fl.* = Flap of Lateral ("Epipodial") streak. *Gl.* = Gland tubules of Lateral ("Epipodial") streak. *Lat.St.* = Lateral ("Epipodial") streak. *Pal.Gl.* = Pallial gland-tissue. *Pal.M.* = Pallial muscle. *Pal.N.* = Nerve in mantle tissue. *Ped.S.* = Pedal sinus. *Sub-Ep.N.L.* = Sub-epithelial nervous plexus. *S.Z.* = Sensory zone of mantle epithelium. *Vac.E.* = Vacuolated epithelium beneath the lateral streak.

Fig. 8*b*. Epithelium of one of the folds of a pallial tentacle in cross-section (after Haller). Highly magnified.

Fig. 9*a*. Horizontal section of a pallial gill. × 30.

Fig. 9*b*. Part of the sub-epithelial nerve plexus of a pallial gill (after Haller), showing connection with sense cell and multipolar ganglion cell (*M. Gang. C.*). Highly magnified.

Fig. 10. The alimentary canal of Patella. See description, page 20. For the sake of clearness this is represented in two parts, the first three coils are shown in Fig. 10*a* and the third (Int. 1) connects at × with the fourth (Int. 2) in Fig. 10*b*. *Y* in Fig. 10*a* is the point at which the stomach folds on itself. The coils of intestine are labelled Int. 1, Int. 2, etc. × 1.

Fig. 11. Dorsal palatal plate. × 10.

Fig. 12. Diagram showing the radular sac, etc. *Rad.* = Radula. × 3.

Fig 13*a*. Dorsal view of the odontophoral cartilages. × 3.

Fig. 13*b*. Ventral view of odontophoral cartilages and muscles. See p. 31 for description. Some muscles are supposed to have been removed. Somewhat diagrammatic. × 3.

Fig. 13*c*. The inturned (median) surface of left half of odontophore cushion. Some muscles have been removed. × 3.

Fig. 14. One row of teeth from the radula. × 25.

Fig. 15. Diagrammatic transverse section of the gullet to show the positions, etc., of the ducts of the buccal glands. × 15.

Fig. 16. Diagram of the gullet and buccal glands in a specimen which had the glands unusually well marked off from one another. × 3.

Fig. 17. Section of a lobule of the hepato-pancreas (after Haller). Highly magnified.

Fig. 18. Surface of one of the transverse folds of the crop. *Pap.Cr.F.* = Papillæ of internal edge of transverse

crop folds. *Sec.F.Cr.* = Radial secondary folds on the transverse crop folds. × 15.

Fig. 19. The bend of the stomach (*Y* in fig. 10*a*) showing the opening of the duct of the hepato-pancreas (*D.H.P.*). *St.Gr.* = Groove in stomach wall. *V.St.* = Valve hindering back flow of the secretion of the hepato-pancreas. × 3.

Fig. 20. Transverse section of ridges and groove in stomach wall of a young specimen (after Haller). Highly magnified.

## PLATE III.

Fig. 21. Transverse section across the rectal papilla. × 20.

Fig. 22*a*—*f*. A series of transverse sections of gullet and crop (the posterior faces of the sections are drawn) showing the migration of the points of attachment of the longitudinal folds (*D.F.G.* and *V.F.G.*) through an angular distance of over 270°. *D.F.G.* = Dorsal fold of gullet. *V.F.G.* = Ventral fold of gullet. × 10.

Fig. 23. Nervous system of *Patella vulgata* ;—*Buc.* = Buccal commissure. *Buc.G.* = Buccal ganglion. *Cer.* = Cerebral ganglion. *Cer.C.* = Cerebral commissure. *C.-Ped.* = Cerebro-pedal connective. *C.-Pl.* = Cerebro-pleural connective. *Lab.* = Labial commissure. *L. Osph. G.* = Left osphradial ganglion. *Op.N.* = Optic nerve. *Ot.N.* = Otocyst nerve. *Ot.* = Otocyst. *Ped.* = Pedal nerve-cord. *Pl* = Pleural ganglion. *Pl.-Ped.* = Pleuro-pedal connective. *Ped.Anas.* = Pedal anastomoses. There are two such anastomoses. *R.Osph.G.* = Right osphradial ganglion. *Subœs.C.* = Sub-œsophageal connective of the visceral loop. *Supint.* — Supra-intestinal ganglion of the visceral loop. *T.N.* = Tentacular nerve. *V.* = Visceral loop. *V.G.* = Visceral ganglion. × 2.

Fig. 24. Dissection of mantle nerves in posterior region to show the anastomosis (*Z*) between the posterior pallial nerves (*P.Pal.N.*) of the two sides. The dissection is supposed to be made from the ventral surface, and a small portion of the skin is left to show the pallial tentacles (see also Fig. 8). × 8. (After a drawing by J. T. Jenkins).

Fig. 25. Longitudinal section of the cephalic tentacle. *T.N.* = Tentacular nerve. × 15.

Fig. 26*a*. Section of eye epithelium. × 800.

Fig. 26*b*. Pigment cell of eye epithelium. × 1,500.

Fig. 26*c*. Sense cell of do. *S.C.* = Sense cell. *P.C.* = Pigment cell. *P.Z.* = Pigment zone. × 1,500.

Fig. 27*a*. Section of otocyst and nerve (after de Lacaze-Duthiers). × 15.

Fig. 27*b*. Epithelium of otocyst cavity.

Fig. 28. Section of osphradium, etc. *Osph.G.* = Osphradial ganglion. *Os.E.* = Osphradial epithelium. *R.G.* = Rudimentary gill (ctenidium). × 180.

## Plate IV.

Fig. 29. Heart of Patella. *N.R.V.* = Veins from the nuchal roof. *Ant.Ao.* = Anterior aorta. *L.Au.* = Auricle (morphologically left). *Post. A.* = Posterior artery. *Vn.* = Ventricle. × 3.

Fig. 30. Right kidney (after Lankester). *A.-D.Lobe* = Antero-dorsal lobe. *P.-V.Lobe* = Peri-visceral lobe. *S.-R.Lobe* = Sub-rectal lobe. *V.Lobe* = Ventral lobe. × $1\frac{1}{4}$.

Fig. 31. Diagrammatic transverse section showing the position of the renal aperture (*R.R.P.*) of the renopericardial canal of the right kidney. The anterior face of the section is drawn. × 80.

Fig. 32*a*. Diagram illustrating the structure of the kidney. *K.C.* = Kidney cavity. × 300.

Fig. 32*b*. Epithelium of kidney. × 1,500.

Fig. 33*a*. A fragment of the ovary in section. × 300.

Fig. 33*b*. Section of young ovum. × 600.

Fig. 34*a*, *b*, *c*. Diagrams showing the development of sperms in the testis (after Gibson). × *ca*. 350.

Figs. 35—42. Figures of the development of Patella (after Patten). Enlarged to various degrees. Fig. 36 is a ventral view. Figs. 37—40 are sections. Figs. 41 and 42 are views of the oral (ventral) side of the embryo. *An.C.* = Anal cells. *Ap.D.* = Apical disc. *Bp.* = Blastopore. *Cil.R.* = Pre-blastoporal ring becoming the prototroch. *Ect.* = Ectoderm. *E.-M.* = Endo-mesoderm. *Mcp.* = Micropyle. *Meso*, or *F.-R.* = Foot rudiments (mesoblastic). *Mesen.* = Mesenteron (endodermic). *Pr.-Tr.* = Prototroch. *Rect.* = Rectal evagination of midgut. *Rad.* = Invagination to form the radular sac.

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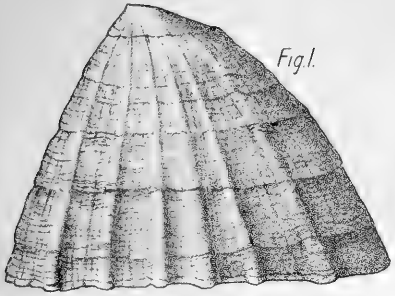

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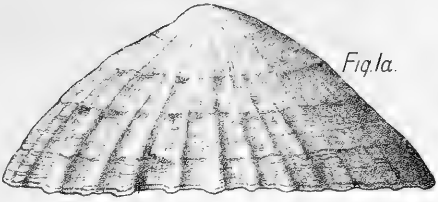

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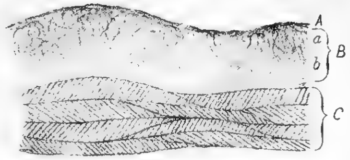

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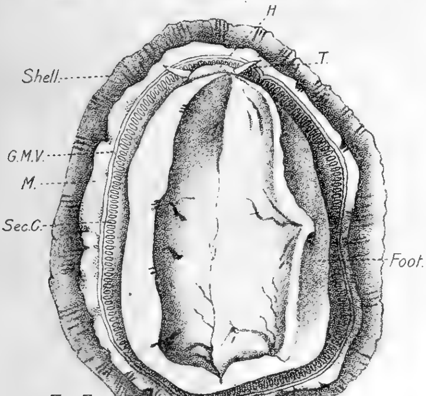

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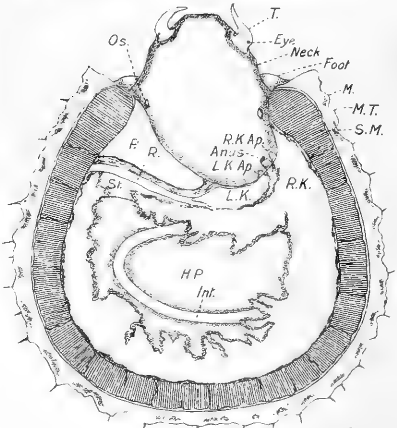

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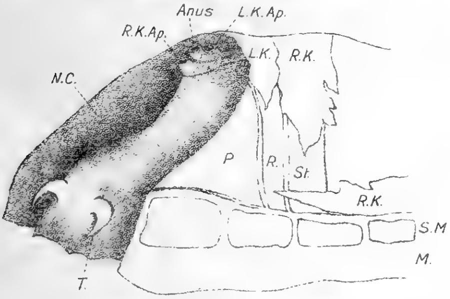

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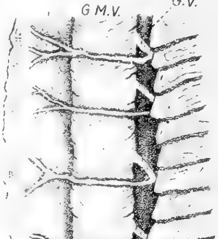

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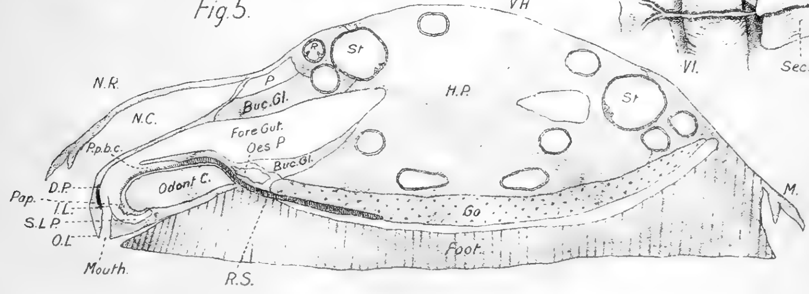


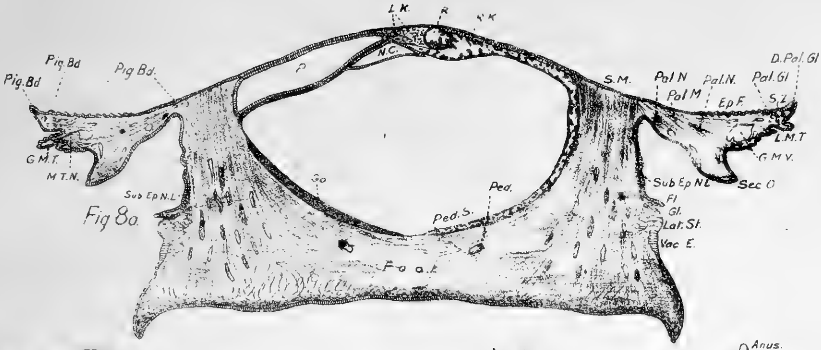
Fig.6.

H.J.F. del.

S.B. lith.

PATELLA.

L.M.B.C. Memoir X. Plate II.



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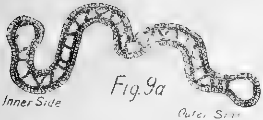


Fig. 9a

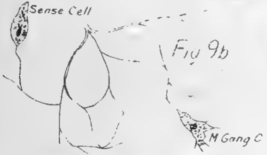


Fig 9b

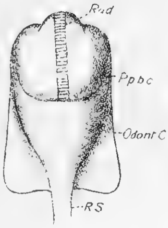
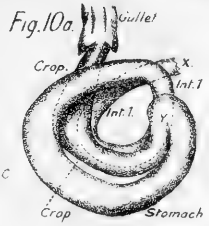


Fig 12



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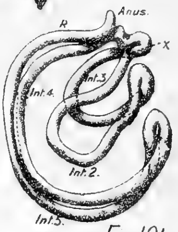

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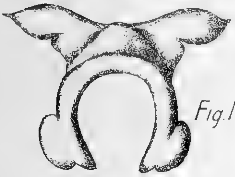
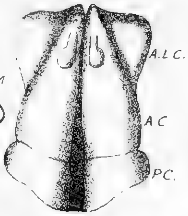


Fig. 11.

Fig. 13c



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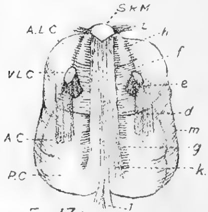

Fig. 13b.

Fig 14

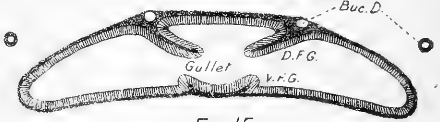

Fig. 15.

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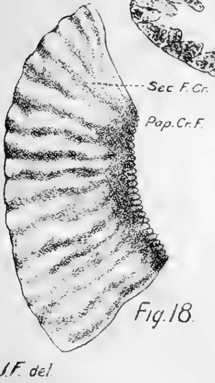

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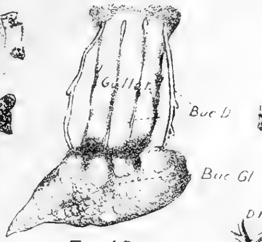

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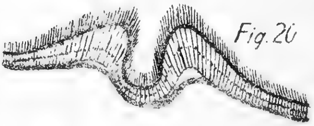


Fig. 20

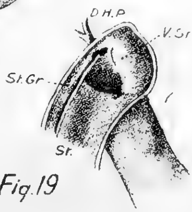


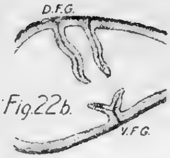
Fig. 19

Fig. 8b.

H.J.F. del. S.b. lith

PATELLA.

Fig. 22a.



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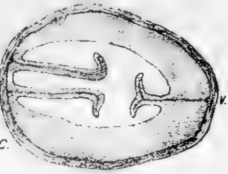

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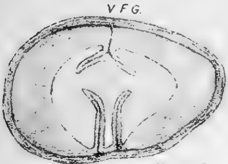

Fig. 22d

Fig. 22e

Fig. 22f

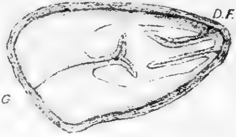

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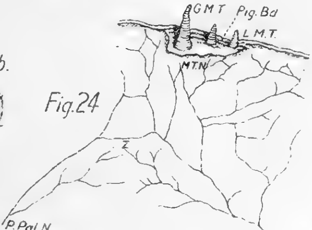
Fig. 27b.



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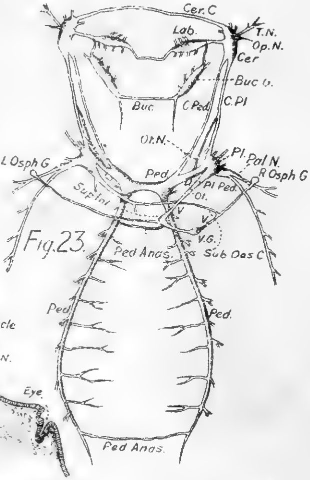

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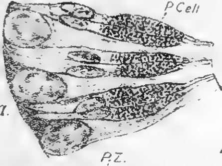

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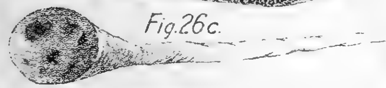

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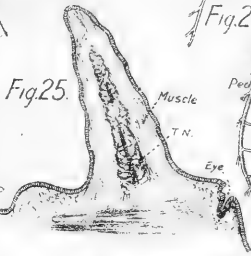

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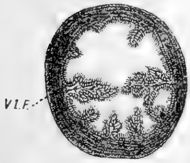

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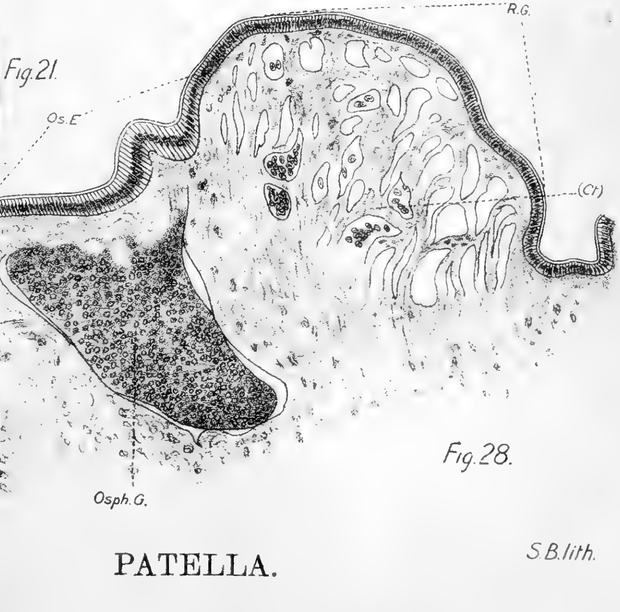
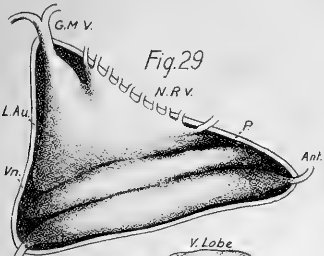


Fig. 28.

H.J.F. del.

PATELLA.

S.B. lith.



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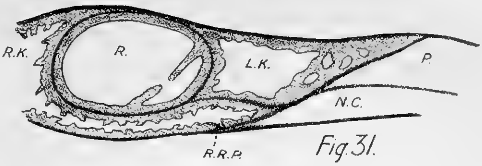

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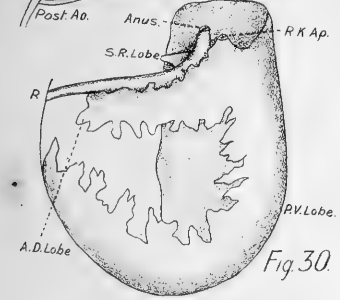

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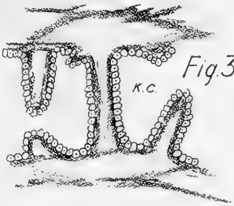

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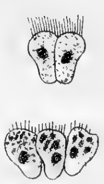

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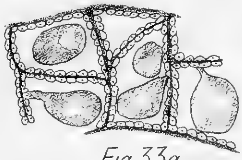

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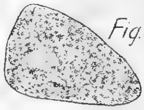
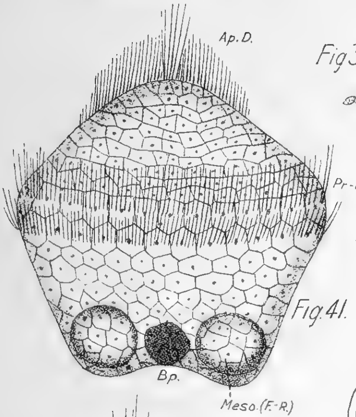


Fig.33b.

Fig 34a

Fig.34b.

Fig.34c.



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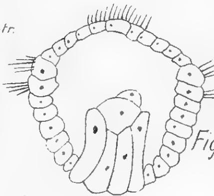

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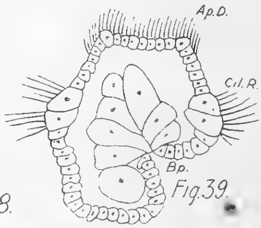
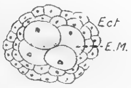


Fig.39.

Fig.35.



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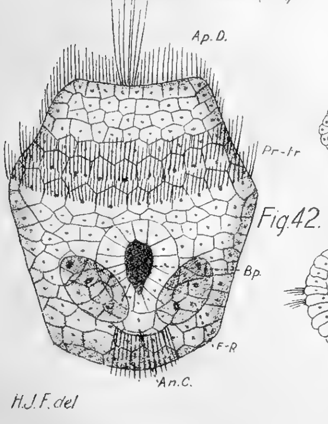

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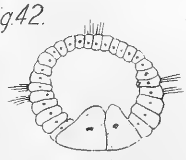

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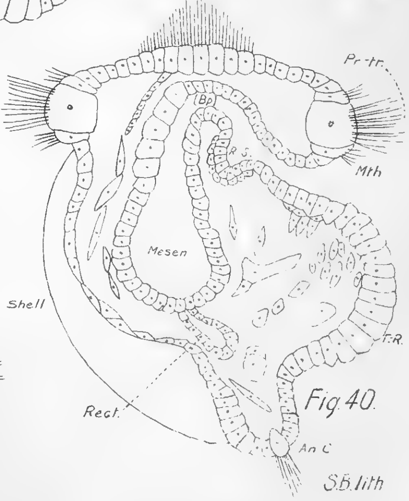

Fig.40.

H.J.F. del

S.B. lith

PATELLA.