

On the Anatomy and Systematic Position of
Incisura (Scissurella) lytteltonensis.

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With Plates 1—5.

WHEN Mr. Geoffrey W. Smith was in Tasmania in 1907–08 I asked him to collect for me any rare or remarkable specimens of gastropod molluscs and preserve them in a form suitable for anatomical and histological examination. Among other forms Mr. Smith obtained for me, through the kind offices of Mr. C. Hedley, of the Australian Museum, Sidney, a number of specimens of the little gastropod which is the subject of the present memoir. They were preserved in Perenyi's fluid, which of course dissolved the shells, but except for the difficulty of staining always resulting from a prolonged immersion in this reagent, the histological condition of the specimens leaves little to be desired.

Scissurella lytteltonensis was described in 1893 by E. A. Smith (16), who noted certain differences between the shell of this and other species of the genus *Scissurella*, but evidently did not consider them of generic importance. In 1904 C. Hedley (8) recalled attention to these differences, and founded the new genus *Incisura* for the reception of the species which, he maintained, is marked off from all other *Scissurellidæ* as also from all *Pleurotomariidæ* by the brevity of the slit in the shell, by the absence of raised rims or keels on either side of the slit, by the subterminal apex,

by the absence of spiral sculpture, and by the remarkable solidity of the shell. He further asserted that his new genus cannot, because of the above-mentioned differences, be included among the Scissurellidæ, and suggested that it is a member of the Fissurellidæ in which development has been arrested, so that the larval characters of the shell have persisted in adult life. Hedley was evidently unacquainted with Pelsener's (12) memoir, containing an account of the anatomy of this very species and of *Scissurella costata*, which, brief as it is, leaves no doubt that the New Zealand and the Mediterranean species are members of the same family, but at the same time discloses so many anatomical as well as conchological differences that they may well be placed in different genera. After some consideration I am of the opinion that Hedley's genus should stand, because the New Zealand species, in addition to the conchological characters enumerated above, differs from the Mediterranean species in the following particulars: (1) In the shape of the radular teeth. (2) In the shape of the foot, which is long and narrow in *S. costata* and *S. crispata*, but short and broad in *Incisura lytteltonensis*. (3) In the absence of cirrhi below the epipodial tentacles in *Incisura*. (4) The greater development of the right columellar muscle, and the more symmetrical disposition of the mantle in *Incisura*. In its general anatomical features *Incisura* bears much the same relation to *Scissurella* as *Septaria* bears to *Paranerita* among the Neritidæ. The systematic position of the Scissurellidæ will more conveniently be discussed at the end of this paper.

Scissurella is placed by most authors among the Pleurotomariidæ, though a few recognise the Scissurellidæ as a separate but closely allied family. A full description of its anatomy is therefore much to be desired, but the accounts that have hitherto been published are insufficient. Vayssière (18) has given a short and, as far as it goes, a good account of the external features of *S. costata* var. *lævigata*, and has figured and described the radula and jaws of this species.

Pelseneer (12), in his well-known memoir on the morphology of primitive mollusca, gives seven figures of sections of *S. costata* and two of *Incisura lytteltonensis* in addition to three figures of the external features of the latter species. The description he gives in the text is concise, and furnishes a good general idea of the anatomy of the family; but he does not give sufficient detail to enable one to make a critical examination of its systematic position. Hence, having sufficient material at my disposal, I have thought it worth while to make a thorough study of the anatomy of *Incisura lytteltonensis*.

Incisura, as Mr. Hedley states in a letter accompanying the specimens, is found on the seaweed *Cystophora* in rock-pools in Lyttleton Harbour, where it is associated with *Rissoina*, *Cantharides*, and *Gibbula*. It may be inferred from its shape and structure that it is semi-sessile in habit, but it is not attached to one spot like a limpet. On the contrary, it is fairly active, and one of the specimens was observed to crawl for a distance of nearly half an inch in the space of a quarter of an hour. When alive it is of a pink colour, and this tinge is sometimes preserved in the shell. The length of the animal, when contracted in spirit, is about 1 mm.

External features.—These have been correctly if somewhat diagrammatically figured by Pelseneer. A three-quarter ventral view of the animal is given in fig. 1. Attention may be called to the following points: The visceral spire is attenuated and much reduced, its coiled apex containing only some lobes of the liver and, in some specimens, a portion of the gonad. The last whorl is greatly expanded laterally, compressed dorso-ventrally, and contains all the important organs of the body. The snout is moderately long, terminating in a trumpet-shaped expansion, on the ventral side of which is the mouth. The mantle is large, and in contracted specimens completely covers the head and the greater part of the snout. The mantle slit, corresponding to the labral incision in the shell, is short, and situated nearly opposite the right eye; its margins are furnished with short digitiform

processes bearing projecting sense-papillæ, such as have been described by Vayssière in *Scissurella costata*. The cephalic tentacles are moderately long, reaching in their contracted state as far forward as the end of the snout. They are fringed with a large number of small, conical sense-papillæ, which, in *Incisura*, are not scattered all over the surface of the tentacles as figured by Vayssière for *S. costata*, but are arranged in two multiple rows on the inner and outer margins of each tentacle (fig. 27), somewhat like the pinnules on the tentacles of an Alcyonarian polyp. The structure of these sense-papillæ will be described further on. The eyes, which are closed and provided with a cornea and lens, are situated on prominences at the outer sides of the bases of the tentacles. Just below and behind the tentacle of each side is a short sub-ocular tentacle which does not bear sense-papillæ like the cephalic tentacles, but is richly ciliated and glandular in structure. In the single male specimen of which I have cut sections, the sub-ocular tentacle of the right side is somewhat enlarged, spatulate in form, and more abundantly provided with gland-cells than in the females. In all the females I have examined the sub-ocular tentacle of both sides is digitiform.

The foot, as is shown in fig. 1, is rather short and triangular in shape, the apex of the triangle being posterior. In shape and in the size of the broad, creeping sole it differs considerably from the narrower elongated foot of *S. costata* and *S. crispata*. The epipodium begins as a low ridge in about the middle third of the foot, and increases in size posteriorly. As described by previous authors it bears three moderately long epipodial tentacles on each side of the body towards the posterior end of its course. These tentacles bear lateral rows of sense-papillæ exactly like those of the cephalic tentacles, but there are no ventral cirrhi in connection with them as in *S. costata*. The epipodial folds meet posteriorly above the posterior end of the foot, and just dorsal to and in front of their union is a muscular opercular lobe bearing the operculum. The last-named structure is small, horny, and

multispiral, as in other Scissurellidæ. It must be regarded as vestigial since, as is the case in *Pleurotomaria*, it cannot be of any use in closing the aperture of the shell. There are two columellar or shell-muscles (fig. 2) symmetrically disposed right and left of the middle of the body, the right muscle being slightly larger and extending rather further back than the left.

As it is almost impossible to make dissections of an animal scarcely exceeding 1 mm. in length, the following account of the anatomy of *Incisura* is mainly founded on reconstructions from sections, but I succeeded in making some satisfactory whole preparations of the ctenidia, and have checked the results of my reconstructions as far as possible by the study of whole specimens cleared in various ways. Fig. 2 is a camera drawing of a specimen stained in picro-carminé and mounted in oil of cloves; it shows as much of the general anatomy as can be made out by this method. Figs. 3, 4, and 5 are reconstructions from sections showing respectively the anatomical relations of the alimentary tract, the kidneys and pericardium, and the nervous system. Figs. 6 to 12 are camera drawings of some of the sections from which the reconstructions were made.

Organs of the pallial complex.—*Incisura* is typically zygo-branchiate, and the position and general characters of the ctenidia, hypobranchial glands, left kidney, and pericardium have been correctly described by Pelseneer.

The ctenidia.—Both right and left ctenidia take their origin from the roof of the mantle-cavity, close to the anterior end of the columellar muscle of their respective sides of the body. The left ctenidium lies almost transversely across the neck of the animal, its anterior extremity reaching nearly as far as the base of the right tentacle (fig. 2), and it is closely compressed between the body-wall and the roof of the mantle. The right ctenidium, on the other hand, lies for the most part in front of the right columellar muscle, and the bulk of it hangs vertically downwards in the space enclosed between the mantle and the outer side of the foot (fig. 7). Pelseneer

has described the right ctenidium as mono-pectinate, but, as may be seen in fig. 7, it is really bi-pectinate; the external lamellæ, however, are few in number, and in some specimens are so feebly developed that they might easily be overlooked. It is at first rather difficult to make out the details of the structure of the ctenidia and to institute an exact comparison between them and those of closely allied Aspidobranchs, but a careful study of sections and whole preparations shows that they are constructed on the familiar pattern. Each ctenidium consists of an axis, the posterior part of which is fused to the roof of the mantle-cavity and extends back in the angle of that side of the mantle-cavity to which it belongs, lying just above the columellar muscle. The anterior end of the axis is free, and the large osphradial ganglion, as is always the case in Aspidobranchia, is situated at the point where the axis becomes free from the mantle. This point, in *Incisura*, corresponds with the anterior end of the columellar muscle. In the case of the left ctenidium that part of the axis which is fused to the mantle bears no filaments, but, as will be described further on, this statement does not hold good for the right ctenidium. Taking the left ctenidium for the purpose of description: its free apex projects into the mantle-cavity in front of the columellar muscle as a thin, triangular lamina, which, as already explained, is bent over to the right, and also is twisted about its own axis from right to left in such wise that the morphologically outer row of filaments become posterior in position, the morphologically inner row anterior. The efferent branchial vessel runs, as is always the case, along the dorsal, here the posterior margin, and the afferent vessel along the ventral, here the anterior margin of the axis. The inner and now anterior filaments borne on the free portion of the axis are short and not more than four or five in number, and are folded backwards over the upper (morphologically ventral) side of the axis, apparently as a result of the latter being twisted from right to left in a narrow space. The morphologically dorsal edges of the anterior filaments are consequently maintained in a dorsal

position. But in the case of the posterior filaments, which are eight in number and much longer than the anterior filaments, the twisting of the axis has brought the ventral surfaces into a dorsal position. Fig. 16 represents a section through the anterior and fig. 17 a section through the posterior row of filaments. Each is more or less quadrangular in outline, its lateral walls formed of long columnar cells bearing long and fine cilia, which in contracted specimens appear to interlock like the cilia of the ciliated discs of filibranch Lamellibranchia. I do not think, however, that their function is to hold the filaments together, but simply to create currents over the surfaces of the filaments. Their interlocking is simply due to their becoming matted together in consequence of the contraction of the gill in spirit. On the ventral surface of each filament is a band of very short cilia. The dorsal edge of the filament bears no cilia externally, but, as shown in the figures, is produced to form a peculiar bolster-shaped swelling, which, as far as I am aware, has no analogue in the gills of any other mollusc. This dorsal glandular ridge, as I will call it, takes its origin from near the free distal end of the filament, and extending along the dorsal face of the latter is closely fused to it for the greater part of its length, but on approaching the proximal end of the filament the glandular ridge becomes free and ends in a small rounded projection. The ridge is traversed throughout its length by a small ciliated canal, which makes no communication with the blood channel of the filament, but opens into the mantle-cavity in the angle between the free proximal extremity of the ridge and the filament. This communication with the mantle-cavity, as seen in section, is shown in the central filament in fig. 17. In the filament on the right hand in the same figure the section passes through the middle of the glandular ridge, and the ciliated canal is seen to be closed in on all sides and to be situated near the ventral, i. e. the filamentary side of the ridge. The same features are shown in the ridge attached to the right-hand filament in fig. 18, but in the case of the left-hand filament in this figure the

section passes through the more distal part of the ridge, and the ciliated canal is seen to be smaller and situated near the dorsal side of the ridge. A little further on it ends blindly. As the figures show, the ridge is made up of a sheath or cortex of elongated, fusiform cells, which pass nearly transversely round the periphery of the ridge, and a medulla of large, closely packed ovoid or fusiform cells having large nuclei and granular cell contents. The cells abutting on the lumen of the ciliated canal are usually larger and more granular than those more peripherally situated, and their histological characters leave little doubt that they are secretory. It is noticeable that there are very few if any glandular cells interspersed among the columnar ciliated cells of the filament, and the glandular ridge appears to have taken over the secretory functions, and to replace the secretory cells scattered over the surface of gill-filaments of other Mollusca. The extreme specialisation exhibited by the formation of a closed canal into which the secretory cells discharge their products is certainly a remarkable feature in *Incisura*.

The central blood-channels of the filaments, as may clearly be seen in the figures, are elongate-oval in shape, and their walls are strengthened, for about half their extent, by flattened, chitinous, skeletal bars, which, as in other molluscs, may be traced to the proximal end of each filament, where they diverge from one another, and curve round to run up in the walls of the blood-spaces of the adjacent filaments (fig. 19). As M. F. Woodward (19) has shown that in *Pleurotomaria* these skeletal bars run along the dorsal edges of the gill-filaments, whereas in *Nucula* they run along the ventral edges, it is of some interest to determine the position of these bars in *Incisura*, which is usually reckoned as belonging with the genera *Scissurella* and *Schismope* to the *Pleurotomariidæ*. It is clear from an inspection of fig. 17, representing a transverse section through the posterior gill-filaments of the left ctenidium, which, as explained above, are turned upside down, that the skeletal bars lie on the dorsal sides of the filaments, and the same thing can be

seen still more clearly by inspection of fig. 7, in which the relations of the gill-filaments to the axis are obvious. In the anterior gill-filaments of the left ctenidium the skeletal bars appear to be ventral in position, but this is because these filaments are reflected backwards and their natural surfaces are reversed. *Incisura*, then, agrees with *Pleurotomaria*, and also with *Trochus* (*vide* Fleure and Gettings) and *Fissurella*, and differs from *Nucula*. But it must be observed that Woodward went further than the facts warranted when he asserted that the position of the gill-bars indicated a more remote affinity between *Pleurotomaria* and the primitive *Lamellibranchia* than is generally supposed. As a matter of fact the skeletal bars differ considerably in position in some not remotely related mollusca. In *Solenomya*, for instance, they are shifted to a more dorsal position than in *Nucula*, and in the *Filibranchia* they are actually dorsal. The fact is, as Woodward himself pointed out, these skeletal bars have a physiological rather than a morphological significance, and are always developed in close relation to the tracts of cells bearing specially long or functionally important cilia. Hence, in *Filibranchia* we find them related to the ciliated discs, which are near the dorsal edges of the filaments.

In so small an object as *Incisura* it is very difficult to make sure of the presence or absence of a septum dividing the blood-channel into an afferent and an efferent moiety, but I am tolerably certain that such a septum exists, as shown in fig. 18. But it is not always placed transversely, but may be oblique or even nearly longitudinal.

The attached portion of the axis of the right ctenidium extends far back in the extreme right-hand corner of the mantle cavity, lying close above the columellar muscle of that side, and gives off some three or four short filaments before reaching the level of the osphradial ganglion. At this spot there is a break in the continuity of the filaments, none being formed in the immediate proximity of the ganglion, but in front of it the ctenidial axis becomes free, and drops vertically down in front of the columellar muscle to hang in

the space between the foot and mantle, as shown in fig. 7. The basal portion of the axis is also enlarged at this point, and gill-filaments are given off from both sides, both of the free apex and of the broad basal portion. These filaments are not simply digitiform like those of the left ctenidium, but are plate-like, with the glandular ridge running along their dorsal margins, as shown in fig. 7. As the skeletal bars and glandular ridges are on the inner side of the filaments of the inner row, the free axis must have been rotated through 45° to bring the dorsal surface inwards. The plate-like filaments springing from the expanded base of the free part of the axis spread out on, and are attached to, the adjacent parts of the mantle; the filaments, or as they more appropriately might be called, the "gill-lamellæ" of the inner row extending dorsally along the inner surface of the mantle, while those of the outer row, two or three in number, pass round the front edge of the columellar muscle and run back for some distance below it as ridges projecting inwards from the dependent margin of the mantle (fig. 8, *m. br.*) The blood supply to the ctenidia will be described in connection with the heart.

The rectum runs diagonally from left to right in the roof of the mantle-cavity, and the anus opens opposite the slit in the mantle edge. In much contracted specimens, such as that from which fig. 2 was drawn, the anus is situated some distance from the slit, but in other less contracted specimens it is close to it.

The hypobranchial glands lie in the roof of the mantle on either side of the rectum, between it and the ctenidia. Both consist of a more or less extensive modified glandular patch of the internal epithelium of the mantle. The gland-cells are very large relatively to the size of the animal, and are of two kinds: large ovoid cells filled with large granules which stain deeply in hæmatoxylin and green in picro-indigo-carmin; these are therefore mucigenous cells. The other gland-cells are of nearly the same size and shape, but have clear or minutely granular contents. The left hypobranchial

gland is much the smaller of the two (figs. 7 and 8); posteriorly it is a narrow strip of glandular epithelium lying between the terminal part of the rectum; anteriorly in front of the anus it becomes broader and extends about as far forward as the level of the mantle slit, but stops far short of the anterior border of the mantle. In this pre-anal region the right and left hypobranchial glands are very closely approximated in the middle line. The right hypobranchial gland has approximately the same anterior extension as the left, but runs backwards on the right side of the rectum nearly to the posterior end of the mantle-cavity. Comparing the arrangement with that described by Woodward for *Pleurotomaria*, it is obvious that the pre-anal portions of the two glands of *Incisura* correspond to the large anterior hypobranchial gland, "partially divided by a median longitudinal furrow into two halves," of *Pleurotomaria*, and the posterior portions of the two glands of *Incisura* correspond to the two "additional mucous glands" lying on either side of the rectum of *Pleurotomaria*. But whereas in the latter genus the left additional gland is conspicuously the larger, in *Incisura* it is the right posterior portion of the gland which preponderates in size, the left gland being small, no doubt because of the relatively large size of the left kidney, for the hypobranchial gland does not extend beneath this organ.

The pericardium, as in all *Rhipidoglossa* except the *Helicinidæ*, is traversed by the rectum. It is relatively of large size, and can always be distinguished in whole specimens as a clear space surrounding the first bend of the rectum on the left side of the body behind the columellar muscle. At this point it lies close to the surface of the body, and its outer wall is very thin and transparent (fig. 11). The exact limits of its extension to the right are very hard to make out, because the left kidney projects into it from above, and its cavity is largely blocked by the auricles. Its extent, as far as I am able to determine it by reconstruction from sections, is represented by the thick black line in fig. 4. The large transverse extension of the pericardial space, as compared

with its narrow limits in *Pleurotomaria*, *Haliotis*, or *Trochus*, is correlated with the tendency towards a secondary bilateral symmetry, the development of two columellar muscles, and the position of the ctenidia wide apart from one another on the right and left sides of the body. The necessary result is an increased breadth of the body, and the blood returning to the heart by the efferent branchial vessels has to traverse a considerable distance before reaching the ventricle. In other words, the auricles are considerably elongated, and the pericardium has to be extended to receive them. Very similar relations are seen in *Fissurella*.

The heart and circulatory system.—The ventricle is placed rather far forward on the rectum; no further forward than in *Fissurella*, but much further forward than in either *Pleurotomaria* or *Haliotis*. The walls of the ventricle are so thin and feebly muscular that they are difficult to recognise, even with the highest powers of the microscope. The auricles also have very thin walls but are more easily recognisable. The left auricle is relatively very large (fig. 10), and its anterior border gives off a number of short and wide sinuses, which penetrate the folds of the wall of the left kidney and vascularise this organ. The right auricle is of smaller size. The course of the blood-vessels, as far as I was able to determine it, is of the usual diotocardiate type, and is diagrammatically represented in fig. 4, which is fully lettered and needs no further description. I was unable to trace the course of the aorta, but the blood, after passing to the foot and the various viscera, is evidently collected in a large sinus lying below the pedal ganglia, and is returned to the afferent branchial vessels by sinuses running over the dorsal side of the great mass of muscle-fibres which diverge on each side of the foot to form the columellar muscles.

The kidneys.—The left kidney (figs. 8, 9, and 13) is of comparatively large size, but its structure and histological characters leave no doubt that it corresponds physiologically to the papillary sac of the *Pleurotomariidæ*, *Haliotidæ*, and *Turbonidæ*, for it is unquestionably phagocytic and not depu-

ratory. It is a triangular sac lying close alongside of the rectum and projecting largely into the pericardium. It opens into the mantle-cavity by a simple slit-shaped aperture with somewhat tumid lips (fig. 9). The majority of the specimens of which I cut sections were females, and in all of them the cavity of the sac was large and but slightly broken up by ridges or papillæ projecting into it. In all the specimens the epithelium lining the cavity of the sac and covering the papillæ had the characters shown in fig. 14. The cells are large and pale, with pale nuclei, and most of them are stuffed with rod-shaped masses which stain very deeply with iron hæmatoxylin. Whatever may be the nature of these rods, which, as shown in the figure, have rhomboid outlines and are apparently crystalline, they have clearly been taken up by the amœboid cells of the left kidney from the adjoining blood-spaces, for these latter are also filled with similar rods, which, however, are smaller, more transparent, and stain less deeply in hæmatoxylin. The left kidney differs considerably in appearance according to its functional activity. In some specimens no rod-shaped bodies can be detected in the cells, and the walls of the kidney sac then appear pale and thin. In other specimens, again, no rod-shaped bodies can be seen in the blood-sinuses, but the kidney-cells are stuffed so full of them that their outlines are no longer distinguishable. In other specimens, again, the rod-shaped bodies are abundant in the blood-sinuses and more or fewer are present in the kidney-cells. A portion of the epithelium of a specimen in the last condition is represented in fig. 14. The fact that the histological character of the left kidney or papillary sac in *Haliotis* and *Trochus* is different from that of the right kidney was established by Rémy Perrier in his careful studies on the kidneys of prosobranch Gastropoda, and Pelseener (11) afterwards showed that the amœbocytes of the papillary sac take up solid particles, such as carmine or Indian ink, injected into the blood-sinuses, whereas the secretory cells of the right kidney eliminate sulphindigotate of soda injected in solution into the blood. Both kidneys of *Patella* are depuratory, that

is to say, they take up sulphindigotate of carmine from the blood, but there is still some doubt as to the very rudimentary left kidney of *Fissurella*. Rémy Perrier (14) describes its histological structure as identical with that of the right kidney, and consequently it has been generally assumed that, like the left kidney of *Patella*, it is depuratory in function, but this is not certain and the subject requires renewed investigation. All observers agree in describing the left kidney of the *Fissurellidæ* as being in a rudimentary condition, and it is possibly nearly if not quite functionless. It may even be absent in some species of *Fissurella*, for I have been unable to find a trace of it in transverse and longitudinal sections of *F. græca*.

In the single male specimen of *Incisura* of which I have sections the left kidney is larger than in any of the females; the papillæ projecting into its cavity are more numerous, are covered with a much more definite layer of epithelial cells, and I could not find any trace of phagocytosis in the latter. Whether this is a constant sexual difference I cannot say, as I was unable to find another male. A section through this kidney is represented in fig. 13, which also shows the left renopericardial canal. The last-named structure is found in the same position in both male and female. It opens into the kidney close to the external aperture of the latter, and runs towards the left as a very fine canal which traverses the floor of the kidney and opens into the left-hand corner of the pericardium, as indicated in the figure. The cells lining the nephric end of the canal appear to bear very fine cilia, but I am unable to speak with certainty on this point. The right kidney of *Scissurella* and *Incisura* has been very briefly described by Pelseneer (12), who figures it as a very small tube lying below the rectum in *S. costata* and to the right of the rectum in *Incisura*. He describes it as being rather narrow in its anterior portion and says further: "Il s'étend partiellement sous le rectum, comme chez *Trochus*, et pénètre dans la masse viscérale, au côté droit de ce corps, sur et entre les convolutions de l'intestin."

I may amplify this account by saying that the right kidney of *Incisura* is a structure of considerable size and importance which may be described as consisting of three lobes. The most anterior lobe varies considerably in size: it lies in the roof of the mantle-cavity to the right of the rectum (figs. 4 and 10) and somewhat posterior to the left kidney. It opens by a simple slit-shaped aperture (fig. 10, *k.r.o.*) into the mantle-cavity, and a few sections further back than the one figured it extends over to the right, forming a considerable projection into the posterior part of the mantle-cavity. Posteriorly it gives off two lobes. That on the right runs nearly vertically downwards close to the right side of the vertical loop of the intestine and passes inward among the viscera, curving round the floor of the middle part of the stomach and eventually coming in contact with the gonad, but it does not effect any communication with this organ. The left posterior lobe passes below the rectum and overlies the anterior cæcal end of the stomach.

The excretory cells of the depuratory kidney of Gastropods are notoriously difficult to preserve, and in my specimens were too much macerated to admit of a satisfactory study of their structure. For the same reason I have been unable to satisfy myself completely as to the relations of the right reno-pericardial canal. For some time I was uncertain whether any communication existed between the right kidney and the pericardium, but the series of sections represented in figs. 22 to 26 demonstrate that this connection does exist, and that, as in *Trochus*, there is an intimate connection between the right reno-pericardial canal and the gonaduct. In fig. 22 the oviduct (*od.*) is seen lying close to the right side of the anterior lobe of the kidney, and from it a narrow canal leads upwards and inwards. The histological features of this canal are not well preserved in any of my specimens, but its walls appear to be formed by cubical epithelial cells containing small, deeply staining nuclei, whose characters as shown in figs. 22 and 23, suggest that they bear cilia and form a ciliated funnel opening into the pericardium. The connection between the canal

and the pericardium is clearly shown in fig. 24, and figs. 23 to 25 show that the lower end of the canal is, in fact, continuous with the gonaduct, and opens along with it into the kidney, close to the external orifice of the latter. It should be noted as a peculiar feature in *Incisura* that there is no distinct duct to the right kidney; its simple slit-like opening into the mantle-cavity is a *Pectinibranch* character.

The gonad, in both sexes, is a simple tubular structure lying to the left side of the stomach, and in the case of the ovary partly embracing this organ. The anterior end of the gonad extends as far forward as the posterior limit of the mantle-cavity and ends blindly below the first bend of the rectum. The cavity of the ovary, in all my specimens, is filled with ova in all stages of development, the ripe ova being very large relatively to the size of the animal, and abundantly supplied with yolk-granules. The testis, in the single male I have been able to examine, is very small, and I think the individual must have been a spent one, as the cavity of the testis only contained a few free spermatozoa and I could find no trace of spermatogenesis.

The course of the gonaduct and its connection with the right kidney has been correctly but all too briefly described and insufficiently figured by Pelseneer. He only says of it: "La glande genitale est unique et occupe le sommet de la masse viscerale. Elle n'a pas d'orifice exterieure; son conduit arrive au rein droit." But it would be difficult for anybody to guess the course of the gonaduct before its arrival at the right kidney by an inspection of his fig. 115, perfectly correct as it is. As shown in fig. 4 the ovary, which in the more anterior and broader part of the visceral mass is on the left side of the stomach, extends into the narrow commencement of the terminal whorl of the spire, and here its posterior end is produced from left to right into a fairly spacious thin-walled sac which lies between the upper and lower of the two posterior lobes of the liver extending into the spire. The walls of this sac are not lined by a germinal epithelium but its cavity often contains a ripe ovum.

It is the commencement of the oviduct. Rapidly narrowing in diameter it passes forward to the right of the posterior end of the stomach and the liver lobes originating from it, and maintaining a position close below the external body-wall, it passes as a very much flattened and very thin-walled duct along the right side of the visceral mass, gradually mounting from a more ventral to a more dorsal position till it arrives above the right-hand loop of the intestine. All this while it has laid close to the outer body-wall, and it is extremely difficult to follow its course, owing to its being flattened between the liver and the external integuments. It turns inward just above and in front of the right visceral ganglion and runs in the roof of the posterior end of the mantle-cavity towards the right kidney (fig. 11). Here its walls become thicker and are lined by a distinct cubical epithelium. The duct does not at once enter the kidney but runs along its outer wall and opens into it in close proximity to the renal orifice. As stated above the gonaduct opens into the kidney coincidentally with a reno-pericardial canal, the relations being very similar to those in *Trochus*. The vas deferens takes the same course as the oviduct.

The alimentary tract.—The buccal bulb is relatively of enormous size. There are two large odontophoral cartilages on either side whose shape, as seen in section, is very similar to that of the cartilages of *Fissurella* as figured by Boutan. As shown in figs. 6, 7, and 8, the anterior and dorsal cartilages are the larger, and support the radula; the posterior cartilages lie ventrad of the hinder ends of the anterior cartilages and have concave upper surfaces, with which the hinder ends of the latter articulate. A similar arrangement obtains in *Trochus*, and has been well described by Randles (15). The musculature of the buccal bulb is powerful, but I have not attempted to follow it out in detail. It is noticeable, however, that the cross-striation, both of the intrinsic and extrinsic muscles of the odontophore, is very well marked. Though it is well known that these muscles are cross-striped in *Gastropods*, I am not aware that the character of the stria-

tions has been carefully studied, and I take this opportunity of giving a drawing (fig. 15) of three fibres of the extrinsic muscles attaching the anterior end of the odontophore to the integuments of the snout. These were specially well-stained, and it is obvious that the ends of the fibres nearest the snout are in a state of contraction, while their odontophoral ends—the lower ends in the figure—are relaxed. The fibres are not round but elongate oval in cross-section. That on the right has been cut through its long axis; in the two fibres on the left the section passes through the shorter axis, near the edge of the fibres. It can be seen that each fibre is a single metamorphosed cell, with a single nucleus situated near its broader end. The central portion of the cell, in which lies the nucleus, is composed of but little-altered cytoplasm, exhibiting an alveolar or reticular structure, differing from the normal only in the fact that the meshes of the reticulum are very regularly disposed in rectangular fashion. This cytoplasmic core of the fibre is invested by a sheath of contractile substance, which is thickest at the two ends of the long axis of the oval, and therefore appears as two bands in the right-hand fibre in the figure, while in the two left-hand fibres only the contractile substance is cut through. The whole is invested by a delicate sarcolemma. The most interesting thing about these fibres is that the reticular arrangement of the cytoplasmic core corresponds exactly with the striations of the contractile substance in the upper part of the fibre on the right side of the figure, and in the left-hand fibre the cross-striations are very obvious and close together in the uppermost contracted part of the fibre, but lower down as the fibre becomes more relaxed, the dark transverse lines become progressively broader and fainter, and each may be seen to be made up of a number of dark longitudinal striæ, which may well be interpreted as nodal thickenings of a reticulum. It is, of course, possible that the difference between the two ends of the fibres is due, not to a difference in the state of contraction, but to a greater specialisation of the broader end. Whichever interpretation is correct, the

appearances lend support to the reticular theory of the constitution of striped muscle-fibre, and are inconsistent with the opposing theory of sarcomeres.

The mandibles occupy the usual position at the sides of the mouth, and are composed of a number of plates or "tesseræ" as described by Vayssière for *Scissurella costata*. Randles has shown that each tessera is the product of a single epithelial cell in *Trochus*, and the same is evidently the case in *Incisura*. The radular sac occupies the usual position. Lying at first between the upper horns of the odontophoral cartilages it maintains a median position to the posterior end of the buccal bulb, and then curves to the right between the right œsophageal pouch and the pedal ganglia and soon terminates in a swollen bilobed extremity lying on the right side of the hæmocœle. The radular teeth are represented in fig. 20. The centrals are squarish, with an expanded basal plate; their anterior margins decurved, and furnished with five very distinct and sharp-pointed denticulations. The next three teeth (medio-laterals) are oblong, with decurved denticulate margins; they decrease somewhat in size from within outwards. The next tooth is much smaller, has a somewhat sigmoid curvature, a thickened base, a narrow neck, and a single recurved marginal denticulation. The next tooth is very large, shaped somewhat like a rake with a crooked handle, its expanded margin decurved and bearing about a dozen denticulations. Then follow the marginals or uncini, which are numerous, curved, slender, with expanded and recurved denticulate margins. The radular formula may be written :

$$\infty 1 (4 + 1 + 4) 1 \infty$$

Vayssière has given a good figure of the radula of *Scissurella costata*, which is similar to but differs in small details from that of *Incisura*. The radula of the *Scissurellidæ* is usually described as resembling that of *Trochus*, but it is much more nearly like that of the *Fissurellidæ*. A reference to Thiele's figures in the concluding chapter of Tröschel's 'Gebiss der Schnecken' shows that the radula of *Incisura*

very closely resembles that of *Submarginula picta*, the shape and relative size of the outer medio-lateral tooth being almost identical, as also the characters of the centrals and uncini. The large and specialised outer lateral tooth, though it differs widely in detail in different species, is characteristic of the *Fissurellidæ*. A close resemblance also exists between the radula of *Incisura* and that of *Emarginula pileolus*, and a less clearly marked resemblance can be seen in the radulae of various species of *Fissurella*. On the other hand, no comparison with the radula of *Pleurotomaria* is possible. A general view of the alimentary tract, as determined by reconstruction from sections, is given in fig. 3, which so far explains itself that little description is necessary. The œsophagus is enormously dilated in the anterior part of its course, forming in addition to the wide lateral diverticula or œsophageal pouches (figs. 9 and 10, *æ. p.*) a spacious ventral pocket or "jabot." These are all lined by a soft-looking glandular epithelium. Behind the level of the pedal ganglia the posterior section of the œsophagus leaves the jabot as a narrow tube with thick, longitudinally ridged walls formed by a long ciliated columnar epithelium. It runs back below the stomach and opens into the latter near its posterior end. Near the œsophageal opening numerous liver cæca open into the posterior end of the stomach. There is no spiral cæcum connected with the entry of the liver-ducts as in *Pleurotomaria*, *Haliotis*, and *Trochus*, but there is a deep ciliated ventral groove, the lips of which are bordered by specially long ciliated columnar cells, extending along the floor of the stomach from the œsophageal opening to the pylorus. A precisely similar groove occurs in the stomach of *Fissurella*, and has been well described and figured by Boutan (2).

Randles has shown that in *Trochus* a cæcal groove, bounded by two conspicuous folds, extends into the spiral cæcum from the œsophageal opening, and that the larger of the two bile-ducts opens into this groove. Though the spiral cæcum is absent there can be little doubt that the ventral groove of the *Fissurellidæ* and *Incisura* corresponds in function to the cæcal

groove of the Trochidæ, and it has the same relation to the liver-ducts. It should be noted in this place that Incisura, in the possession of numerous biliary apertures, resembles Fissurella and differs from Trochus, which has two, and Pleurotomaria, which has only one bile-duct. The intestine leaves the stomach on the ventral side of the anterior third of the stomach in Incisura. Beyond it the stomach narrows rather abruptly, and is continued forward as a small cæcal diverticulum, the front end of which is inserted in the loop formed by the left-hand bend of the rectum. The walls of the blind end of this diverticulum are covered internally by a thick chitinous layer, and thrown into complicated folds and ridges, but the cæcum is not spirally coiled, and situated as it is at the end of the stomach furthest from the bile-ducts, it cannot be homologised with the spiral cæcum of Pleurotomaria, Haliotis, or Trochus. It must, however, be the cæcum referred to by Pelseneer (12). The walls of the intestinal end of the stomach of Incisura have the columnar cells with striated borders and thick cuticle so fully described by Randles for Trochus.

The intestine is provided throughout its length with a single longitudinal ridge or typhlosole. On leaving the stomach it makes a sharp bend from left to right, passes vertically upwards to above the level of the stomach, thence turns sharply to the right, describes a wide loop on the right hand, as shown in fig. 3, and bending sharply again to the left, passes nearly straight across the body till it reaches the left-hand corner of the pericardium, when it turns upward and to the right in the mantle roof, and becoming rectum, traverses the pericardium in its diagonal passage across the roof of the mantle-cavity to end in the anus opposite the mantle-slit.

The liver cæca, as may be seen in figs. 3 and 11, are few in number, of relatively large size, with large lumina bordered by large secretory cells. As far as I could determine they do not branch, but have somewhat convoluted courses, and open independently into the œsophageal end of the stomach.

A few details may be added relative to the structures connected with the buccal cavity and œsophagus.

In the mid-dorsal line the roof of the buccal cavity is deeply folded to form a median ridge containing a narrow lumen T-shaped in transverse section. This lumen of course communicates freely below with the buccal cavity. This median fold or ridge is deepest anteriorly over the mouth, and extends backwards for about two thirds of the length of the buccal bulb, gradually shallowing posteriorly till it dies out altogether. The walls of this ridge are composed of simple columnar cells, the internal ends of which have a striated border, and bear short cilia. On either side of the anterior part of this mid-dorsal ciliated groove is a somewhat shallower but still conspicuous groove appearing on the dorsal surface as a pair of folds lying close and parallel to the median ridge. These may be called the salivary grooves, for the small, simple, tubular buccal or anterior salivary glands open into them near their anterior extremities (fig. 21, *sg.* and *s. d.*). These anterior salivary glands are simple short cœca lined by an epithelium, consisting mainly of large finely granular secretory cells with a few columnar supporting cells between them. The salivary grooves die out posteriorly at the point where the œsophagus leaves the buccal cavity, and at this level a second or posterior pair of salivary glands opens into the roof of the buccal cavity, just to the outside of the salivary grooves. These posterior salivary glands are very small tubular structures with minute lateral diverticula. They correspond in position to, but are much smaller than, and not so much branched as the second pair of salivary glands in *Fissurella*. Otherwise the structures just described are identical in the two genera. As soon as the œsophagus is separated from the buccal cavity its right and left walls are produced into the broad and flattened œsophageal pouches, but from the first the right-hand pouch is considerably larger than the left. The T-shaped lumen of the dorsal ciliated groove may be traced for some way along the roof of the œsophagus, but presently it dies out, and is replaced by a

band of ciliated cells which diverges towards the left, and eventually passes completely over to the left side and passes into the narrow posterior part of the œsophagus. Ventrally, to the right side of the narrow œsophageal tube, the floor of the spacious anterior œsophageal cavity is produced into a capacious pouch or "jabot," which runs back for some distance alongside of the narrow œsophageal tube (fig. 11, *j*), and eventually ends blindly. The deviation of the œsophagus to the left and the preponderant size of the right œsophageal pouch have been noted by Boutan in *Fissurella*, and it is indeed a common feature in the *Rhipidoglossa*, indicative, as Anandrut has pointed out, of the larval torsion which brings about the asymmetry of the adult Gastropod.

The nervous system.—Fig. 5 is a diagram of the principal ganglia and nerve-trunks, as reconstructed from sections. Pelseneer's description of this system in *Scissurella costata* and *Incisura lytteltonensis* is as follows: "Dans les deux espèces, les cordons pédieux sont dans la masse musculaire du pied, et s'étendent jusqu'à la partie postérieure. À leur extrémité tout à fait antérieure se trouvent des ganglions pleuraux bien distincts. La commissure viscérale naît de ces derniers; elle est croisée et porte un ganglion supra-intestinal presque accolé au ganglion branchial ou osphradial gauche, comme dans *Trochus*. Tout ce système nerveux ressemble donc beaucoup plus à celui de *Trochus* qu'aux parties correspondantes connues de *Pleurotomaria*, telles que les ont décrites Bouvier et Fischer." Since this was written we have had the more complete account of the anatomy of *Pleurotomaria* by M. F. Woodward, and the difference between the nervous system of this genus and that of the *Scissurellidæ* is even more apparent than before.

As may be seen from the diagram, the nervous system of *Incisura* is at once typically *Rhipidoglossate* and specialised. As the nervous systems of various *Rhipidoglossa* have been described in great detail by sundry authors, it will only be necessary here to mention the more important and peculiar features.

The cerebral commissure is long and situated far forward in front of the anterior pair of salivary glands. It is a true nerve, not ensheathed by a layer of ganglion cells, differing in this from *Pleurotomaria*. The cerebral ganglia are of large size, sub-triangular in transverse section, and produced into prominent lobes at the origins of the more important nerves. The tentacular and optic nerves have separate origins from the cerebral ganglia, *Incisura* agreeing in this point with *Trochus* and *Fissurella* but differing from *Pleurotomaria*. The labial lobe is very large, and forms a long, conical, tapering, antero-ventral process of the cerebral ganglion, which curves inward below the odontophore on either side, maintaining its thickness for about two thirds of its course towards the middle line. Then it tapers abruptly to form a thin labial nerve, which passes between the muscles of the lower lip, and as far as I can determine is connected by an extremely fine prolongation with its fellow of the opposite side, thus completing the labial commissure. The buccal commissure is given off from the labial lobe about half way between the cerebral ganglion and the mid-ventral line. It passes inwards among the muscles of the odontophore and at once turns abruptly upwards to run between the extrinsic and intrinsic muscles to the top of the buccal bulb. Here it enlarges to form a ganglion of considerable size, lying close to the inside of the cerebral ganglion, and from this a stout nerve—a true nerve without a sheath of ganglion cells—passes inwards and backwards over the top of the odontophore and enlarges below the origin of the œsophagus into a small ganglion, which is connected by a very short commissure with its closely adjacent fellow of the opposite side. Bouvier (3) has figured and described two swellings at the ends of each of the elongated buccal ganglia of *Turbo setosus*, but I infer from his description that they are not separate ganglia, but merely swellings at the ends of a long and ill-defined ganglion. I find precisely the same arrangement in *Fissurella græca*, but Boutan figures four clearly defined ganglia in *F. reticulata*. The sub-division of this elongated ganglion into two distinct

ganglia is an indication of specialisation and a peculiar feature in *Incisura*. For the rest the characters of the cerebral ganglia, the size of their labial lobes, and the relations of the buccal ganglia are very similar in *Turbo*, *Fissurella*, and *Incisura*.

The cerebro-pleural connective, as is commonly the case, is larger than the cerebro-pedal; both are true nerves, devoid of any sheath or local accumulations of ganglion cells. The pleural ganglia are distinct and that of the right side is relatively large, but both are fused to the dorsal surfaces of the pedal ganglia. The visceral commissure is typically streptoneurous, and for the same reason that the osphradial ganglia are situated far forward, the whole commissure is contracted antero-posteriorly as in *Patella*; on the other hand, it is considerably extended right and left. The sub-intestinal ganglion is distinct, but elongated and rather ill-defined; as Pelseneer remarks it is connected by a very short nerve with the large left osphradial ganglion. The left symmetrical pallial nerve passes straight out from the left pleural ganglion almost immediately below the supra-intestinal ganglion, and traverses the posterior fibres of the left columellar muscle, turning nearly vertically downwards to enter the thickened border of the mantle. Before turning downwards it gives off a very fine branch, which makes connection with the short nerve uniting the supra-intestinal with the osphradial ganglion, thus establishing a left-hand dialyneury very similar to that of *Trochus*.

The subintestinal nerve is very stout, and crosses over the dorsal surface of the hinder part of the pedal ganglia almost at right angles to the long axis of the body. The sub-intestinal ganglion is fairly large and distinctly indicated by an accumulation of nerve-ganglion cells. It is triangular in shape, and from its right-hand lower corner the visceral nerve, and from its right-hand upper corner the osphradial nerve is given off. The latter is a very slender nerve, which passes into the substance of the columellar muscle, and turns vertically downward and then forward along the dependent edge of the mantle, running in this part of its course at the base

of the gill-filaments, which, as has been explained above, run back along this region of the mantle. At the anterior edge of the columellar muscle the nerve expands to form the large right osphradial ganglion. The right symmetrical pallial nerve takes its origin from the ventral side of the right pleural ganglion, just where the latter becomes fused to the pedal ganglion. It runs outward, traverses the columellar muscle some way in front of the osphradial nerve, and takes a direct course to the right osphradial ganglion, which it crosses dorsally, and in so doing enlarges and makes an intimate connection with it. Just in front of the osphradial ganglion the pallial nerve divides into two branches. The posterior branch, which is slender, runs back along the thickened border of the posterior part of the mantle. The anterior branch runs forward to the mantle-slit, where it expands to form a small ganglion, indicated by a distinct accumulation of nerve-ganglion cells, and is here joined by a slender nerve from the anterior end of the osphradial ganglion. This little ganglion at the hinder border of the mantle-slit gives off an external branch supplying the posterior sense-papillæ of the mantle-slit, and a stout anterior branch which passes round the mantle-slit and is continued forward as the peripheral pallial nerve, meeting and uniting with its fellow of the opposite side on the anterior border of the mantle. There is thus a very intimate dialyneury on the right side. These relations are very hard to make out, and require careful study with high powers of the microscope, but I can vouch for the correctness of the account here given of them. The relations in *Fissurella* are somewhat similar, but the proportions of the lengths of the nerves differ greatly, and apparently differ in different species, for in my sections of *F. græca* the sub-intestinal is close to the right osphradial ganglion, whereas in *F. reticulata* Boutan figures them as far apart and connected by a long slender nerve, as in *Incisura*. The origin of the right symmetrical pallial nerve from the upper surface of the pedal ganglion rather than from the right pleural ganglion is identical in *Incisura* and *Fissurella*.

The visceral loop bears three distinct accumulations of ganglion cells, forming as many ganglia. The right ganglion lies close below the gonaduct and gives off a slender nerve to that organ. The pedal ganglia, as may be seen in fig. 5, are very much concentrated. Anteriorly they are rather flat, but in about the middle of their length they increase considerably in thickness, this increase being due to the addition of a considerable ventral thickening to each ganglion. In this region, in fact, each pedal ganglion consists of a dorsal and a ventral moiety, as is the case in all Rhipidoglossa (fig. 9). Here also the whole of the pedal ganglia lies in the hæmocœle, as is the case with the more elongated pedal cords of Fissurella. But in Incisura the dorsal moieties of the pedal ganglia have very little posterior extension. The ventral moieties, on the other hand, extend back behind the dorsal moieties, and, narrowing in diameter, plunge into the muscular substance of the foot (fig. 10). There they are continued backwards for a short distance, giving off nerves from their outer edges, and diminishing rapidly in diameter, partly because of fibrils given off to the different nerves, but also largely because of the thinning out and eventual disappearance of their coating of nerve ganglion cells. Posteriorly the cords become simple nerves, and end some distance in front of the posterior end of the foot. Pelseneer states of *Scissurella costata* and *Incisura lytteltonensis*: "Dans les deux espèces, les cordons pédieux sont dans la masse musculaire du pied, et s'étendent jusqu'à la partie postérieure." This is certainly not the case in *Incisura*; the left pedal cord, or rather nerve, dies out at a distance of 125 μ from the posterior end of the foot in two specimens in which I calculated its extent, and remembering that the animal is only 1 mm. long this is a considerable distance. In short, one can hardly speak of pedal cords. The pedal centres, particularly the dorsal portions of them, have become concentrated into two clearly defined pedal ganglia, and it is only the ventral portions that are continued backwards to represent in some measure the elongated pedal centres of other Rhipidoglossa. In addition

to the thick anterior commissure connecting the dorsal portions of the ganglia, there is a single anterior thin commissure connecting the ventral portions, but this is the only trace of the usually numerous cross commissures of other lowly organised Gastropoda. Such a concentration of the pedal centres is very unusual if not unique among Aspidobranchia, and indicates that *Incisura*, and, if one may judge from the similar relations indicated in Pelseuec's figures of *S. costata*, the Scissurellidæ in general are highly specialised. Much has been written about the significance of the dorsal and ventral moieties of the pedal cords of archaic Gastropods. The French authors hold that the upper moiety is pleural, or, as they say, pallial, the lower moiety pedal in character. Pelseuec and most English and German authors hold that both moieties represent pedal centres. The facts in *Incisura* seem to uphold the latter view. I have no wish to re-enter upon a controversy which has become almost wearisome by repetition, but may state that in *Incisura* the cerebro-pedal connectives certainly join the dorsal moieties of the ganglia; that the epipodial nerves are certainly given off from the dorsal moieties, and that whereas the left symmetrical pallial nerve is undoubtedly given off from the left pleural ganglion, the right symmetrical pallial nerve certainly appears to be given off from the dorsal moiety of the right pedal ganglion and not from the right pleural, both in *Incisura* and *Fissurella*. Advocates of the French view will take this last fact as evidence in support of their theory. The nervous system of *Incisura* certainly bears no resemblance to that of *Pleurotomaria*. On the whole it most nearly resembles that of the *Fissurellidæ*, in which family the pedal cords, though still elongate and ganglionic, and provided with several cross-commissures, have undergone a considerable reduction in length as with those of other *Rhipidoglossa*.

The sense organs.—The eyes, as already stated, are closed and provided with a distinct lens. Their structure resembles that of the eyes of the *Fissurellidæ*, and differs from the eyes of the *Pleurotomariidæ* and *Trochidæ*, which are open.

The otocysts occupy the usual position on the dorsal surfaces of the pedal ganglia and present no unusual features (fig. 9).

The osphradia are strips of modified epithelium running for some little distance along the lower side of the gill-axes in front of the osphradial ganglia and just ventral to the osphradial or branchial nerve (fig. 16). They are very similar in structure and position to the osphradia of *Fissurella græca*.

Sense-papillæ occur not only on the cephalic tentacles but also on the epipodial tentacles, all round the margins of the mantle and on the cirrhi bordering the mantle-slit. Those on the cephalic tentacles are by far the largest, those on the margins of the mantle are very minute, but all have essentially the same structure. Fig. 28 represents a longitudinal section through three of the papillæ of the cephalic tentacles. Each papilla is a conical projection of the integument of the tentacle and is composed of a number of elongated cells of two kinds, closely packed together like the cells in a taste-bud from the human tongue. The larger cells with larger, pale nuclei are evidently supporting cells, their characters being similar to the adjoining epithelial cells. The more slender, finely granular cells with smaller, deeply staining nuclei are the sense-cells, and each ends in a short stiff cilium projecting from a small cup-shaped depression at the end of the cone. According to Vayssière these cilia are in constant movement in the living animal. The tentacles of *Fissurella* are clothed with a vast number of minute papillæ giving a velvety texture to the surface. These papillæ, though not so highly specialised, have each a single apical sense-bulb, the structure of which is similar to that of the sense-papillæ of *Incisura*.

Finally, mention may be made of the pedal glands. The anterior pedal gland consists of a mass of unicellular glands lying in the hæmocœle below the buccal bulb (fig. 7, *p. gl.*). It extends back nearly as far as the pedal ganglia. Anteriorly these glands become more deeply seated and pass into the muscular mass of the foot, where they debouch into a median ciliated duct (fig. 6) which runs forward and opens

on the anterior face of the foot in the groove between it and the lower surface of the snout. The posterior pedal glands are a mass of unicellular glands lying above the epithelial cells of the sole of the whole posterior surface of the foot. Each unicellular gland has its own duct, which runs between the epithelial cells to open on the surface.

The genera *Scissurella*, *Schizotrochus*, *Incisura* and *Schisnope*, which have been grouped as a separate family *Scissurellidæ* by some few authors, are generally placed in the family *Pleurotomariidæ* because they are zygobranchiate *Rhipidoglossæ*, with a labral incision of variable length and position in the shell. There is no frontal veil between the cephalic tentacles, an epipodial ridge is present, and there is a corneous multispiral operculum. Fischer (5) writes: "Quelques auteurs distinguent deux familles, *Scissurellidæ* et *Pleurotomariidæ*, mais les différences qui existent entre ces deux types n'ont pas plus d'importance que celles qu'on constate entre les divers groupes de *Trochidæ*. Je les considère comme des sous-familles." Pelseneer (13), who had studied their anatomy, retains these forms in the family *Pleurotomariidæ*. Yet it is obvious, from what precedes, that the *Scissurellidæ* cannot possibly be retained in this position. The differences in the radula alone are sufficient to distinguish the two types. But in addition to this the *Scissurellidæ* differ from the *Pleurotomariidæ* in a number of characters, which may be summarised as follows:

(1) The *Scissurellidæ* have two columellar muscles; *Pleurotomaria* has only one.

(2) The eyes of *Scissurellidæ* are closed; those of *Pleurotomaria* are open.

(3) The subocular tentacles of the *Scissurellidæ* are absent in *Pleurotomaria*.

(4) The epipodium of *Pleurotomaria* is destitute of tentacles, cirrhi, or lappets.

(5) The wide distance apart of the ctenidia, the large size of the pericardial cavity, the forward position of the ventricle of the heart, and the more distinct shifting of the organs of

the pallial complex into a median position in the roof of the mantle-cavity are all points in which the Scissurellidæ differ from Pleurotomaria.

(6) In Pleurotomaria the right kidney has a distinct duct, with thickened glandular walls in the female; in the Scissurellidæ there is no such duct.

(7) There is no spiral cæcum to the stomach in the Scissurellidæ, and the form of the stomach differs largely from that of Pleurotomaria.

(8) The hepatic orifices are numerous in Scissurellidæ, whereas there is only a single orifice in Pleurotomaria.

(9) The nervous system of the Scissurellidæ differs in detail in almost every point from that of Pleurotomaria, particularly in the concentration of the cerebral ganglia; the extreme fineness of the labial commissure; the presence of distinct pleural ganglia; the well-developed symmetrical pallial nerves establishing a right and left dialynenry; the presence of distinct supra- and sub-intestinal ganglia; the shortness of the visceral loop; the concentration and abbreviation of the pedal centres.

Not only are the Scissurellidæ distinct from the Pleurotomariidæ, but they are clearly less closely related to them than the Haliotidæ or even than the Trochidæ and Turbonidæ, for the last-named families, though they have lost the labral incision in the shell, as also the right ctenidium and the structures correlated to it, have retained many anatomical features which find their counterpart in Pleurotomaria.

Where, then, shall we find the nearest relatives of the Scissurellidæ? Though Mr. Hedley was clearly in error in removing Incisura from the Scissurellidæ, I think he came very near the truth in suggesting the affinity of this genus with the Fissurellidæ. His comparison of the adult Incisura with the post-larval stage of Fissurella is a just one. Almost all the differential external features which serve to distinguish the adults disappear on comparison of the adult of the one type with the post-larval stage of the other. In the young Fissurella we see a coiled shell with spiral sculpture, a labral incision of considerable length to the right of the middle line.

There is a pair of ciliated post-ocular tentacles on either side of the head (I find vestiges of these structures in the adult of *F. græca*), a well-developed pair of ciliated epipodial tentacles in the vicinity of the opercular lobe, and a corneous multispiral operculum. Even the gills, if one may judge from Boutan's figure (Pl. xlii, fig. 8), have a close resemblance to those of a Scissurellid. If the animal were sexually mature one would not hesitate to place it among the Scissurellidæ. In the next or Rimuliform stage the epipodial tentacles are multiplied; Boutan figures six in addition to the sub-ocular tentacles in *F. reticulata* and two in *F. gibba*. The labral incision has been converted into a foramen by the approximation of its edges at the labrum, but a suture still connects the foramen with the margin of the shell. This condition is exactly paralleled by the Scissurellid genus *Schismope*. Subsequent development leads to the assumption of Fissurellid characters. The visceral spire, and with it the spiral coils of the shell, become obsolete. The foramen in shell and mantle become situated at the summit of the Patelliform shell, the post-ocular and epipodial tentacles (which obviously belong to the same series) degenerate, the operculum is cast off, and the opercular lobe disappears. In short, the Fissurellid develops along lines which remove it further and further from the Scissurellid condition of the larva.

But, as must be apparent from the preceding pages, there is a considerable number of anatomical features in which the adult Scissurellid more nearly resembles the adult Fissurellid than any other family of the Rhipidoglossa. These features may be shortly recapitulated, *Incisura* being taken as a type of Scissurellid structure.

The jaws of *Incisura* in position and structure very closely resemble those of a *Fissurella*. The radula of *Incisura lytteltonensis* finds its nearest counterpart in the radula of *Submarginula picta*, and in general is distinctly Fissurellid in character. In the alimentary tract the characters of the salivary glands and œsophageal pouches, the absence of a spiral cæcum in the stomach, the presence of an œso-

phageo-intestinal groove in the capacious stomach, the existence of numerous hepatic ducts, are all points in which *Incisura* agrees with *Fissurella*, and differs, to a greater or less degree, from the *Pleurotomariidæ*, *Haliotidæ*, *Trochidæ*, and *Turbonidæ*. The presence of a right and left columellar muscle in the *Scissurellidæ* is evidently an antecedent stage of the horse-shoe shaped columellar muscle of the *Fissurellidæ*.

The eyes, which are open in *Pleurotomariidæ*, *Haliotidæ*, and *Trochidæ*, are closed in both the *Scissurellidæ* and the *Fissurellidæ*.

The subocular and posterior epipodial tentacles of the *Scissurellidæ* are paralleled by the similar larval organs in the *Fissurellidæ*.

In both the *Scissurellidæ* and *Fissurellidæ* the increased size of the last whorl of the shell and the diminution of the visceral spire has led to a broadening of the dorsal part of the body, in consequence of which the bases of the ctenidia are widely separated on the right and left sides of the body, the pericardium is transversely elongated, and the heart and kidneys are shifted towards the mid-dorsal line in the roof of the mantle-cavity. In these respects *Incisura* is intermediate between *Fissurella* and the other families of *Rhipidoglossa* enumerated above.

The nervous system of *Incisura*, though much specialised, shows more resemblance to that of the *Fissurellidæ* than to that of any other *Rhipidoglossa*, as has been explained in detail in the descriptive part of this paper. The correspondence in the labial commissure, the buccal ganglia, and the visceral commissure is very exact. The pedal centres of the *Scissurellidæ* have undergone great concentration, but this is foreshadowed in the pedal cords of the *Fissurellidæ*, which are much shortened in comparison with the elongated scalariform pedal centres of such families as the *Pleurotomariidæ*, *Haliotidæ*, and *Trochidæ*.

There can be little doubt, then, as to the affinity of the *Scissurellidæ* with the *Fissurellidæ*, but the exact relationship of the two families remains to be considered. In my opinion

it is not exact to say, as Hedley has, that *Incisura* represents an arrested stage of development of a *Fissurellid*. It is a more reasonable inference from the facts that the two families have descended from a common stock, and have diverged in different directions. There are several arguments in favour of this inference. One which in my opinion has great weight is derived from the condition of the left kidney in the two families. In the *Scissurellidæ*, as I have shown, the left kidney is relatively of large size, and is a true "papillary sac," phagocytic in function like the left kidney of the *Plenrotomariidæ*, *Haliotidæ*, and *Trochidæ*. In the *Fissurellidæ* this organ is reduced to a mere rudiment, and may, I believe, disappear altogether in some species, for I have failed to find a trace of it in transverse and horizontal sections of *F. græca*.

Remy Perrier (14) has stated that the epithelium of the left kidney of *Fissurella* is identical with that of the right kidney, but there is some doubt about this, and a renewed investigation of the left kidney of several species of the *Fissurellidæ* is much to be desired. But there is no doubt that it is a vestigial organ, and that in this respect the *Fissurellidæ* have been specialised along a different line to the *Scissurellidæ*, which have retained the left kidney in a fully functional state. Per contra, while the *Fissurellidæ* retain to a large extent the primitive scalariform character of the pedal centres, the *Scissurellidæ* have in this respect surpassed them in specialisation, for their pedal centres are concentrated to a degree elsewhere unknown among the *Rhipidoglossa*. The divergence of the two types is obvious, and one may conclude that both have been derived from a stock very nearly represented by the so-called Emarginuliform larva of *Fissurella*, which had a spirally coiled shell with a large umbilicus, spiral sculpture and a considerable labral incision. A corneous multi-spiral operculum and a well-developed epipodial ridge bearing sub-ocular as well as posterior epipodial tentacles were present. The left kidney was a well-developed papillary sac, and the pedal centres were

elongate and scalariform. Such an ancestral form would not be far removed from a *Pleurotomaria*, but would differ from it in the development of a double columellar muscle and in the tendency to acquire a secondary symmetry always correlated with the doubling of this muscle. The *Scissurellidæ* have retained most of the features of this parent form, but have undergone considerable specialisation in the nervous system. The *Fissurellid* branch must early have acquired a "sessile" habit, and have been much modified in connection with it, but its members have largely retained the primitive condition of the pedal centres. The *Scissurellidæ*, though for the most part constant to the primitive type, are also undergoing modification in the same direction as the *Fissurellidæ*. In *Incisura* the visceral spire is reduced, the shell is becoming thick and solid, the spiral sculpture is absent, the margins of the aperture are in one plane, the foot is becoming short and broad, and its whole organisation is indicative of a semi-sessile habit. Further specialisation along these lines would give it *Fissurelliform* or rather *Emarginuliform* characters. It is interesting to note that another member of the family, *Schismope*, while retaining its spiral coil and widely open umbilicus, has undergone specialisation in another direction, for the labral slit has been converted into a foramen by the approximation of its edges, so that although distant from the margin it is connected with it by a suture. In this respect it closely resembles *Semperia*, a sub-genus of *Emarginula*. *Semperia* leads on to *Rimnla*, and as we have seen there are *Emarginuliform* and *Rimuliform* stages in the development of *Fissurella*. This is an undoubted example of the developmental stages of one form resembling the adult stages of other forms, a phenomenon the occurrence of which some persons are inclined to deny nowadays, though the evidence in favour of it is very large.

The parallel stages of evolution among the *Scissurellidæ* and *Fissurellidæ* afford interesting examples of the phenomenon of convergence, and illustrate a principle which, I think, has not been sufficiently attended to in drawing inferences as to

the affinities of animals from morphological evidence, namely, that a similar environment and similar habits of life reacting on a similar organisation may often produce very similar structural results. Not, however, identical, for however similar the results may appear at first sight in all cases of convergence a close analysis will always disclose differences which exclude the idea of direct descent of the animals in question. This instance is particularly instructive; the Haliotidæ, Scissurellidæ and Fissurellidæ have all inherited the same structure from a presumably Pleurotomariid ancestor, viz. the slit in the mantle and the corresponding labral incision in the shell. It has been variously modified, and similar modifications are displayed independently by different groups, the similarity of the evolutionary series being, as far as one can judge, correlated with the adoption of similar habits.

ADDENDUM.

It is long since I first read the short but profound essay of Sir Ray Lankester (9) "On the Use of the term Homology in Modern Zoology, and the Distinction between Homogenetic and Homoplastic Agreements." On referring again to this essay, I find that the conclusions arrived at in the foregoing paragraph, as also similar conclusions arrived at after a detailed study of various members of the Neritidæ (1), are unconsciously expressed in nearly the same words that he used forty years ago. I have to beg Sir Ray Lankester's pardon for not making specific reference to his essay in my former paper. But I find a certain satisfaction in not having had the form of his argument clearly in my mind while I was working to the same conclusion from evidence gathered from the study of the probable lines of descent of animals belonging to a different class to that which he used to illustrate his original thesis. Had I consciously set out to prove, or even to disprove, his contention, I could not have avoided a certain amount of bias. To have arrived unconsciously—or subconsciously, for the idea of homoplasy inculcated by him was

always present to my mind—at an identical conclusion is to give unequivocal support to the validity of the arguments by which it was sustained. In the essay in question Lankester showed that the term homology, which really belonged to the platonic school of the natural philosophers of the end of the eighteenth and the beginning of the nineteenth century, acquired a new connotation after the publication of the ‘Origin of Species.’ But this new connotation was indefinite. On the one hand structures were said to be homologous which “are genetically related, in so far as they have a single representative in a common ancestor.” For this kind of homology Lankester proposed to substitute the term “homogeny.” On the other hand, various organs were described as homologous which could not possibly be included under the idea of homogeny, because, over and above general resemblances such as might be referred to inheritance from a common ancestor, they exhibited a number of detailed resemblances such as could not possibly be supposed to have been represented, in like detail, in a generalised ancestral form. Therefore, Lankester pointed out, there must be a second quantity covered by the term homology, and he described it in the following words: “When identical or nearly similar forces or environments act on two or more parts of an organism which are exactly or nearly alike, the resulting modifications of the various parts will be exactly or nearly alike. Further, if, instead of similar parts in the same organism, we suppose the same forces to act on parts in two organisms, which parts are exactly or nearly alike and sometimes homogenetic, the resulting correspondences called forth in the several parts of the two organisms will be nearly or exactly alike. . . . I propose to call this kind of agreement homoplasia or homoplasia. . . . What exactly is to be ascribed to homogeny and what to homoplasia in the relations of a series of structures is a matter for careful consideration.” Somewhat further on in the essay homoplasia is defined as “depending on a common action of evoking causes or moulding environment on homogenous (= homogenetic)

parts, or on parts which for other reasons offer a likeness of material to begin with."

The term "homoplasy" has passed into current use, and the principle expressed by it has been freely used to explain numerous large and general resemblances which have obviously been evolved independently, such as the general resemblances between different kinds of patelliform gastropod shells, e. g. between *Patella*, *Fissurella*, *Septaria*, *Capulus*, and *Siphonaria*, or the general resemblances of external morphology of fishes and cetacea. But the term homogeny has not been so generally accepted, and many, if not most, zoologists have preferred to retain the old word homology, and in so doing it is clear that many of them have failed to distinguish between the two quantities contained within the single term, of which the differences were so clearly pointed out in Lankester's essay. For it must be evident to anybody who is well acquainted with the morphological literature of the last thirty years that, so far from attempting to distinguish between homogenetic and homoplastic resemblances, a large number of authors have shown a vast amount of ingenuity in referring the most minute resemblances in the organs of animals, which are certainly not very closely related to one another, to homology. The most extreme instances of this tendency to ascribe every resemblance, however detailed, to inheritance, ignoring the possibility that similar structural changes may be induced by the incidence of similar forces, are to be found in the works of those authors who attempt to derive the lower members of one phylum of the animal kingdom from highly differentiated members of another phylum.

It is, of course, true that several of the most thoughtful and best informed among contemporary zoologists have been fully aware of the error lurking in the indiscriminate use of the term "homology," notably Gegenbauer and Fürbringer in Germany; Cope, W. B. Scott, E. B. Wilson, and Osborn in America. It is not my present intention to enter upon a long discussion of this subject, which I hope to return to on a future

occasion. But I take the opportunity of dealing with an interesting and suggestive essay by Osborn (10), in which Gegenbauer's admirable analysis of the different forms of resemblances obtaining among animal structures is largely quoted.

In the first place Osborn makes it evident that I, in common with others, have fallen into an error in using the term "convergence" to denote the parallel stages of evolution among the Fissurellidæ and Scissurellidæ. In the common meaning of the word, convergence might appropriately be used to signify that apparent approximation of structural characteristics which not infrequently leads to two forms being classified together in the absence of sufficiently complete information as to their internal anatomy. But it has acquired a special meaning, defined by Osborn as the "independent similar development of unrelated animals, bringing them apparently closer together." As it has been the purpose of my paper to show that the families of Molluscs treated of are related, and closely related, the term convergence is not applicable to resemblances recurring in those families. But when I come to consider whether other resemblances between various mollusca should be described as due to "parallelism" or "homoplasy" I find myself in a difficulty. Parallelism is defined as the "independent similar development of related animals, plants, or organs"; homoplasy as the "independent similar development of homologous organs or regions giving rise to new parts." It is added that homoplasy always involves homology, while parallelism and convergence may or may not involve homology.

In *Incisura* the reduction of the visceral spine, the obliteration of spiral sculpture, the levelling of the margins of the aperture, the alteration in the shape of the foot are changes parallel to those observed in the ontogeny of a Fissurellid, and they involve homogenetic organs; the parallelism in this case involves homology and should be called homoplasy. In *Schismope* the conversion of the labral slit into a foramen is a change parallel to that observed in the

ontogeny of a Fissurellid and it involves a homogenetic character, therefore it also is due to homoplasy. On the same reasoning the resemblances in the shell, foot, and mantle of more distantly related forms, the Patellidæ, Septaria, the Capulidæ, and Siphonariidæ are homoplastic. But should the pallial branchiæ of a Patella and the gill of a Siphonaria, be attributed to parallelism or homoplasy? They are certainly not genetically derived from the typical molluscan ctenidium, and to this extent are deficient in the element of homology which Osborn says should always be associated with homology. On the other hand they are vascular outgrowths of the mantle, which is assuredly a homogenetic structure in all the forms in question, and therefore there is an element, though a more remote element, of homology. In this case it is simply a question of the importance attached to the degree of homology whether these structures should be ascribed to parallel or homoplastic development. But Lankester's term, homoplasy, as originally defined, covers all the cases. It appears to me that, while there is a contrast between homoplasy and convergence, there is no such contrast between homoplasy and parallelism, and that for the sake of clarity the last term should be abandoned, homoplasy being retained in the sense originally defined by Lankester. It has the priority over Fürbringer's term homomorphy, which, as Osborn points out, has the same connotation; and it has the advantage of indicating a resemblance due to the moulding influence of environment, whereas homomorphy only calls attention to similarity of form.

In the latter half of his essay Osborn raises a most interesting question, which has presented itself with various degrees of insistence to workers in various groups of the animal kingdom. Drawing his evidence from palæontological as well as recent types, he points out that the accessory cusps in the molar teeth of Mammalia arise in the same order and with the same relations to the primary cusps in groups which can be proved to have diverged widely from one another before any complication of the tooth pattern arose. Here, then, are

examples of detailed resemblances which cannot be due to inheritance nor yet can they be due to external forces acting upon homogenetic parts, for the teeth are formed below the gum and the cusps are in place before any mechanical forces are brought to bear on them. The characters of the teeth are clearly congenital, and the resemblances between the patterns which have arisen independently in different groups cannot be accounted for by the preservation of fortuitous variations by natural selection, for palæontological evidence shows that variation has in each case proceeded along one line and not along several lines, one of which has been selected.

Calling to mind Lankester's suggestion of the "common action of evoking causes . . . on parts which for other reasons (than homogeny) offer a likeness of material to begin with," Osborn pleads for the recognition of a latent or potential homology, by which term I understand him to mean a tendency or capacity to produce a definite structure, which capacity must have been present in the ancestors of the existing orders of Mammalia, but has only manifested itself in such groups as possessed or were subject to the co-operating factors necessary for evoking the latent capacity, and thus producing the structure in question.

The objections to a principle of this kind are that, in the first place, as Osborn himself admits, it leads us on the dangerous ground of teleological speculation; and, in the second place, that it might, if loosely applied, be used to explain anything or everything by a phrase.

Nevertheless, I think that some such principle may be admitted, with due caution, in explanation of a large number of difficulties which present themselves, with increasing insistence, to every class of zoological workers. In a recent paper on the Neritidæ I alluded to the great difficulty of finding a satisfactory theory to account for the distribution of the fresh-water Neritids, described as species of the subgenera *Paranerita* and *Septaria*, in remote oceanic islands. As their general anatomical and conchological characters

differ in a very small degree from those of the marine species of the genus *Nerita*, abounding in the seas in which the oceanic islands inhabited by the fresh-water Neritids are placed, it did not seem an unwarrantable assumption that in each locality the marine species had ascended from estuaries into rivers (just as prawns do in so many parts of the tropics), and had been similarly modified as a result of the fresh-water environment. But when I found that the accessory generative organs of the fresh-water species from different localities were always alike, and differed in the same direction and to the same degree from the accessory generative organs of the marine species from the same localities, particularly in the fact that the female gonaducts of the freshwater species are always triaulic, whereas those of the marine species are diaulic, I was no longer able to sustain the opinion that I had first formed as to the possibility of the independent but similar modification of the marine species in different parts of the world. It seemed to me impossible that the triaulic condition should have been evolved several times over. The problem, however, is of the same kind as, though of less magnitude than, that presented by the cusps of mammalian molar teeth. If we can conceive the presence in the germ-plasm of Neritidæ of factors competent to produce the triaulic condition of the genital ducts, but that the activity of these factors is only excited by the co-operating action of other factors—in this case by reduction of the salinity of the water—the detailed resemblances between structures existing in animals living so far apart but under similar conditions are susceptible of explanation.

A few years ago such an explanation would have been inadmissible. But since Mendelian experiments have shown that definite changes affecting parts of the organism in a similar manner may require the co-operation of two or more factors, and cannot be produced unless those factors are brought together; and since such experiments as those of Stockard on *Fundulus* have shown that a relatively slight change in the salts dissolved in water may induce profound

changes in certain organs of developing embryos, it is no longer possible to reject such suppositions as fanciful and incredible.

Those who have given unprejudiced consideration to the objections raised against the all-sufficiency of natural selection, must have felt that a term is wanting somewhere in the current forms of argument used to explain resemblances between structures which are only doubtfully homogenetic. The missing term may possibly be found when we have a more exact knowledge of the kinds of factors whose co-operation is necessary to produce specific structure. Some of these factors must be germinal, but evidence is accumulating that germinal factors are not simple but compound, and may be split into subordinate factors which, taken alone, do not produce the specific result. There is further evidence that germinal factors react differently to different external factors, and if this be so many kinds of resemblances and differences may be accounted for by laws of interaction of which we are as yet only dimly aware.

The evidence on these matters is insufficient to enable us to arrive at definite conclusions, but it is at any rate sufficient to earn respect for a suggestion supported by such a large number of positive facts as that of Osborn.

I believe that in the future morphologists, in conjunction with systematists, will be largely occupied in attempting to discriminate between the different kinds of resemblances among animal structures, between similarities due to the "common action of evoking action or moulding environment," and similarities due to direct descent, and I venture to think that such morphological studies, carried out with scrupulous attention to detail, are not useless, but will give precision to, and perhaps modify our views on, the causation of modification of animal structure.

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EXPLANATION OF PLATES 1—5,

Illustrating Mr. Gilbert C. Bourne’s paper “On the Anatomy
and Systematic Position of *Incisura (Scissurella)*
lytteltonensis.”

LETTERING FOR ALL THE FIGURES.

An. Anus. *a. g. f.* Anterior gill-filaments. *au. l.* Left auricle. *au. r.* Right auricle. *B.* Buccal ganglia. *b. b.* buccal bulb. *b. c.* Buccal cavity. *br. n.* Branchial nerve. *b. sk.* Branchial skeleton. *b. v.* Blood-vessel. *C.* Cerebral ganglia. *car.* buccal cartilage. *c. c.* cerebral commissure. *cil.* Cilia. *cil. c.* Ciliated canal of dorsal ridge of gill-filament. *cil. l.* Lateral ciliated cells. *c. pd.* Cerebro-pedal connective. *c. pl.* Cerebro-pleural connective. *di. l.* Left dialyneurous connection. *d. g. r.* Dorsal glandular ridge of gill-filament. *e.* Eye. *ep.* Epipodium. *ep. n.* Epipodial nerve. *ep. t.* Epipodial tentacle. *F.* Foot. *f. c.* Frontal cilia. *g.* Ganglion behind mantle-slit. *g. f.* Gill-filaments. *g. n.* Genital nerve. *hy. g. l.* Left hypobranchial gland. *hy. g. r.* Right hypobranchial gland. *i.* Intestine. *i. v.* Vertical loop of intestine. *j.* Jabot. *ju.* Jaws. *k. l.* Left kidney. *k. r.* Right kidney. *l. b.* Left branchial ganglion. *lb. l.* Labial lobe. *l. c.* Labial commissure. *l. c. m.* Left columellar muscle. *l. ct.* Left ctenidium. *li.* Liver. *li. d.* Liver-ducts. *l. œ. p.* Left œsophageal pouch. *lt.* Lateral tooth of radula. *m.* Mouth. *m. c.* Mantle-cavity. *md. t.* Medio-lateral teeth of radula. *m. f.* Median dorsal fold of buccal cavity. *m. s.* Mantle-slit. *mt.* Mantle. *n.* Nucleus. *od.* Oviduct. *od. o.* Opening of oviduct into right kidney. *œ.* Œsophagus. *os.* Osphradium. *ot.* Otocysts. *ov.* Ovary. *P.* Pedal ganglia. *pa.* Pallial nerve. *pc.* Pericardium. *p. g. f.* Posterior gill-filaments. *p. gl.* Pedal gland. *phg.* Phagocytic cells of left kidney. *pl. l.* Left pleural ganglion. *pl. r.* Right pleural ganglion. *p. n.* Pedal nerves. *p. v.* Pallial blood-vessels. *R.* Rectum. *r. b.* Right branchial ganglion. *r. c. m.* Right columellar muscle. *r. ct.* Right ctenidium. *rd.* Radula sac. *r. œ. p.* Right œsophageal pouch. *rp. d.* Reno-pericardial duct. *sb. i.* Sub-intestinal ganglion. *sg.¹* Anterior salivary glands. *sg.²* Posterior salivary glands. *sn.* Snout. *s. o. t.* Sub-ocular tentacle. *sp. i.* Supra-intestinal ganglion. *sp. l.* Left symmetrical pallial nerve. *sp. n.* Supra-intestinal nerve. *sp. r.* Right symmetrical pallial nerve. *st.* Stomach.

sy. p. Sensory papillæ. *T.* Cephalic tentacle. *tn.* Tentacular nerve.
un. Uncini. *V.* Ventricle of heart. *v. aff.* Afferent branchial vessel.
v. eff. Efferent branchial vessel. *v. g. l.* Left visceral ganglion. *v. g. r.*
 Right visceral ganglion. *v. n.* Visceral nerve.

[All the figures are of *Incisura lytteltonensis*.]

Fig. 1.—A specimen viewed from the left side and below to show the size and shape of the foot, the operculum, the epipodial tentacles, etc. \times about 40.

Fig. 2.—Dorsal view of a female specimen which has been stained and mounted as a transparent object. \times 80.

Fig. 3.—A reconstruction of the alimentary tract; semi-diagrammatic. \times 80.

Fig. 4.—A diagram showing the relations of the right and left kidneys, the heart, pericardium, ovary and oviduct. The extent of the pericardial cavity is indicated by a thick black line. \times 80.

Fig. 5.—The nervous system as determined by reconstructions from sections. \times 80.

Fig. 6.—♂. A transverse section through the posterior part of the head, including both eyes. \times 135.

Fig. 7.—♂. A transverse section taken just behind the mantle-slit, showing the bi-pectinate character of the right ctenidium. \times 135.

Fig. 8.—♂. A transverse section through the anterior ends of the pedal ganglia. \times 135.

Fig. 9.—♀. A transverse section through the hinder ends of the pedal ganglia. Note the position of the left kidney, *k. l.*, and its opening into the mantle-cavity; the size and extent of the right and left œsophageal pouches, *r. œ. p.* and *l. œ. p.*; the size and position of the right and left pleural ganglia, *pl. r.* and *pl. l.*, and the supra-intestinal ganglion, *sp. i.*; the pedal ganglia, *P.*, are clearly seen to be composed of a dorsal and a ventral moiety. \times 135.

Fig. 10.—♀. A transverse section passing through the posterior end of the mantle-cavity, showing the large size of the left auricle, *au. l.*; the orifice of the left kidney, *k. r. o.*; the pedal nerves, *p. n.*, which are the posterior continuations of the ventral moieties of the pedal ganglia shown in fig. 9. \times 135.

Fig. 11.—♀. A transverse section passing through the posterior end of the foot. Note that the large pedal nerves shown in the previous figure do not extend into the hind part of the foot. \times 135.

Fig. 12.—♀. A transverse section taken near the terminal part of

the visceral spire, showing the opening of the oviduct, *od.*, into the hinder end of the ovary, *ov.* × 135.

Fig. 13.—♂. A section through the left kidney showing the reno-pericardial duct, *rp.d.* Note the band of ciliated cells, *cil.*, on the floor of the mantle-cavity opposite the opening of the left kidney. × 225.

Fig. 14.—♀. A portion of a section through the left kidney showing the rounded phagocytic cells, *phg.*, which have taken up solid rod-shaped bodies from the subjacent blood-vessel, *b.v.* × 1000.

Fig. 15.—Striped muscle-fibres attaching the anterior end of the buccal bulb to the integument. × 1000.

Fig. 16.—A transverse section through the anterior filaments of the left ctenidium. Note the osphradium, *os.*, lying under the branchial nerve, *b.n.* × 535.

Fig. 17.—A transverse section somewhat posterior to that drawn in fig. 16, passing through the posterior filaments of the left ctenidium. In this and the previous figure note, *d.g.r.*, the dorsal glandular ridges of the gill-filaments. × 535.

Fig. 18.—A transverse section through two gill-filaments of the right ctenidium; *cil.c.*, the ciliated canal traversing the dorsal glandular ridges of the filaments. × 1000.

Fig. 19.—The left ctenidium stained and viewed from above as a transparent object. × 225.

Fig. 20.—A portion of the radula. × 800.

Fig. 21.—Part of a transverse section passing through the anterior end of the buccal bulb to show, *m.f.*, the median dorsal fold of the buccal cavity and, *s.g.¹*, the anterior salivary glands and their ducts. × 535.

Figs. 22–26.—A series of transverse sections through the right-hand posterior corner of the mantle-cavity showing the relations of the oviduct and the right reno-pericardial duct to the right kidney and the pericardium. × 225. (These figures are drawn as seen reversed under the microscope.)

Fig. 27.—A cephalic tentacle showing the two multiple rows of sensory papillæ. × 225.

Fig. 28.—A longitudinal section through three sensory papillæ of a cephalic tentacle. *n¹*, pale nucleus of a supporting cell; *n²*, deeply stained nucleus of a sense-cell; *cil.*, cilia borne at the ends of the sense-cells. × 1000.