Loxosoma loxalina and Loxosoma saltans —Two New Species.

Bv

Richard Assheton, M.A., Lecturer on Biology in Guy's Hospital, University of London.

With Plates 6 and 7 and 4 Text-figs.

The genus Loxosoma is remarkable among Polyzoa in having the lophophore placed more or less obliquely to the main axis of the stalk instead of being at right angles as in other Polyzoa, and in being solitary, for the buds, which are formed readily enough, drop off before they have reached any great size, and attach themselves to the surface of some other organism or neighbouring object by means of diverse forms of adherent arrangements in the end of the stalk or foot, which varies a good deal in shape. The species, of which rather more than a dozen have been described, are all commensals living fixed on to other organisms or upon the tubes inhabited by other organisms, which may be Polychætes, Sponges, Ascidians, Gephyreans, and probably other animals as well.

Among these there is a form called Loxosoma annelidicola, which was originally mistaken for a Platyhelminth, and called Cyclatella annelidicola, having been found by P. J. Van Beneden and C. E. Hesse in 1865 on certain Maldanid Polychætes, but which subsequently was recognised as an Entoproct, and so described by Prouho in 1891.

Prouho found the species on the Clymenians Nicomache lumbricalis and Petaloproctus terricola.

More recently a species of Loxosoma, the first actually described from the American side of the Atlantic, has been made the subject of an interesting paper by N. S. Nickerson, and named L. Davenporti, also from the tube of a Maldanid, namely Clymene producta. This species clearly has close affinities with the other Maldanid Loxosoma, L. annelidicola, as is shown for instance, by the possession of the wing-like expansion of the body and the arrangement of the foot muscles, but is quite distinct in many characters, such as the far longer stalk, peculiar epidermic "flask organs," the more numerous tentacles, and the curious "mammary organ" which the female of L. Davenporti possesses. The two new species which form the subject of this present paper are also from the tubes of Maldanid worms, and, as one might expect, bear certain resemblances to L. Davenporti and L, annelidicola, but they are clearly distinguishable from these, as may be noted from a glance at prepared specimens.

LOXOSOMA LOXALINA.

Loxosoma loxalina was found in September, 1909, in the Sound of Mull, near the entrance to Loch Aline, in association with a Maldanid, of which I have only an imperfect specimen, and which I have been unable to identify.

External Characters.—It is characterised by its long stalk as compared with the other known Maldanid associates, the stalk being longer than the body and calvx together, though very much shorter than the stalk of L. Phascolosomatum, and the presence of curious projecting glands placed with some regularity on the sides of the body (fig. 1), which, though more numerons and smaller, are no doubt comparable to the "flask organs" described by Nickerson on L. Davenporti, although they occupy a different position. Ectodermic glands, unicellular or multicellular, occur on other species, e.g. L. Tethyæ, L. crassicauda, and L. phascolosomatum, though in these cases they are sunk

entirely beneath the surface rather than raised above it, but probably all such organs may be said to be generally homologous. In L. loxalina they have undergone a special development and differentiation, and though projecting from the surface, do not stand out so clearly as in L. Davenporti or in L. saltans, the second species to be described here. In all specimens that I have examined these organs are generally similar: they occupy more or less corresponding positions, and are differentiated in like manner. There are usually two pairs on the calvx and two pairs on the body, and they tend to give the animal a somewhat angular appearance. Sometimes extra pairs occur on the body. There are none on the stalk, which is sharply marked off from the body. In L. Davenporti they are borne about the spot where the body passes into the stalk. Although glandular is a convenient term to use, there is no sign of any secretion exuding from them. Figs. 1, 15, 16 and 17 indicate clearly enough the structure of these organs, but their function must remain for the time being a mystery. Fig. 1 represents the most usual condition. I have never found less than the four pairs here indicated, but I have in some specimens seen additional pairs. The two pairs on the edge of the calyx are less prominent than the others, and are not very different from the unicellular glands of Salensky, L. tethyæ. The lower pairs are either connected with, or lie in close juxtaposition to, rows of large deeply stained cells (figs. 1, 3, and 6 [k.]). On the body there are two pairs, the upper of which is on the ventro-lateral surface at the level of the lower margin of the two appendages of the stomach. The lowest pair of all is different from the rest, and is never absent. Whereas the others vary a good deal in form and degree of development, this lowest pair is constant. Each organ consists of a group of long cells, the nuclear ends of which are deeply imbedded in the body, and the outer ends, projecting a short distance beyond the surface, form a conical eminence with a small crater-like depression on the centre. Fig. 17 (a.) represents, in diagrammatic form, the structure of these and the other epidermic glands of L. loxalina, and may be compared with the figures of sections of the similar organs of L. saltans (figs. 15 and 16), which resemble far more closely the "flask organs" of Nickerson on L. Davenporti. It is pretty clear that they are all essentially similar morphologically, whatever their function may be. From the distinct character and constancy in position of the lowest pair we may assume that these particular ones have a special function. They are more deeply set than the others.

The foot is circular and devoid of any special gland such as L. tethyæ and L. leptoclini possess. It has, however, a peripheral row of unicellular structures, which may be mucous or some form of adhesive gland which project beyond the general contour as the toes of a frog project beyond the web (fig. 13). But quite possibly they may be of firmer consistency and serve as stiffening rods.

The lophophore of this species as well as L. saltans is not circular in outline, but slightly indented along the oral region, at first sight suggesting the condition in the Phylactolæmata, but in them the inflection is of the anal region. The tentacles in every case I have counted number sixteen, and are not all of the same size. Four along the anterior or indented part are longer than the rest, and a gap occurs between the two inner ones of the four. The same characters are seen in L. saltans, and apparently also in L. tethyæ according to Salensky, though only two tentacles are shown by his figures to be longer than the others.

Alimentary Canal.—The whole body is very much compressed in the oro-anal axis, but does not show any features very strikingly different from those of other species of Loxosoma. The rectum is carried far along the hood of the lophophore, so that the anus lies near the rim of the lophophore as in L. crassicauda, but unlike L. Davenporti, where the rectum ends about the centre of the lophophore hood. The rectum is wider than the intestine and its walls contain cells with brown inclusions, which are probably excretory products (vide L. saltans). The whole body being longer in L. loxa-

lina than is usual, the alimentary canal is longer, and the lower or proximal part of the stomach is more distinct and forms a triangular or conical-shaped chamber. There are well-marked lateral swellings which form the glandular portion of the alimentary system (fig. 1, ld. pd.).

The mouth is bounded posteriorly by an epistome and anteriorly by the edge of the lophophore, which in the middle line is raised up into a little knob which in L. saltans bears stiff hairs. The mouth leads into a wide funnel-shaped chamber quickly narrowing into an æsophagus lined by long cilia. The cells which form the walls of the æsophagus contain a dark olive-green pigment lying deep in the cells and which occurs nowhere else in the animal.

There are really two pairs of diverticula from the alimentary canal, an anterior or proximal pair, though actually lying nearer the foot than the lophophore region, and strictly lateral, and a posterior or distal pair less sharply constricted and lying rather more towards the ventral surface. Fig. 1 of L. loxalina and figs. 10, 20 of L. saltans illustrate this well enough.

The alimentary tract is ciliated over a great part of its surface, though in certain regions the cilia are longer than in others. The whole of the œsophagus bears long cilia, the lower chamber of the stomach is lined with short cilia, while the diverticula are devoid of them. The intestine is ciliated throughout by short cilia. The character of the cells forming the walls of the alimentary canal seem to be similar in the two species, L.loxalina and L.saltans, and some further details are given in the next section.

I shall not dwell upon the histological details of L. loxalina, as although I have over a hundred specimens of this species, they were all obtained from the tube of a single worm, and were preserved alike in Perenyi fluid, which is not a suitable reagent for fixing this animal's tissues. In fact the specimens were not discovered until some time after preservation in the bottle containing the sand tube and portions of the Maldanid worm. I have not succeeded in coming

across the species again, so that I have not seen it alive. The Maldanid worm was the only one obtained, and that was got some feet below low-water level of a spring tide.

Nervous System.—The only part of a nervous system observed is the paired ganglionic mass which lies between the intestine and the reproductive gland as shown in fig. 3, in a position corresponding exactly with that of L. saltans, fig. 14, and other species.

Excretory System.—The poor histological condition of the specimen makes it very difficult to determine the character of the excretory organs. There are certain structures which are probably of that nature which lie in the body just above the glandular expansion of the stomach. Firstly, there is a pair of large rounded masses of deeply staining cells which have rather the appearance of yolk-glands or testis, and are no doubt part of the reproductive system (fig. 6). Closely applied to these and extending from them to the skin are very peculiar cells arranged in tiers, pagoda-like, as in fig. 1 (k), and fig. 6 (k), the larger cells being at the bases. Next the skin are some small rounded cells. It is not possible to make out a duct, nor is it easy to make these structures correspond with anything hitherto described as excretory organs of polyzoa. Nevertheless, as will appear in the next section, it seems to me possible to derive them for the structure which must be regarded as excretory organs in L. saltans.

Reproductive system.—This consists of a pair of large gonads (figs. 1 [g.] and 4 [g.]), from which wide ducts run inwards towards a mass of large granular cells lying in the median plane just behind the nerve ganglion and æsophagus. This mass may be of the nature of a shell-gland (c f. Nickerson), or possibly a yolk-gland, and from it a single median duct runs to open into the atrium between the epistome and the lophophore.

The gonads are not very well preserved, but at any rate I can say that each is a more or less spherical sac with thick walls and a small central cavity from which the gonoduct runs. The walls bear the reproductive cells, and I am inclined to

think that they are hermaphrodite; but I do not wish to commit myself absolutely. Figs. 3, 4 and 6 illustrate these points. There seems to be an anterior duct or opening (fig. 5, k.d.) on the epistome. Whether this is renal or reproductive I cannot determine.

Muscular System.—The contractile tissue is well developed in connection with the stalk, foot and tentacles. The long peduncle contains longitudinal fibres which run parallel with the surface between the body and the foot, and closely applied to the surface. At the proximal end some of these fibres bend across and become continuous with the walls of the alimentary canal. I cannot make out that they divaricate in so marked a manner at the distal end in reaching the foot as one would expect from the condition described in L. annelidicala or L. Davenporti. There is a strongly developed circular band of fibres developed on the inner rim of the lophophore.

The surface of the stalk contains longitudinal rows of larger cells, and one especially well-developed row extends down the mid-dorsal line. This also occurs in L. Davenporti and others.

LOXOSOMA SALTANS N.S.

An allied form of Loxosoma living also in the tube of a Maldanid occurs farther north in the sands of the shores of Skye, in the neighbourhood of the Kyle of Loch Alsh, some three or four feet below low-water level.

This is sufficiently different from Loxosoma loxalina of the Sound of Mull to deserve a different specific name, though it, together with L. Davenporti and L. annelidicola and even L. crassicauda, form a group showing special affinities. All these species live commensally with tubicolous Polychætes. The difference is distinctly indicated in the two figures, 1 and 20 on Pls. 6 and 7, which are drawings of typical specimens of the two forms after preservation. Fig. 10 gives a better idea of the living animal, L. saltans. The Skye

form is shorter and broader, and has a smaller body in proportion to the size of the lophophore than L. loxalina. The curious gland-like processes are quite different. They are less numerous and far larger in the Skye species, in which I have never found more than two present. They arise from the ventro-lateral surface about half way down the body—whereas in L. loxalina there are usually four pairs set more on the lateral edges. They resemble very closely the flask organs of L. Davenporti, but are larger and placed higher up on the body.

In the Skye species these curious organs may be altogether wanting, or one alone may be present. They are pedunculate, whereas in L. loxalina they are partially sunk beneath the surface. Specimens with buds, which buds arise from the ventro-lateral surface anterior to the spikes, are found with or without spikes, so that there is no correlation between these organs and the buds. Figures 15 and 16 represent sections taken rather obliquely through these organs. It will be seen how in fig. 15 the epiblast is ruptured at one side, thus indicating how easily they may become detached. They are in all cases entirely epidermic.

The character which suggests the name I propose for the species Loxosoma saltans is the peculiar mode and highly developed power it possesses of locomotion. When freshly taken it is extremely active, moving over the body of the worm or along the lining of the tube in a manner fascinating and unique by a series of gymnastic efforts, which combine the agility of the kangaroo and the deliberation of a geometer caterpillar.

It is possibly in correlation with this habit that there is a modification of the lophophore, which is not perfectly circular as is usual among the Entoprocta (except L. loxalina), but is elongated in the oro-anal plane, and shows a slight tendency to a separation into right and left halves, and is inflected along its oral region (fig. 19).

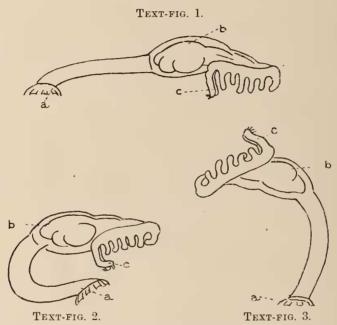
The tentacles, as a rule, number sixteen, so that we have a right and left series of eight very slightly separated from

each other by the occurrence of a rather wider interval between the first of the right and the first of the left and last of the right and last of the left. A papilla bearing stiff hairs lies between the two series at the oral end. The special modification in connection with the habit of jumping is in the four oral tentacles, that is to say the first and second of the two series, forming the four on the inflected edge of the lophophore. These are longer than the rest, and when closed down over the mouth fold outside and across the tentacles of the lateral parts of the lophophore as in fig. 19. These four usually work together and are raised off the floor of the calyx quite independently of the others. When the animal moves its position these four tentacles play a part in the action.

The stalk of the animal is extremely strong and muscular, and can swing the body about in any direction with ease and rapidity. The calyx may be directed ontwards from its point of attachment, so that where expanded it shows a campanulate form as in fig. 10, which resembles the ordinary Pedicellina condition rather than that typical of the genus Loxosoma, and in this respect it is more like Urnatella.

When lying prone, as presumably it must often do while between the worm and tube, we may suppose that it lies with its oral surface towards the object to which it is attached, as this is the position it more usually takes when not waving outwards. Prouho's figures seem to show that L. annelidicola lies the other way. It is in this position that locomotion is possible. This is effected by the animal bending down its body and lophophore into contact with the surface over which it is about to move, but contact is made only by the tips of the four large oral tentacles, which are provided with special stiff bristles on their outer tips (fig. 10), which do not occur in the other tentacles. These no doubt serve to give it a hold. The four tentacles are then suddenly bent backwards, that it to say outwards, and at the same moment the peduncle is whisked forwards with great rapidity, and the adhesive foot applied in a fresh situation, as in Text-fig. 1.

It appears to be a distinct jump; there is a moment when neither foot nor tentacles are in contact with the surface over which the animal is progressing. It is not quite like the looping of a caterpillar; it is more like the action of the boy playing "leap-frog." The animal can either bring its foot directly forward, or swing it horizontally according to space.



Three successive attitudes of L. saltans during the act of jumping. a. Foot. b. Gut. c. Tentacles used in jumping.

As I have not succeeded in obtaining Loxosoma loxalina alive, I cannot say whether it leaps, but from the fact that there is the same difference between the oral tentacles and the others it seems probable that it does. Salensky's figure suggests that a similar modification also occurs in L. tethyæ.

As far as I know no such agility on the part of a Polyzoan has been observed before; Cristatella, of course, is known to move, but that is motion of a very different kind. It seems

possible that a somewhat different though less lively mode of progression may be possessed by L. Davenporti from what Nickerson says, though there is no modification, nor similar action, of the four oral tentacles. Nor is the oral part of the lophophore rim indented. In L. Davenporti there are certain cells at the base of each tentacle on its outer surface, "the cuticula over the cell" being "thickened to form a flattened or sucker-like protuberance." Nickerson continues (p. 355): "If a number of specimens in clear sea-water in a smooth glass vessel be observed attentively, individuals may often be seen lying on the dorsal surface with the lophophore fully expanded. If a current of water from a pipette be directed against an animal in this position it becomes evident at once that the creature is attached quite firmly by the lophophore margin; and though the foot end may be lifted up by the motion of the water, the hold of the animal is loosened only by a very strong current. This observation makes it evident that the cells in question serve as a means of attachment. They are to be regarded as unicellular suckers, which are of use to the animal in enabling it to keep a hold upon its host while changing its foot attachment."

External Form.—The living animal is almost transparent and colourless except for the excretory organs and alimentary canal, which is throughout slightly yellow, and at certain points it is strongly pigmented and shows up brightly. The pigmented portions are the two distal and lateral swellings on the stomach, which vary from a bright yellow or orange to brown (fig. 19), and the latter part of the alimentary canal or rectum which is wider than the intestine. The two smaller and proximal diverticula of the alimentary canal, which in sections are seen to take stain more readily than any other part of the alimentary canal, are almost quite devoid of any colour in the living animal. Fig. 19 illustrates the colour of the living animal and fig. 10 the general form and character. In this specimen there were two large pedunculate "flask organs," of which one is shown in fig. 10,

and two buds; one of these is well advanced. The figure shows the way in which the lophophore expands and the small tentacles spread out, though always slightly curved inwards. The four oral tentacles are usually moved together and often thrown back as in the act of jumping. None of my specimens, nine in number, had more than two buds.

The stalk is shorter than in L. loxalina, and the foot is slightly larger, but resembles the foot of L. loxalina with its toe-like organs very closely. I think there are twelve to sixteen of these organs.

Alimentary Canal.—The general character of the alimentary canal is indicated by the figs. 11 and 12. It differs from that of L. loxalina only in the greater size of the distal, more ventral diverticula, which are the most pigmented parts, the long cells being filled with yellow granules. Fig. 11 is a slightly oblique section which passes through the esophagus and the edge of one of these thick-walled diverticula, which are composed of elongated cells with the nucleus at the outer end and loaded with spherical vellow inclusions (figs. 11 and 22). I think the gut lining is throughout a single cell in thickness which cells vary greatly in length. The œsophagus opens into the stomach low down on the anterior face. As in L. loxalina, the anterior and posterior walls contain granules of dark colour, but they are of a deeper brown and less refractive than in the former species. The intestine leads from the stomach by a gradual narrowing of that organ, but along the whole dorsal wall of the stomach there is a groove (which is continuous with the lumen of the intestine) of low ciliated epithelium. This iu its turn is continuous with the conical lower apex of the stomach and with the entrance of the esophagus, all of which is ciliated. The only parts not ciliated are the four glandular tracts. The longest cilia are in the œsophagus and at the entrance of the esophagus to the stomach. Figs. 11 and 12 illustrate the character of the epithelium of the apex of the stomach, where it is low, columnar (and I think really ciliated) with a few mucous glauds (mu.). The section also shows the

proximal diverticula of long cells with small nuclei at their bases and filled with fine granules of quite a different character to the cells of the larger distal pair. The cells of the apical part of the stomach and the intestine contain many granules at their basal ends which are blackened by osmic acid and are probably fat-globules. This part of the stomach may be regarded as absorptive (figs. 11 and 12). The characters of the proximal pair of diverticula suggest secretion of some digestive juice, the cells being filled with very fine granules not unlike the granules of vertebrate pancreatic or salivary gland-cells. The margin of these cells or of some of them are irregular like those of mucous cells or other actively secreting cells, and probably indicate the pouring out of secretions into the general digestive cavity. These surfaces are devoid of cilia.

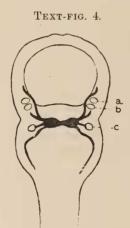
On the other hand, the larger, thicker-walled diverticula on the more ventral surface, which are yellow in the living animal, are formed of long large cells loaded with spherical masses of various kinds, some staining purple with hæmatoxylin, others yellow and various shades of brown. Some stain intensely with thionin, others not at all. The characters indicate active constructive metabolism, and suggest a function to these parts of the alimentary tract more comparable to that of a liver.

The intestine has a narrow lumen, is circular in transverse section, and has a thick, homogeneous wall richly ciliated until it reaches the hood of the lophophore. Here the lumen widens, and fæces are collected, and the walls contain yellow pigments probably of an excretory nature. The anns is extremely small. I presume that it exists, but in no section have I been able to see it as an actual opening. Its position is indicated, however, by a proctodæal depression and a suture which is probably caused by its coalesced edges.

Nervous System.—The central nervous system, as in L. loxalina, is a conspicuous object lying between the intestine and reproductive gland (fig. 14, n.g.). It consists of a pair of ganglia connected by a thick band of nerve-fibres. Peri-

pheral nerves radiate from the ganglia to the lophophore and body-kidneys (if such they be), the body-wall, gut-wall, and lophophore, which in plan can be represented by the accompanying diagram. But I must confess that I have not succeeded in tracing out the termination of the finer branches.

In specimens which have been left alive in sea-water containing methylene-blue there are rows of cells along the stalk which stain blue (fig. 21), and one particularly prominent row runs along the mid-dorsal line of the stalk (fig.



L. saltans. Nervous system (thick lines). a, b. Lophophoral kidneys. c. Body kidney.

21). This prominent row is confined in L. saltans to the stalk; it dies away as the stalk passes into the body and also as it joins the foot. A similar row of cells has been described by Salensky for L. crassicauda and L. tethyæ (though Harmer (4) did not find it in L. tethyæ), and by Nickerson in L. Davenporti. Salensky considered them to be gland-cells, and Nickerson appears to agree with him, although "no conditions have been observed which point to a discharge of the contents." It seems to me not improbable that these cells may be nervous, or neuro-muscular, forming perhaps a kind of muscle plate centre of nervous impulse in

connection with the highly developed and rather complex character of the movements of which the stalk of L. saltans at any rate is capable.

The paucity of specimens prevented me from making an exhaustive study of the nervous system of this interesting little acrobat.

I cannot see in these cells any real resemblance to gland-cells. Their arrangement as a regular single file is more suggestive of co-ordinate action than glandular activity, which more usually is connected with diffuseness and irregularity of form.

One speaks of the foot as being an adhesive disc, and, as Nickerson says, containing unicellular gland-cells. I cannot believe that the toe-like cells which project round the edges of the foot are adhesive in the sense that they excrete any adhesive material. The rapidity and ease with which the animal relaxes its hold and swings its foot round and takes a new grip suggests a complicated nervous and muscular action, involving some action, such as suction, as the means of attachment rather than a simple adhesion by secretion. The so-called glands (fig. 13) may be of the nature of rods which stiffen the expanded rim of a sucking disc. One can imagine that such an arrangement would enable the animal to obtain hold and relax with great facility.

Sense-hairs are borne by the tentacles, and upon the hypostome and on the lophophore at the point of its greatest inflection in the oral region.

Excretory Organs.—I endeavoured to find some evidence of flame-cell tubes in the living animal, and although not working under very favourable conditions, I shall be surprised if such organs are found by anyone else in this species. I could find no trace of any ciliary action in any part of the animal excepting the alimentary canal and tentacles.

Animals which have been living some twenty-four hours in sea-water containing methylene-blue become generally coloured by the dye, but certain parts become an intense blue. When transferred back again into pure sea-water the dye disappeared from the general tissues, but was retained by certain parts. On placing the animals into Hermann's or Flemming's solution afterwards the blue parts were intensified, and some from which the blue had disappeared stood out again in a kind of indigo blue-black.

The organs affected permanently are, I believe, the nervous and excretory tissues. The brain is coloured blue, but not very strongly; I could not trace by this method any nervetrunks passing from it. The alimentary canal, I think, was hardly affected, with the exception of the rectum, the cells of which became an intense blue. It is hardly probable that the walls of the rectum are in any way modified with reference to the nervous system. The lines of cells on the stalk, as before mentioned, are also slightly coloured blue (which became intensified after fixation by Flemming's or Hermann's fluids). It is quite probable that the rectum cells may have special excretory functions. The other parts which are intensely coloured are a pair of organs in the base of the lophophore, and a similar pair rather lower down in the body just above the "liver diverticula."

These are probably excretory organs. I have already referred to them as the lophophore and body kidneys respectively. They, it is true, receive very distinct nervetrunks from the brain, but their whole appearance is that of an excretory organ rather than a sense-organ. There is a pair of spaces bounded by an irregular layer of cells still lower and nearer the sides which adjoin the second pair of excretory bodies, which I have not noticed to be coloured by the methylene-blue. This latter corresponds more in position with the curious "pagoda"-like organs described as an excretory organ in L. loxalina.

The two pairs of organs (figs. 7, l.k. and 8, b.k.) are clearly the organs described by Prouho in L. annelidicola and by Nickerson in L. Davenporti as excretory organs. They are composed of several large highly vacuolated cells closely pressed against one another and are slightly yellow in the living animal.

I have seen no trace of any duct in connection with the body pair. In connection with the lophophore organs there is a trace of a duct (vide figs. 5 and 7, k. d.), but I cannot follow this tube either to the exterior, though it runs close to the surface of the epistome, nor to the cells themselves, although, as seen in the figures, it lies close against them. Prouho found a duct which was ciliated and open to the exterior, and Nickerson a similar one, but was doubtful about the ciliation. I feel pretty sure there is no ciliated duct. It is quite possible that the above-mentioned tube is a duct to the surface in connection with the lophophoral kidney, and that the much larger open space lined by irregular cells mentioned above as lying to the outside of the body-kidneys may be the duct of the body-kidney, but I cannot say whether it opens to the exterior or not.

The walls of the rectum in all probability are an important part of the excretory system. Figs. 20, 21 and 24 show how clearly certain cells of the side walls take up the methyleneblue, even more distinctly than the lophophoral and body "kidneys." In the normal condition the side walls of the rectum are yellow like the walls of the liver diverticula of the gut. In each case the colour is due to spherical bodies within the cells of varying tint, but whereas the liver-cells or inclusions are hardly affected by the methylene-blue, the rectal ones stain deeply.

In sections of the rectum one sees more clearly what the process probably is. Fig. 24 represents a section of the rectum taken transversely and stained with thionin, eosin and orange G. The cells forming the anterior and posterior walls are ciliated and do not form excretory granules like the sidewall cells, which are larger and non-cilitated. In these there are large vacuoles containing masses of granules, some of which take the thionin, others the orange stain. These grains are seen to be forming in the deeper parts of the cells (fig. 24, ex. gr.) and passing into the vacuoles. Some of the vacuoles (vac.) are deep down, others (vac.') are closer to the surface, and some I have found at the surface. It is

quite likely that the vacuoles burst eventually and discharge the contained excretory granules into the rectum. I have not observed such a discharge of a vacuole in a living specimen, nor am I prepared to say that the ruptured vesicles seen in sections are not due to artificial causes, but the whole appearance of the epithelium strongly supports the view put forward above. Harmer, in his paper on the excretory processes in ectoproctous Polyzoa, describes the excretion of granules containing artificial pigment from various parts of the alimentary canal thus (p. 154): "This process takes place by the separation of small round vesicles from some part of the wall of the alimentary canal, and probably from the cæcum. These vesicles contain granules of Bismarck-brown, and may be seen in the stomach, intestine, or rectum, where they are no doubt on their way to the exterior." Then, again, in discussing, on p. 162, the nature of the natural colouring matter of the "liver" part of the alimentary canal he writes: "Without going into the question of the excretory value of the processes which take place in the vertebrate liver . . . I may express my conviction that this appearance of pigments like indigo carmine, carminate of ammonium, and Bismarckbrown in the granules of the walls of the alimentary canal in Polyzoa, taken in conjunction with the normal appearance in the same place of a natural pigment and the ultimate passage of much of that pigment into the brown body, is to be regarded as, in part at least, a process of excretion." I would suggest that L. saltans indicates that the function of excretion, so far as the alimentary canal is concerned, is concentrated in the expanded terminal part of the intestine, and that the yellow pigment of the liver diverticula is of a different nature. The cells of the rectum which produce the excretory pigment have an utterly different character to those of the liver diverticula. In fig. 22 the former, and in fig. 24 the latter type of cell may be seen. In the rectal excretory cell the nuclei are deep down and horizontally placed, as so often occurs in the secretory cells, and the granules appear to be forming near the nucleus and passing ontwards towards the

vacuole, which is clear and obvious. In the liver-cell there is no vacuole at all, the nucleus is large and spherical, rather less deeply placed, and the granules appear to be forming in the inner or more superficial part of the cells and to be accumulating towards the base. The difference in appearance seems to me to indicate the physiological difference between katabolic and anabolic metabolism.

The curious pagoda-like arrangement of cells seen at the sides of the body of L. loxalina (fig. 6, k.) is probably excretory, and may perhaps be comparable in structure to the excretory organs described by Harmer for L. crassicauda, but the histological detail is insufficiently good for me to determine its exact nature. If it is so, the position would indicate an external opening on the side of the body just below the posterior lophophoral ectodermic gland and not on the epistome as in L. crassicauda, which is a considerable difference of position. It may be that the type of excretory organ described here for L. saltans and in others, as, for instance, L. Davenporti by Nickerson, is derived from such a condition as the above, but it might have been correlated more closely with such cells as those known as leucocytes in the Ectoprocta, which have been shown by Harmer to have an excretory function.

Reproductive Organs.—I have seen no trace of a hermaphrodite condition such as Nickerson describes for L. Davenporti, and which, I think, may occur in L. loxalina, though it is not possible to say that one individual may not produce ova at one time and sperm at another, as Harmer has suggested. It is possible that of my nine specimens of this species none was fully mature, but I do not think so.—I find also that the gonad is single and median.—In no instance have I seen a trace of a paired gland in either sex.—Fig. 14 passes through the ovarian follicle of an individual which contains what appears to be a nearly fully grown occyte.—The follicle opens by a narrow duct into the atrium between the intestine and the epistome (fig. 9, g. p.).—The oviducts project so as to form a little papilla, which is seen cut across in fig. 9.—I cannot find

any other organ which is undoubtedly connected with the function of reproduction in the females. There is nothing which I could compare with Nickerson's mammary gland, nuless the slightly modified epithelium on the inner surface of the epistome may indicate a function of this nature (fig. 9, m. e.).

The male organs seem to me to be as simple as the female organs. There is a single follicle with duct opening on a papilla in the same place into the atrium, namely, between the intestine and epistome. The follicle contains spermatozoa instead of an oöcyte, and there is no modification of the external epithelium of the atrium.

I am not convinced that there is any glandular mass which can be compared with the so-called shell-gland of L. Davenporti and L. annelidicola or L. loxalina. So it will be seen that the reproductive system is as simple as possible, and remarkably different from the condition in other species of Loxosoma.

Body-wall.—The general parenchyma presents no special features. It is very sparse in L. saltans, and is dense where it occurs. In L. loxalina it is more abundant and less dense. There is a complete absence of any lateral expansions into alæ characteristic of L. Davenporti and L. annelidi-The epidermis is distinct and a single layer of cells throughout, but varies, as we have seen, in different localities, giving rise to the peculiar "flask organs," the rows of large cells in the stalk and the supporting structure on the foot. The lophophore is drawn out into the sixteen tentacles, the structure of which is as follows: There is a central single row of dense cells, fig. 18 (mes.), round which are about five rows of ectodermal cells. The two outer rows are sharply defined, lightly staining cells, while on the inner face are three rows of larger cells with less well-defined boundaries. These three rows bear long stiff cilia which vibrate vigorously in the living specimen from time to time. On the outer surface there are one or two single stiff non-vibratile hairs, probably sense-hairs comparable to those described by Harmer on L. crassicauda, and shown by Prouho on L. annelidicola. On the four large oral tentacles there is a little tuft of hair on the tip of each on its outer border as shown in fig. 10. These are the ones which seem to aid in locomotion.

Budding.—I have had so few specimens that I have been unable to study the development of buds. In no case did I find more than two buds; nor were these buds very large. It would be rash to say that two buds is the limit of the number borne at once by an individual, seeing that in other forms so many may be carried at the same time. On the other hand, it is not improbable that two should be the limit in this species, for, as one may well imagine, a little species like this which is capable of such active locomotion might not find it advantageous to be encumbered by more than a couple of buds at a time.

The only other Loxosoma that I have found in Scotland is L. phascolosomatum in the Kyles of Bute.

Two new species of Loxosoma have recently been described by Nilus in the 'Trav. nat. C.R. séances St. Petersburg,' vol. xl, and named L. murmanica and L. Brumpti respectively These are very unlike the two species described in the above, and resemble L. tethyæ more closely, having a small circular lophophore with only six tentacles, with no very evident epidermic gland-organs, and with many buds arising low down on the body-wall.

SUMMARY.

(1) Loxosoma loxalina n.s.—Lophophore larger than the body and bears sixteen tentacles, of which four are longer than the others. These four are on the oral part of the lophophore, which is slightly inflected along that region. The stalk is considerably longer than the calyx, and terminates in a circular foot with radiating supporting cells. There is no foot-gland. The body and the lophophore are beset with deeply placed ectodermal organs along the lateral margins,

of which organs there are usually four pairs, giving a somewhat angular appearance to the calyx. It was found living commensally with a Maldanid worm (which was not identified) on the Morven shore of the Sound of Mull in Scotland.

- (2) Loxosoma saltans n.s.—Lophophore larger than the body and bears sixteen tentacles, of which four are longer than the others and are moved separately, and are always outside and over the others when contracted. They bear stiff hairs on the outer edge of their tips. As in L. loxalina the oral part of the lophophore is indented. The specific name indicates its habit of locomotion by jumping, in which action the four large tentacles take a part. The stalk is shorter, or only slightly longer than the calyx, and terminates in a circular foot as in L. loxalina. There is no foot-gland. The glandular diverticula of the alimentary canal are highly developed. The body has two ectodermal organs, or less, which are pedunculate and attached to the ventro-lateral surface just below the buds. They are larger and placed higher than the corresponding organs of L. Davenporti. The species was found in the tube of a Maldanid worm Clymene ebiensis on the Skye shore of the Kyle of Loch Alsh in Scotland.
- (3) The alimentary canal of L. saltans is differentiated more markedly into glandular, absorptive and excretory regions than L. loxalina. Two very distinct proximal diverticula appear to secrete some substance into the cavity of the gut, probably digestive in action; a more distal pair of diverticula seem to be more of the nature of a liver. The whole alimentary canal is a single layer of cells.
- (4) The nervous system consists of the usual pair of gauglia in both species. In L. saltans the main nerves can be traced to lophophore, body-wall, kidneys and gut. Sensory hairs occur on the tentacles. A chain of cells along the stalk may be nervous.
- (5) In L. saltans the excretory organs are divided into (i) lophophoral and (ii) body-kidneys, which are large vacuolated cells which perhaps lie in contact with ducts, but the external

openings could not be traced. No sign of ciliation of any part of these ducts is apparent in the living L. saltans.

In L. loxalina the excretory organs are on a rather different plan.

In L. saltans the (iii) rectum takes an important part in excretion, certain cells accumulating excretory products in vacuoles which presumably burst into the cavity of the rectum.

(6) In L. loxalina the reproductive glands consist of a pair of gonads which may be hermaphrodite, with ducts joining in the median plane where there is a shell-gland, whence a median duct runs to open into the atrium between the epistome and the lophophoral hood.

In L. saltans the gonad is single and median, with the duct opening on a papilla between the epistome and lophophoral hood.

(7) In neither species is there any lateral expansion of the body into alæ. The general mesodermal tissue is more abundant in L. loxalina than in L. saltans.

I desire to express my sincere thanks to Professor W. C. McIntosh, LL.D., F.R.S., for his kindness in identifying the Maldanid worm upon which L. saltans was found; to Dr. G. F. Harmer, F.R.S., for certain references to the literature of Loxosoma; to Miss Marie Krull for assistance in the preparation of the specimens; and to Miss Dorothy Thursby Pelham for drawings numbered 4, 5 and 6 upon Pls. 6 and 7.

References.

- Annandale, N.—"The Fauna of Brackish Ponds at Port Canning, Lower Bengal ('Loxosomatoides')," 'Rec. Ind. Mus.,' 2, pl. i, p. 14, 1908.
- 2. Van Beneden et Hesse.—"Recherches sur les Bellodes et les Trematodes marins" ('Memoirs presenté à l'Academie,' le 8 Novembre, 1861); 'Memoires de l'Academie royal de Belgique,' t. xxxiv, 1864, pp. 83-84, pl. xii, figs. 12-20.
- Ehlers, E.—"Zur Kenntnis der Pedicellinen," 'Abhand. d. Kön. Ges. d. Wiss. Göttigen,' 1890.

- Harmer, S. F.—"On the Structure and Development of Loxosoma," Quart. Journ. Micr. Sci., vol. 25, pp. 261-337, 1888.
- On the Nature of Excretory Processes in Marine Polyzoa,"
 Quart. Journ. Micr. Sci., vol. 33, 1892.
- 6. —— 'Camb. Natural History,' vol. "Polyzoa, etc.," London, 1896.
- Keferstein, W.—"Untersuchungen über nieder Seethiere: viii, Ueber Loxosoma singulare, gen. et. sp. n.," 'Zeits. f. wiss. Zool., Bd. xii, S. 131, 1863.
- 8. Kowalewsky.—"Beiträge zur Anatomie und Entwickelungsgeschichte des Loxosoma neopolitanum, sp. n.," 'Mem. de l'Acad. Imper. des Sci. de St. Petersbourg,' viie sér., t. x, No. 2, 1866.
- Leuchart.—"Bericht über Leist. in der Naturgesch. der niederen Thiere, während des Jahres, 1863," 'Arch. f. Naturges,' t. xxx, Bd. ii, 1864.
- Nickerson, W. S.—"On Loxosoma Davenporti (sp. nov.)" 'Journ. of Morphology,' vol. xvii, 1900.
- 11. ———"Double Loxosoma," 'American Naturalist,' vol. xxxiv, November, pp. 891–895. Abst. 'Journ. R. Micr. Soc.,' London, 1901, p. 43.
- 12. Nilus.—"Loxosoma Murmanica brumpti," 'St. Petersburgh Trav. Soc. Nat. C. v. Sćance, 40-41, p. 157.
- Nitsche, H.—"Beiträge zur Kenntniss der Bryozoan; Ueber der. Bau und Knospung im Lox. Kefersteini," 'Zeits. f. wiss Zool., Suppl. Bd. xxv, p. 343, 1875.
- Pronho, H.—"Étude sur le Loxosoma annelidicola," 'Archives de Zool. Expr. et Gen., vol. ix, Ser. 2, p. 91, 1891.
- 15. Salensky, M.—"Études sur les Bryozoanaires entoproctus," 'Ann. des Sci. Nat.,' 6 sér., Zool., t. v, No. 3, 1877.
- Schmidt.—"Die Gattung Loxosoma," 'Arch. f. mikr. Anat.,' Bd. xii, S. 1, 1876.
- Schmidt, O.—"Bemerkungen zu den Arbeiten über Loxosoma,"
 Zeits. f. wiss. Zool., Bd. xxxi, S. 68, 1878.
- Vogt, C.—"Sur le Loxosoma des Phascolosomas (Loxosoma phascolosomatum"), 'Arch de Zool. Exper. et Gen.,' t. v. p. 305, 1876.

EXPLANATION OF PLATES 6 AND 7.

Illustrating Mr. Richard Assheton's paper on "Loxosoma loxalina and Loxosoma saltans—Two New Species."

LETTERING.

- a. Atrium. b. Bud. b. k. Body-kidney. c.c. Ciliated cell of stomach region. ec. ex. External ectoderm of tentacles. ec. o. Ectodermal spike or flask-like organs of L. saltans. ec. or. Ectodermal organ of L. loxalina. ect. Ectoderm. ect. ii. Ectodermal organs of L. loxalina. ect. iv. Ectodermal organ of many cells deeply placed of L. loxalina. ep. Epistome. ex. r. Excretory cells of rectum. ex. gr. Excretory granules in rectal cell. d. l. Dorsal row of large ectodermal cells (nervous?). gl. c. Gland-cell (or supporting rod?). g. gonad. g. d. Duct of gonad. g. p. Genital papilla. int. Intestine. k. Kidney. k. d. Kidney-duct. l. d. Liver diverticulum. l. k. Lophophoral kidney. m. e. Modified epithelium of atrium. mes. Mesodermal core of tentacle. m. Mouth. mu. Mucous cell. n. g. Nerve-ganglia. as. Esophagus. o. f. Ovarian follicle. oöc. Oöcyte. p. c. Cell of pancreatic diverticulum. p. d. "Pancreatic" diverticulum. r. Rectum. sh. gl. Shell-gland. st. Stomach. ten. Tentacle. tes. ! Testis?. v. Ventral wall of rectum. ciliated. vac. Vacuole in rectal cell. vac.' Granule entering vacuole.
- Fig. 1.—Loxosoma loxalina. Preserved specimen seen from the ventral surface. The character of the alimentary canal and the position of the gonad and excretory organs (?), the nerve ganglia and ectodermal organs in their most characteristic form are in icated.
- Fig. 2.—L.loxalina. Vertical longitudinal section of a corresponding specimen showing the mouth, alimentary canal and anus, which is placed near the edge of the lophophore.
- Fig. 3.—L. loxalina.—Transverse section through the brain, esophagus and intestine. One of the ectodermal organs has been cut and alongside of it the group of cells which are arranged in tiers and are probably excretory cells. Part of the reproductive system, probably the shell-gland, lies between the brain and esophagus.
- Fig. 4.—L. loxalina. A section taken transversely so as to cut the intestine (int.), the gonad (g.) and the edge of the brain (n. g.). A portion of the gonoduct is seen at g. d. running towards a group of granular cells (sh. g.), which are probably shell-gland.
- Fig. 5.—L. loxalina. A vertical section through the epistome showing the opening of two ducts. One on the epistome may be excretory

the other one (g. d.) is a duct which leads from the group of cells of figs. 3 and 4 to the space between the epistome and the lophophore.

- Fig. 6.—L. loxalina. A section taken horizontally through a gonad (g.) and a curious row of cells (k.), which are probably not connected with the gonad, but are of the nature of an excretory organ. These large vacuolated cells bear some resemblance to those of the excretory nephridium of L. crassicauda (v. Harmer).
- Fig. 7.—L. saltans. Horizontal section cutting through the epistome and lophophoral kidney. The two fine kidney ducts are seen cut obliquely as they pass towards the epistome.
- Fig. 8.—L. saltans. A section through the lophophoral kidney, which is seen to consist of several large, much vacuolated cells closely pressed together and bounded by a capsule.
- Fig. 9.—L. saltans. Transverse section through the atrium passing through esophagus, intestine and papilla upon which the oviduct opens.
- Fig. 10.—L. saltans. A figure drawn from a living specimen to show the way in which the lophophore and tentacles are carried. The four long tentacles usually work together. The fine stiff hairs, used either as touch sense-cells or grasping organs, are seen on these four tentacles. The specimen bore one well-developed bud, one rudimentary one, and two of the peculiar "flask"-like ectodermic organs of unknown function. One of these is shown in the figure.
- Fig. 11.—L. saltans.—A slightly oblique section which passes vertically through the esophagus, one nerve ganglion, one "liver" diverticulum, but misses the rectum. The character of the liver-cells containing many granules is seen.
- Fig. 12.—L. saltans. A horizontal section through the pancreatic diverticulum and stomach. The cells of the wall of the stomach are really ciliated, except the mucus-producing cells (mu.), but not the cells of the glandular diverticulum.
- Fig. 13.—L. loxalina. Part of the foot shows the large rod-like cells which project beyond the general margin as either adhesive or supporting elements.
- Fig. 14.—Loxosoma saltans. Transverse section through the brain, esophagus, and intestine, the brain consisting of two ganglia connected by a thick band of nerve-fibre. Between the brain and esophagus lies the ovary, consisting of a single follicle containing a single oöcyte. On each side the body-kidney is seen in section.
- Fig. 15.—L. saltans. A section taken through the base of one of the pedunculate ectodermal organs, which consists of four modified ectodermal cells contained within a capsule of ordinary cells.

- Fig. 16.—L. saltans. A section of the second on the same animal showing the ectoderm cut through on one side. These organs appear to be easily lost.
- Fig. 17.—L. loxalina. Diagram of similar ectodermal organs on the species L. loxalina, in which they are never pedunculate. (a) The organ next the stalk; (b) any of the others.
- Fig. 18.—L. saltans. Sections which illustrate the structure of the tentacles. Each consists of a core of mesodermal cells, a single row, and a coat of ectoderm of which the innermost are ciliated. Sense-hairs are borne by some of the outer cells, but these are not shown in the figure.
- Fig. 19.—L. saltans. A figure drawn from a living specimen with tentacles retracted, showing the way the four large ones bend over the smaller lateral ones. The colour of the various parts of the alimentary canal are shown. The kidneys are also very slightly yellow, but these are not shown in the drawing.
- Fig. 20.—L. saltans. A figure of a living specimen after twenty-four hours in sea-water containing a weak solution of methylene-blue. The parts brightly coloured are the young growing tissues, especially the ectoderm of the buds, the central nervous system, and the lateral walls of the rectum.
- Fig. 21.—L. saltans. Another specimen which had been in seawater with methylene-blue for some hours. The coloured parts are the kidneys, the rectum (also excretory), and a chain of cells along the dorsal wall of the stalk.
- Fig. 22.-L. saltans. Two cells of the liver-like diverticula or thickening of the alimentary canal.
- Fig. 23.—L. saltans. Two cells of the pancreatic diverticulum of the gut, and one ciliated cell of the "stomach" region.
- Fig. 24.—L. saltans. A section through the rectum stained with thionin, orange G, and eosin. The dorsal and ventral walls are ciliated. The latter walls are composed of excretory cells. The excretory products are seen collecting in the large vacuoles.
- NOTE.—The specimens of L. loxalina were all fixed in Perenyi. Those of L. saltans in Flemming's or Hermann's fluid.

