THE INTERNAL INFLUENCES THAT DETERMINE THE RELATIVE SIZE OF DOUBLE STRUCTURES IN PLANARIA LUGUBRIS.

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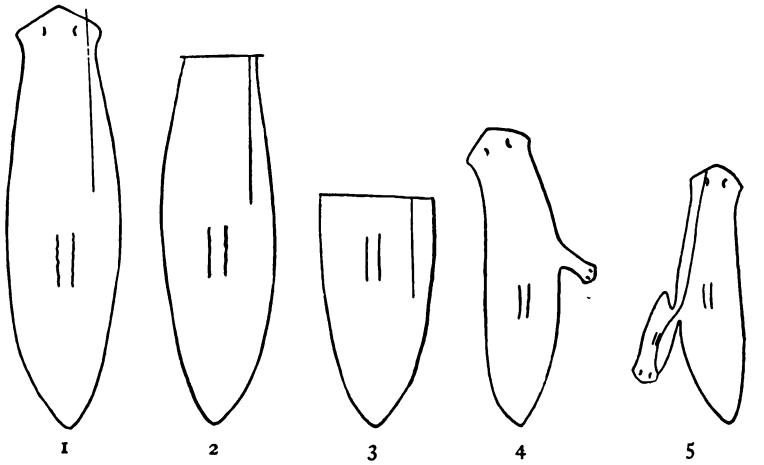
In a previous paper[1] I attempted to determine what internal factors regulate in planarians the limit of size of each of two heads when such are present. Two conditions appeared to have an influence on the result: (1) The width of the region connecting the part to the rest of the organism, (2) the length of the new part. By the following experiments I have attempted to gain the further insight into the conditions:

In one series the planarians were split lengthwise into unequal parts, as shown in Fig. 1; or else the head was first cut off, and then the posterior piece was split lengthwise, as shown in Fig. 2. Under both of these conditions the head on the smaller piece is much smaller than that on the larger part. The purpose of the experiment was to see if by abundant feeding the size of the smaller head could be brought up to that of the larger; or whether its size is determined by the width of the region connecting the small head with the larger piece. If the longitudinal cut does not extend as far posteriorly as the old pharynx, a new pharynx does not, as a rule, come into the smaller part. If, however, the cut is extended posteriorly as far as, or beyond, the old pharynx, a new one may come into the small part. The same end can be reached by cutting off the worm in front of the pharynx as shown in Fig. 3, and then splitting the posterior piece lengthwise. The side piece will be, of course, shorter in the last case.

The results show that the size that the new smaller head attains is determined largely by the presence or absence of a new pharynx in the small part.

The following cases will serve to illustrate some of the ways in which the regeneration takes place. A narrow piece was split off in one case as shown in Fig. 1. A small head developed at

[1] *Roux's Archiv*, XIII., 1901.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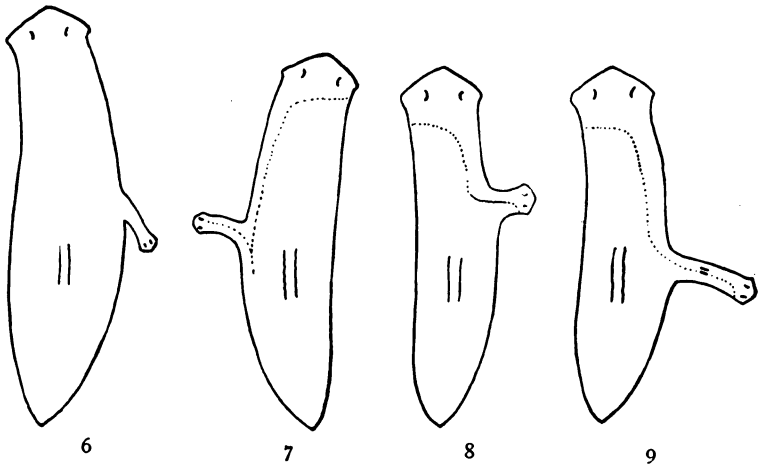
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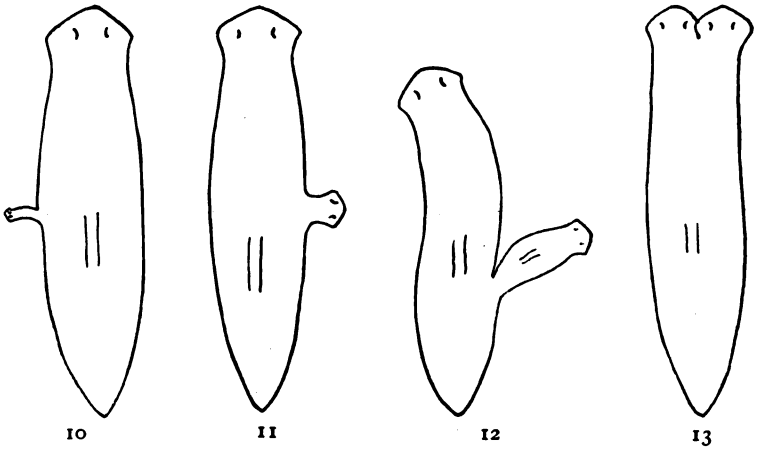
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its anterior end, but there was no pharynx present. The small piece was attached to the main body at the side and just in front of the anterior end of the pharynx, Fig. 4. Five months later it had not grown any larger (although the worm was kept well fed), but, in fact, appeared to be smaller than at first, Fig. 6. In two other cases the split had extended so far back that a pharynx developed in the small piece, Fig. 5. A tail also grew out at the new side behind the new pharynx. Subsequently the two pieces pulled apart. In another series the old head was cut off by a cross-cut, and then a split made down one side, right or left, Fig. 2. The condition of the two heads a month and a half later is shown in Figs. 7, 8, 9. In the first and second cases a pharynx is absent, but in the third a pharynx has developed in the middle of the smaller worm. The latter condition of these three worms, five months after the operation, is shown in Figs. 10, 11, 12. In the first the head at the side is smaller than it was before ; in the second it has remained about the same size ; while in the third, which contains a pharynx in the smaller piece, the head and the piece as a whole have increased in size.

In another series the heads were split exactly in the middle line. In some of these the split was made only in the anterior end—the cut not extending posteriorly to the pharynx—in others the cut extended into the pharynx region. In other cases the head was first cut off and then the worm split in the middle line. When the head was split for only a short distance, each half completed itself—if the parts were kept from reuniting—as shown in Fig. 13. The head remained smaller in size than the normal head, and even after seven months had not increased any further in size. The inner sides of the heads were a little smaller in size than the other. If the split extends further posteriorly [1] the new heads become larger than in the last case, but still not full size, Fig. 14.

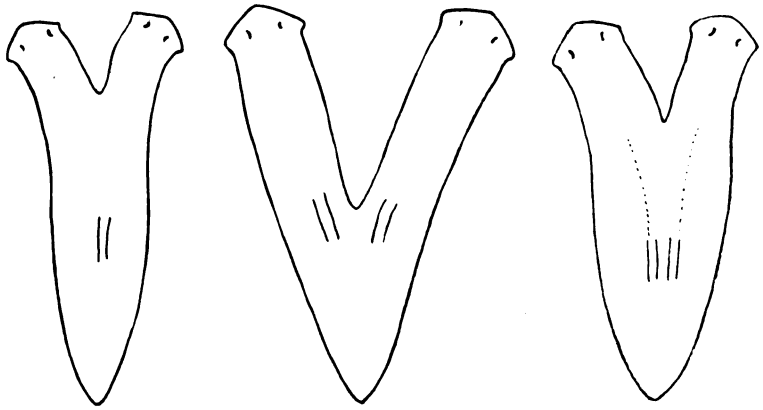
If the cut extends into the region of the pharynx so that two proboscides are formed, one in each half, Fig. 15, the two new heads appear to become larger than in the preceding case, but still do not attain full size. Each appears to be proportionate in size to the part of the body on which it is found, and its size is

[1] The old head had been first cut off.

determined by that of the rest of the part. If the latter should grow to the normal full size the heads would, no doubt, also become full size. Since the parts would become full size if they were separated from each other the explanation of their failure to enlarge beyond a certain size is unquestionably connected with the fact of their union with each other. Very often the pieces partially reunite after the operation, and two proboscides are formed as shown in Fig. 16. In such cases the body at, and beyond, the region of the proboscis is broader than normal, and in consequence the heads at the anterior ends may be larger than when only a single proboscis is present, as in Fig. 14.

In order to see how important a factor the extent of the surface regenerating a head is, as compared with the size of the area of union of the parts, the following experiment was made. The old head was first cut off, and then by an oblique cut, as shown in Fig. 17, a triangular piece was partially cut off. Pieces of this sort tend to unite and must be for a time kept apart. The new head develops on the anterior cut surface of the triangular piece, and the other head on the anterior edge of the oblique cut surface. A new pharynx develops along the posterior edge of the oblique cut in some cases, Fig. 18 and 20, in others not, Fig. 19, depending, in part, on the extent to which the pieces are kept apart after the operation, in part on the nearness of the cut to the region of the old pharynx. As soon as the two new heads have been fully formed it is seen that their size bears no relation to the fact that one has developed on the cross-cut surface and the other on the oblique surface. Their sizes depend rather on the size of the part from which they have developed, Figs. 18, and 19, and whether a new pharynx has appeared in the triangular piece, and also on the relation of the part to which they belong to the rest of the worm. The following examples may make this clearer. In the first case, Fig. 18, the triangular piece has rather a broad attachment to the other part and contains a pharynx. The larger of the two heads belongs to the old part. In the second case, Fig. 19, the triangular piece is much smaller and ends in a smaller head. It does not contain a pharynx and is attached to the other part by only a narrow area.

The third case, Fig. 20, shows that the triangular piece is



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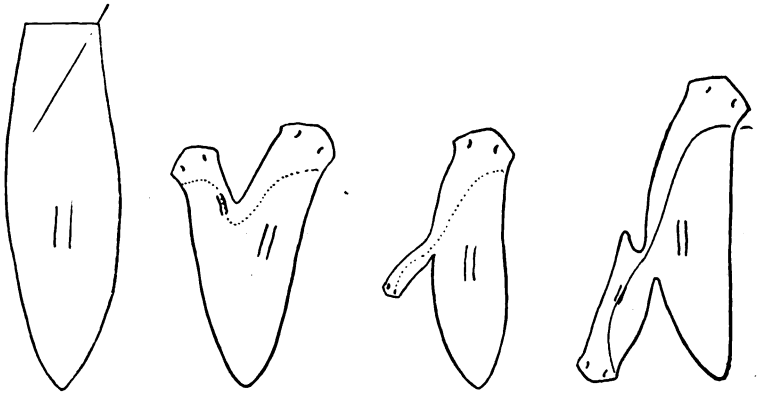

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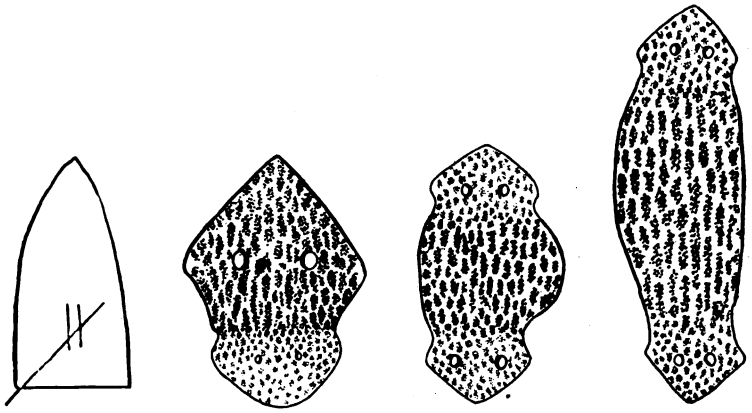

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united to the other part by only a narrow connection. It contains a pharynx, and a new tail has begun to grow out near the area of attachment. This piece pulled apart later. Practically the same results were obtained when the pieces were cut as shown in Fig. 21. In this case the worm was first cut in two near the old pharynx and then by means of an oblique cut, the triangular piece was separated in such a way that a part of the old pharynx was left in each piece. A new pharynx developed in both pieces, and the same relations between the sizes of the new heads, that were described in the first and third cases above, hold here also.

Conclusions.

The results show clearly that the presence of a pharynx in a new part is an important element in the subsequent growth of the part. A part containing within itself a new pharynx behaves more like an independent worm. The most natural interpretation would be, perhaps, that this is due to the part being able to feed for itself; but while this may to some extent account for the result, yet is probably not the whole explanation. My reason for thinking so is that when the animal feeds the digestive tract of the side piece is also filled with food material. If, therefore, the planarian is kept well fed, the side piece does not lack food material even where there is no pharynx in this part.

There are some facts in connection with the mode of regeneration of planarians that may throw some light on this lack of enlargement of pieces without a pharynx. If the anterior end of a worm is cut off, the new pharynx appears, in the anterior piece, at the posterior edge of the old material. It is, at first structurally, too, the head. If the piece is fed so that the old part loses as little as possible, a new region is intercalated in front of the pharynx, and this region continues to enlarge until the normal proportions have been attained. Again, if a piece of *Planaria lugubris* is cut off behind the old pharynx, a new head arises at the anterior end, and a new pharynx, also at the anterior end just at the border between the new and the old parts. The head and pharynx are in this case also too near together, but a new region of growth is established between the head and the pharynx so

that the two are carried further and further apart. These results show that the principal growing region in the new worms lies in front of the pharynx, and it is conceivable that in the absence of the pharynx this region of growth is not formed.

The influence of the width of the region of attachment—a factor to which I ascribed some influence in my last paper—should also be taken into account here. If a pharynx is present in the part the area of union seems to play a less important rôle than when there is no pharynx present. It is probable that it is not simply the area of union as such that plays the important part, but it is the connection between the internal organs—possibly the digestive tract—that is chiefly involved in the result.

THE FORMATION OF HETEROMORPHIC HEADS IN PLANARIANS.

The formation of a heteromorphic head in *Planaria lugubris*, when the old head is cut off just behind the eyes, has been described in several of my preceding papers. In the past summer I succeeded in obtaining one such case in *Planaria maculata*, but only after a large number of trials, and furthermore in this successful case the cut was not immediately behind the eyes, as seen in Fig. 22. At the same time I cut a large number of worms into short cross-pieces, keeping all pieces of the same length together. To my surprise I found that the only pieces that produced a head at the posterior end, as well as at the anterior end (Figs. 23 and 24) were those taken just behind the old pharynx in the region of the reproductive pore. Two possibilities suggest themselves, viz., the presence of the reproductive organs in the piece, or the cut being made through the region at which this planarian pinches off pieces of itself to form new worms. If the posterior edge of the cross-piece lay in the region of constriction, where the new head of the new worm would develop, it is conceivable that this might cause the development of the heteromorphic head in the cross-piece. A similar series of cross-cuts were made on *Planaria lugubris*, but double-headed pieces were never formed on the cross-pieces from the region of the reproductive pore. In this species, however, new worms are not formed normally by pieces constricting off from the posterior end.

Neither of these possibilities seems to me to give a satisfactory

explanation of the presence of a heteromorphic head. In order to see if any internal condition is present in these double forms that may account for the results, the two preceding pieces from the posterior end, as well as two other similar pieces, were cut into sections. In three of these no pharynx was present, but parts of the old reproductive organs were present in the middle of the piece; in the fourth a pharynx was present, but the pharyngeal chamber did not open to the exterior. There was nothing in the presence of the digestive tract to give a clue as to the cause of the development of a heteromorphic head. It is true that the branches of the digestive tract were united behind, but this in itself furnishes no proof that such a union can account for the result. The sections show that a brain, nerve-cords, and eyes are present in both heads. Whatever the factors are that determine the result, the fact that the heteromorphic head appears only in short pieces will probably also have to be taken into account, for it is very improbable that a heteromorphic head would appear if whole worms were cut through in this region.

BRYN MAWR, PA., May 25, 1902.