SPIRAL MODIFICATION OF METAMERISM.

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THE unusual forms of metamerism recorded below are by no means uncommon in the Annelids. They are to be found in the most widely separated groups, but for briefness and simplicity of treatment I confine myself here to the more important results obtained on *Allolobophora fætida*.

In a lot of 318 worms, 218 were found normal with respect to the metamerer, and 100 abnormal. That is to say, in the proportion of about one to two, or, one worm out of each three was abnormal.

These abnormalities were of several kinds, some of these being described below. Many of the worms showed more than a single abnormality. Thus out of the above hundred : —

With	1	abnormality		65
"	2	abnormalities		16
"	3	"		10
"	more than 3	"		9
				<hr/>
				100

One of the commonest forms of abnormality, and also the simplest, is what we may speak of as the split-metamere, although

FIG. 1.

the term is, as I hope to show, misleading. This is shown in Fig. 1, *a*, *b*, *c*, giving the dorsal and ventral views of several rings. Fig. 1 *a* shows the dorsal view, *b* the ventral, and *c* an imaginary construction representing the split-metamere as opened ; the dotted lines represent the under surface. The middle metamere of the three is split.

On one side (left in *a*) of the split-metamere the usual conditions prevail, while on the other (right in *a*) all of the important structures are doubled, — setæ, nephridia, etc. *There is a half-septum with double walls corresponding to the split.* Twenty-eight cases of simple splitting were found in this lot.

The most interesting abnormality and also the most frequent is what I have spoken of as spiral metamerism. Thirty-seven such cases were counted in the one hundred abnormalities given above. These spirals are of all lengths, from the simple spiral involving a few metameres to those involving more than twenty metameres. The highest degree of complication amongst these spiral forms comes in what I shall speak of as the double and triple spirals.

The accompanying diagram (Fig. 2, *a*, *b*, and *c*) illustrates a spiral of a medium length. The spiral begins with a split-meta-

FIG. 2.

mere. The upper (right) division of the split forms a ring below with the whole of the other (left) side, in this way leaving free the lower division of the split, which begins to wind around the body as shown in *c*, passing completely around four times, and ending in the split-metamere at the bottom. Here the spiral comes to an end in a split-metamere opening in the reverse direction from the upper split. All combinations between the split-metameres and the spirals that are geometrically possible (and there are several variations) are actually found in the worms, provided a sufficient number of forms be examined.

It is not necessary that the spirals should begin in a split-metamere, although this is the commonest method of procedure. The greatest complexity is found in the double and triple spirals. For instance, if the first metamere of Fig. 2 had been split twice instead of only once, then it will be seen that two sets of spirals will be started, twisting around the body. Or the same result is obtained if a split-metamere be interpolated in a spiral so as to increase the number of half-metameres on one side. Lastly, if two split-metameres be interpolated, as in the last case, then a triple spiral will be formed. On the ventral side of the spiral the usual number of setæ are present, *i.e.* two pairs to each turn. Within the body, the nephridia follow the usual law. But by far the most interesting conditions are to be found in the septa. *The septa follow the spiral arrangement of the metameres.* It will be seen at once that this results in a corkscrew-like arrangement of the septa. That is to say, that instead of a series of septa *there is a single spirally winding septum, beginning with the half-septum of the split-metamere above and ending in the same below.* Or it may be said that there is a continuous body cavity lying between the coils of the septum, and this cavity is continuous from the top to the bottom of the spiral. I cannot dwell further on this here, or discuss the variations to be found in the septa.

Let us turn now to another side of the problem. Keeping capsules containing embryos of *Allolobophora foetida*, I was enabled to examine young worms immediately on their emergence from the cocoon. These embryos showed all the common forms of abnormalities to be found in the adult worms. In one lot there were 120 normal embryos to 25 abnormal, or as 1 : 5. In other words, there are fewer cases of abnormalities in the young worms (1 to 5) than amongst the adults (1 to 2).

This apparent contradiction finds largely its explanation in the fact that the adults are often found regenerating lost metameres, and proportionally the number of abnormalities in these newly formed parts is greater than in the embryos. Thus, out of a lot of 525 worms, 40 were found showing regenerating metameres behind. (More than this number probably had regenerated metameres, for after a certain stage it is impossible to distinguish the new metameres from the old.) Out of these 40 worms, there were 2 in which the metamerization had not yet

appeared, leaving 38 in all. Of these only 2 were completely normal, or the proportion of abnormal to normal was as 38 to 2 or 19 to 1. For this reason, I think we are enabled to account for the greater number of abnormalities in complete (adult) worms than in the newly hatched embryos.

Lastly, an attempt was made to find an interpretation of the spiral and split-metameres. To do this the anterior region of the worms was studied where one may be guided by definite landmarks. To take a single example: It is known that the external openings of the vasa deferentia occur on the 15th metamere. Now, if split segments can be found anterior to or including the 15th metamere, we are furnished with a clue to their interpretation. Such abnormalities are to be found, but are not very common, and a very large number of individuals had to be examined in order to obtain sufficient material to reach a safe conclusion.

At the very outset, however, I met a disturbing factor. It had to be first determined whether the openings of the vasa deferentia *always* appeared on the 15th metamere. Such is not the case. Thus, in 799 worms, 20 were found in which this was not true. That is to say, 20 worms showed abnormalities as to the position of the external openings of the vasa deferentia. The following table indicates the position of the external openings of the vasa deferentia in 12 of the 20 cases:—

1 ex. vas d. occurred on 10th metamere.				
1	"	"	11th	"
2	"	"	12th	"
4	"	"	14th	"
			Normal.	
4	"	"	16th	"

In cases in which the external vas deferentia were found on segments anterior to the 15th, this may be explained *in some cases* as due to injury or loss of the anterior metameres,¹ but I believe that this does not account for all such cases. These results show at least that care must be taken in utilizing the 15th segment as a fixed point. In all cases due weight has been given to this factor.

In this same lot of 799 worms there were 32 cases (after removing the 20 above) in which abnormalities (splits, spirals,

¹ I am collecting experimental evidence on this point at present.

etc.) were found anterior to the ex. vas. d., or in the proportion as 1 to 25. It is highly improbable, I think, that in these 32 abnormalities (found in 799 worms minus 20 leaving 779) many cases of an unusual position of the openings could have been present; for, as we have seen above, it occurs only once in 40 worms. This disturbing factor cannot, then, vitiate to any great degree our general conclusion in the present case.

One of the most instructive cases is given in Fig. 3 *a*. This shows a ventral view of a worm. The 10th metamere is split on the left side (right of figure) into two parts, remaining single on the right side. The dorsal view of the split-metamere is seen in *b*. Now, corresponding to this condition, we find that the openings of the vasa deferentia have also been shifted, so that now they come to lie on different metameres.

FIG. 3.

If we count the metameres (half-metameres) of the left side (right of figure *a*), we find that the openings are on the 15th metamere of *that side*. Counting the half-metamere of the opposite side (left of figure), we find again that the opening is on the 15th of *that side*. That is to say, *that the vasa deferentia open on their proper half-metameres, and, therefore, on account of the split-metamere, the two cannot be on the same metamere, but on consecutive ones.*

This gives us, I believe, a clue by which to interpret the split-metamere. We know that in the embryo the metameres are laid down right and left of the middle line of the body in blocks of mesodermal tissue; that under normal conditions these hollow blocks come to lie exactly opposite (right and left) of one another, so that the opposite pairs unite across the median dorsal and ventral lines. If we conceive that the blocks are slightly misplaced on one side, or that two consecutive blocks of one side are smaller than two of the opposite side, we will have as a necessary mechanical result of the relative position of the blocks a split-metamere. Thus, in the last case, if we suppose the 10th and 11th blocks of the left side smaller than

the 10th of the opposite side, the three half-metameres of these blocks will form together a split-metamere. Now, if the vasa deferentia still appear, each on its proper half-metamere, or mesodermic block, they must, as explained above, appear at a different level. Moreover, we gather from Fig. 3 that the half-blocks 10 and 11 of the left side of the worm are each equivalent to a simple block of the opposite side, as is indicated by the displacement of the openings of the vasa deferentia. It follows as a corollary, therefore, that the half-blocks 10 and 11 of this side cannot be looked upon as a single half-metamere itself, divided into equivalent halves; for, if this were true, we would not expect to find the shifting of the reproductive organs. I think, therefore, it is more correct and simpler to fall back upon the interpretation given above, and to regard the two half-blocks 10 and 11 as true half-metameres. That this is the correct interpretation of the splitting is further shown in the fact that the splitting always takes place in the sides, right or left, and never entirely above or below.

Moreover, we have seen that the number of abnormalities is greater in regenerated parts than in the embryos, and this finds its explanation as soon as it is seen that the formation of the body cavities is here a much more irregular process (as I have determined in regenerating metameres) than in embryonic growth. Furthermore, the same explanation that accounts for the split-segment is equally applicable to the spiral modification. If we imagine one of the mesodermic blocks of one side to be larger either above or below (but not both above and below), so that above (let us say) it opens into two body cavities of the opposite side, while below it opens into but one, then we have produced the conditions necessary to start the spiral. Each of the consecutive blocks on the same side as the larger block will open *below* into its proper opposite block; but above (on account of the first displacement) into the one lying in reality behind it. Reference to Fig. 2 *a* and *c* may make this clearer; but it is difficult to put into words what a model will show at a glance. The spirals when once started do not run on continuously, but end after passing around the body several times. The ending likewise finds its explanation in the inequality of the blocks of opposite sides. I have found these spiral methods of metamerism growth in widely separated genera

of Oligochæta, and also in many different genera of Polychætous Annelids. Whatever, therefore, be the cause of the phenomena, it must be a very fundamental one.

My work is still in progress, and I reserve for the future a fuller discussion and a more extended account of these occurrences. There are a few general considerations that have grown out of the work that I find full of suggestion, and as such I offer them here.

1. A very similar splitting (but not the spiral) has been described and figured for the Cestodes. I have also seen these. The occurrences of such similar processes of growth in both Cestodes and Annelids suggests that metamerism in the two groups has the same fundamental (though not phylogenetic) explanation.

2. On the conventional assumption that metamerism in the Annelids is to be explained by a theory of budding, it seems evident from the facts outlined above that the right and left sides may bud independently. This leads to the improbable conception that the Annelid is formed of two parallel rows of buds, and that a single worm may have more of these buds on one side than on the other.

3. The conversion of the opposite arrangement of metameric blocks into the alternate producing the spiral finds its explanation in the relative size and position of the blocks of the two sides. Similarly in plants, the arrangement of the leaves into opposite, alternate, or spiral finds its explanation in the packing of the leaves in the bud ; and the transition from the one method to the other, often in the same plants, is explained by processes of cell growth. This may indicate that a fundamental interpretation may be found for both.

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