FACTORS OF FORM REGULATION IN HARENACTIS ATTENUATA

II ABORAL RESTITUTION, HETEROMORPHOSIS AND POLARITY

BY

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WITH TWELVE FIGURES

Changes in polarity, including both the so-called reversal of polarity and other changes occur very readily in *Harenactis*, probably more readily than in any other actinian which has thus far been made the subject of experiment. The present paper is chiefly concerned with the description and discussion of these changes.

I THE REGIONAL FACTOR IN ABORAL RESTITUTION

I Aboral Restitution in the Œsophageal Region

The method of closure of aboral cut surfaces within the œsophageal region is the same as that of oral surfaces in the same region (Child, '09b), i. e., the contraction of the parts injured by the operation approximates the cut margins of body-wall and œsophagus and union occurs. The consequence of this method of union is that the œsophagus opens aborally to the exterior instead of into the enteron, and no connection exists between the enteron and the exterior. In this respect *Harenactis* resembles *Cerianthus* and all other species of actinians which I have examined.

The further history of such œsophageal pieces depends to a considerable extent upon their length; short pieces from the oral part of the œsophageal region—e. g., distal to the line *a* in Fig. 1—usually do not live for more than a week or two and the regulatory changes at the aboral end rarely proceed beyond the closure of

the wound. Longer pieces—e. g., distal to the line *b* or between the lines *a* and *b* in Fig. 1—may live for several weeks and in such pieces tentacles very often appear at the aboral end.

Fig. 1 Diagrammatic outline of *Harenactis*, indicating levels of section.

But partial isolation of some portion of the œsophageal region by a lateral incision extending only part way through the body is a more satisfactory method for the production of heteromorphic tentacles than complete isolation. After partial isolation the part in question lives indefinitely and in every case that I have observed gives rise to heteromorphic tentacles. For convenience the two methods and their results are considered separately.

Complete Aboral Discs in the Œsophageal Region

Pieces from the œsophageal region with a cut surface at each end often contract irregularly or so strongly that the œsophagus is more or less completely extruded from one end and closure is delayed or prevented: otherwise these pieces give the same results as those with cut surface at the aboral end only. In order to avoid these irregularities pieces including the original oral end of the animal and the old tentacles may be used, e. g., pieces including all of the region distal to the level *b* in Fig. 1. Such œsophageal pieces show a much higher death rate than pieces of equal size from other regions of the body. In my experiments 50 per cent or more of these pieces died without producing aboral tentacles. Pieces that remain in good condition for a week or more usually produce aboral tentacles. These tentacles arise in the same manner as oral tentacles, but less rapidly. In general when a given level of the body, e. g., the level *b* in Fig. 1, forms the oral end of a piece, tentacles appear much more rapidly than when the same level forms the aboral end of a piece. At the level *b*, for example, oral tentacles usually became visible in my experiments about forty-eight hours after section, while aboral tentacles appear after six days or more.

The heteromorphic tentacles may reach a length of eight to ten millimeters and would undoubtedly become longer, were it not for the fact that the distension in these œsophageal pieces gradually decreases until they are completely collapsed, after which death soon occurs. As the distension decreases the original oral tentacles undergo gradual decrease in size and atrophy at the tips until they are the same size as the aboral tentacles: in later stages the aboral tentacles also undergo decrease and atrophy as the distension decreases still further, until both oral and aboral tentacles may be reduced to short stumps. In general the history of these œsophageal pieces is similar in *Harenactis* and *Cerianthus* (Child, '04) except that in *Cerianthus* heteromorphosis has been observed only very rarely (Child, '05).

Fig. 2 shows a diagrammatic longitudinal section of an œsophageal piece with heteromorphic tentacles. At the stage figured the

oral tentacles are undergoing atrophy at their tips, but the smaller aboral tentacles are still intact.

The ability to produce tentacles at the aboral end exists throughout the œsophageal region of *Harenactis*. Every piece from this region which does not collapse and die within the first few days after section produces them. Their number and relation to the mesenteries is the same as at the oral end; in fact an aboral disc thus formed can scarcely be distinguished after a few days from an oral disc, except by the smaller size of its tentacles.

Fig. 2. Œsophageal piece (between lines *a* and *b*, Fig. 1) in section with oral and heteromorphic tentacles.

Partial Aboral Discs in the Œsophageal Region

Partial isolation of some portion of the œsophageal region from the regions aboral to it is readily accomplished by a lateral incision involving both body-wall and œsophagus on one side (Fig. 3). This is the method employed for the production of lateral partial discs in *Cerianthus* (Child, '05), and partial discs arise in the same manner in *Harenactis*.

The course of restitution in these cases is briefly as follows: The contraction following the operation approximates the cut margins of œsophagus and body-wall above and below the cut and union occurs as indicated in Fig. 4, leaving a new lateral opening into the œsophagus. Within two or three days tentacles begin to develop proximal to this opening, their number being determined by the number of intermesenterial chambers cut across by the incision: thus far these cases show the same results as *Cerianthus*. A few days later, however, tentacles also begin to develop distal to the opening, i. e., at the aboral end of the partially isolated œsophageal region (Fig. 5). When the incision lies proximal to the level of the mesenterial ostia these heteromorphic tentacles

may attain the same length as the others (Child, '09a), otherwise both they and the tentacles directly distal to them at the original oral end undergo gradual atrophy and the whole strip finally disappears as in *Cerianthus*.

Fig. 3 Oral region of body in longitudinal section; dotted line indicates the operation for producing lateral mouths.

Fig. 4 Early stage after the operation indicated in Fig. 3.

Fig. 5 A later stage, showing heteromorphic tentacles above the lateral opening.

Fig. 6 Surface view from side, showing lateral mouth with normal tentacles below and heteromorphic tentacles above.

In these cases then a partial aboral disc is formed distal to the lateral opening and a partial oral disc with the same number of tentacles—except in cases of irregularity of closure—develops

proximal to the opening. Fig. 6 shows an individual with oral and aboral partial discs after the tentacles have attained complete development.

These heteromorphic discs developed in every case—some twenty-five—where lateral incisions involving both œsophagus and body-wall were made.

Certain interesting modifications of the results occur when the lateral incisions are made in animals with the oral end more or less completely invaginated. These cases often occur against the will of the experimenter, for when the animals are first brought into the laboratory they are extremely sensitive and a very slight stimulus is sufficient to bring about invagination. Consequently it often happens that more or less invagination has occurred before the scissors reach the œsophagus. Two cases will serve to indicate what may occur under these conditions.

In the first of these cases the relation between the incision and the œsophagus and body-wall was approximately that indicated in Fig. 7. The œsophagus and disc had undergone a certain amount of invagination before the incision reached the œsophagus, consequently the portion of the œsophagus distal to the incision is shorter than the portion of the body-wall, as the figure shows. Union between œsophagus and body-wall above and below the incision occurred as usual in this case, but the regions of union occupy positions different from those in the preceding cases. Distal to the cut the body-wall and œsophagus unite at *a*, Fig. 8, i. e., at a point facing the lumen of the œsophagus when the animal is extended. Proximal to the incision the union occurs at *b*, Fig. 8. The results are exactly the same as if a lateral incision extending obliquely toward the distal end of the body had been made while the animal was fully extended. The new tentacles arise as usual in relation with, but a short distance from the line of union both above and below the incision. Consequently the tentacles below the incision, i. e., the oral tentacles on the proximal portion, arise somewhat further proximally than in the preceding cases and the partial disc is somewhat oblique (compare Fig. 8 with Figs. 4 and 5). In later stages this obliquity gradually disappears in consequence of growth of the body-wall proximal to these tentacles.

In the region distal to the incision, however, the new heteromorphic tentacles arise in the lumen of the œsophagus (Fig. 8). It is evident from the figure that their origin at this point does not constitute a change from the usual relations of tentacles to the line of union. They arise at or rather very near the aboral end of this partially isolated region of the body-wall exactly as in other cases described (Figs. 2 and 5). In cases of this kind the tips of these aboral tentacles can often be seen protruding from the lateral mouth when the animals are fully extended and distended, though they sometimes extend down the œsophagus and are not visible at all from the exterior. Under these conditions the heteromorphic tentacles do not usually attain any great length. This failure to develop is undoubtedly due to the fact that the pressure of other parts upon them prevents their distension and consequent growth. When the animal is distended the region proximal to the incision presses upon the aboral end of the distal region and the walls of the œsophagus are usually more or less closely applied to each other, so that conditions for the growth of tentacles are very unfavorable. In a number of cases I have seen these aboral tentacles gradually crushed out of existence.

The second case of this kind to be described is shown in Figs. 9 to 11. Here invagination has proceeded so far before the incision was completed that the disc instead of the œsophagus was involved (Fig. 9). Fig. 10 indicates the relations of parts after union had occurred and the animal had become distended again. Distal to the incision the cut aboral surface of the body-wall had united with the cut surface of the disc so that the line of union was at *a* (Fig. 10). Proximal to the incision union between body-wall and œsophagus occurred at *b*.

As in the preceding case the tentacles appear in relation to the cut surfaces of the body-wall, but in the case of the oral partial disc proximal to the incision regulation gradually brings the parts into the usual positions (Fig. 11). In the region distal to the incision, however, the heteromorphic tentacles arise between the old tentacles and the mouth (Fig. 11) on what is apparently the disc, so far as its position is concerned, though it is actually the aboral end of the partially isolated region of the body-wall, as is

Figs. 7 to 11 Lateral operations and their results in partially invaginated animals: in longitudinal section.

Fig. 7 Operation on slightly invaginated animal.

Fig. 8 Result of operation: the heteromorphic tentacles are located at *a*, within the œsophagus.

Fig. 9 Operation on individual more completely invaginated.

Fig. 10 Early stage following operation of Fig. 9: *a* and *b* indicate the regions of union of cut margins of body wall and œsophagus.

Fig. 11 Later stage of same individual: heteromorphic tentacles appear on the upper surface near the original oral tentacles.

evident from Fig. 10. In all cases of this kind both the old tentacles distal to the incision and the new aboral tentacles undergo atrophy and the whole region disappears because the mesenterial ostia are always proximal to the incision, and this region, therefore does not share in the distension of other parts of the body (Child, '09a). The atrophy at the tip of the old tentacles is shown in Fig. 11.

All possible gradations between the condition represented in Fig. 11 and the usual condition (Figs 4 and 5) can be obtained according to the degree of invagination existing at the time the incision is completed. Attention may again be called to the fact that in all such cases the new tentacles appear in the same relation to the cut surfaces, though their space relations to other parts may differ widely.

2 Aboral Restitution in the Suboesophageal Region

Under certain special conditions to be described in a later section heteromorphic tentacles may appear in regions aboral to the oesophagus, but where the closure of the wound occurs in the usual manner, i. e., by approximation of the parts of the aboral cut surface of the body-wall and the formation of new tissue between them, as described in the preceding paper, tentacles have never been observed at the aboral end.

Even when the level of section is immediately proximal to the oesophagus (c, Fig. 1) closure occurs to form an aboral end, at least so far as appearance is concerned. Oesophagus and body-wall never unite with each other unless a cut surface is present on each: moreover, these two surfaces must be connected by continuous cut margins of mesenteries in order that such union may occur. These conditions exist only when the section involves the oesophagus, never when the level of section lies aboral to the oesophagus.

Section at any level proximal to the oesophagus is followed by closure of the aboral end, though the closure may be more or less delayed by protruding muscles and mesenteries. No outgrowth of a new aboral end such as is found in *Cerianthus solitarius*

(Child '03, pp. 257 to 259) ever occurs, but the area of new tissue enlarges somewhat as the body becomes distended after closure. The actual restitution of the aboral portions removed is accomplished, so far as it occurs, by the gradual growth and redifferentiation of the more proximal portions of the piece.

Fig. 12 Restitution in a piece including the whole œsophageal region.

The question as to whether complete aboral restitution occurs at all levels of the body requires some consideration. Fig. 12, for example, represents the distal piece resulting from section of the body at the level *c*, Fig. 1. In this case practically the whole region containing the retractor muscles has been removed and the piece represents little more than the œsophageal region. Such pieces may live for months without food, though they of course decrease in size. During this time the œsophageal region increases somewhat in length, but never attains anything like the usual proportions, at least never within the four and a half months over which my observations extended. Restitution of the retractor muscles in such individuals does not occur to any great extent and they remain wholly incapable of invagination. Moreover, I have never observed attachment to the substratum by the aboral end in these cases.

There can be little doubt that the absence or small amount of aboral restitution in these cases is, at least in large part, the consequence of the conditions of existence. In an earlier paper (Child, '08b) I described certain regulatory changes in shape and structure which occurred when the animals were kept for long

periods without sand in which to burrow. Briefly stated, these changes consist in a very great decrease in length with considerable atrophy of the more proximal regions, including the retractor muscles. Pieces undergoing regulation were kept under the same conditions, and since under these conditions reduction and atrophy of the more proximal portions of the body occurs to a considerable degree in unmutated individuals it cannot be expected that restitution of these parts shall be complete. In short the condition of physiological equilibrium differs widely from that existing under the usual conditions in nature, i. e., when the animal is in its burrow in the sand. Consequently restitution under these altered conditions consists in an approach to the new condition of equilibrium determined by these conditions, not in an approach to the original condition of equilibrium determined by conditions which no longer exist. In such cases as Fig. 12 then, restitution is approximately complete for the conditions under which the individual is living, though it is not complete with reference to the animal as we usually find it in nature.

There is nothing inherent in *Harenactis* which determines the restitution of these missing parts irrespective of the environmental conditions. As regards certain features, at least the form and structure of the species are the product of its constitution and the environment and with respect to these same features the same is true for restitution. Under the conditions of the experiments in question there is not and cannot be any stimulus for the restitution of the proximal regions of the body in the form characteristic of the species in nature, since these conditions determine reduction and partial disappearance of these parts in individuals which originally possessed them.

In *Cerianthus solitarius* (Child '03, etc.) the shape and structure of the body are much less dependent upon external conditions, though not wholly independent of them, and there removal of a proximal region of the body is followed by at least partial restitution. *Cerianthus æstuarii* (Child '08a) occupies a position intermediate between *C. solitarius* and *Harenactis* in this respect. When kept without sand marked decrease in length occurs and the more proximal portions undergo some degree of reduction, and

correspondingly restitution at the aboral end in pieces kept under the same conditions does not proceed much beyond closure of the wound, though when the animals are allowed to burrow in sand it is much more nearly complete.

In my experiments with *Harenactis* I endeavored to place pieces like Fig. 12 under natural conditions, i. e., I embedded them in sand with only the oral ends protruding, but their movements always resulted in their gradual emergence from the sand. Their emergence was due to the fact that since the aboral end was not firmly fixed in the sand contraction often drew the aboral end upward instead of the oral end downward and the sand gradually filled the space beneath the body. Longer pieces are more likely to remain in the sand since the more proximal portions are less likely to be dislodged by the contractions. I have no doubt, however, that if these shorter pieces can be kept in the sand aboral restitution will at least proceed much further; in all probability they will attain the usual form of the species. I hope to obtain further data on this point at a future time.

As noted above aboral restitution in the subœsophageal region does not show any marked regional differences. So far as I can determine, the amount of redifferentiation is in some degree proportional to the size of the portion removed, i. e., short pieces like Fig. 12 representing the more distal portions of the body proceed somewhat further in the restitution of the proximal parts than do longer pieces. If restitution consists in an approach to the condition of physiological equilibrium characteristic for the existing conditions, as I believe it does, this difference is to be expected, for when we remove the whole subœsophageal region we remove some portions which are characteristic of the condition of equilibrium under the experimental conditions.

One regional difference in aboral restitution does occur, however, though, macroscopically it is physiological rather than morphological. This difference concerns the functioning of the aboral end of the piece as a foot. As I pointed out in an earlier paper (Child '08b) the region of attachment shows no marked differences in structure from other regions of the body-wall. As a matter of fact, however, the more proximal the level of section the more

often does attachment of the aboral end thus formed occur. Pieces like Fig. 12 have never been observed to attach themselves and often pieces comprising almost the whole length of the body do not, but my notes record the occurrence of attachment more frequently in longer than in shorter pieces. The question of the localization of the power of attachment was discussed in my earlier paper (Child '08b, p. 11): I need mention here only that it is more marked toward the proximal end and that its limits apparently differ more or less widely according to conditions.

3 Analysis of the Experimental Data with Reference to the Regional Factor

The facts are briefly as follows: at all levels within the oesophageal region restitution from an aboral cut surface results in the formation of structures normally characteristic of the oral end; when the operation involves the whole cross-section of the body a complete disc with twenty-four tentacles is formed similar to that at the oral end, and when incisions involving only a part of the circumference are made partial discs with tentacles corresponding in number to the number of intermesenterial chambers cut across by the incision are formed. At all levels proximal to the oesophageal region aboral restitution results in the formation of structures normally characteristic of the aboral end, though environmental conditions may prevent complete restitution of the parts removed. The formation of heteromorphic structures is then limited to the oesophageal region in the cases under consideration.

This definite localization of heteromorphosis may apparently be determined by one or both of two possible regional factors or factor-complexes, viz: first, the physiological character or constitution of the oesophageal and suboesophageal regions and, secondly, the method of closure of the aboral end in the two regions. My experiments show clearly that external factors are not concerned.

As regards the first of these factors, the physiological character or constitution, it is evident that the formation of heteromorphic discs and tentacles would be impossible if the parts concerned did

not originally possess or acquire after isolation a certain definite reactive capacity. The question as to whether this capacity is an original possession of the parts in question or whether it is acquired after isolation leads at once to the consideration of the second factor, viz: the method of closure, since this is, so far as can be determined, the only other regional factor possessing the same localization as the heteromorphic reaction.

The method of closure in the œsophageal region is always the same at both oral and aboral ends (Child, '09b) and consists in the union of the cut surface of the body-wall with that of the œsophagus, so that the œsophagus does not connect with the enteron but opens externally at each end. In the preceding paper attention was called to the fact that this method of closure follows necessarily from the structural relations of parts in the œsophageal region and the character of the wound reaction, which consists in the contraction of all parts involved. This method of closure brings the various parts at the two ends of the piece into similar space relations and into similar relations of organic continuity with each other, and it seems at least possible that the establishment of these conditions in two complexes of similar parts may be a factor in determining that the two complexes shall react similarly. Under these conditions the correlations between the parts in each complex must be similar, consequently a similar constitution being postulated, similar reactions are to be expected. On the other hand, the establishment of similar relations of space and organic continuity in two complexes can scarcely be expected under similar external conditions unless the two complexes consist of similar parts. In short, since the two ends of an œsophageal piece of *Harenactis* are very similar in structure and behave similarly under like conditions we are forced to the conclusion that they are essentially similar physiologically. In restitution their structural and physiological similarity determines that closure of the wound shall occur in the same manner, this method of closure in turn determines that similar relations of space and organic continuity, i. e., similar physiological correlations, shall be established, and these finally determine the occurrence of similar reactions, i. e., in the present case the restitution of similar structures.

Clearly then the experimental evidence leads us to the conclusion that no essential qualitative axial, i. e., polar, differences in constitution exist in the œsophageal region of *Harenactis*. Quantitative axial differences undoubtedly do exist, as is shown by the fact cited in the preceding paper (Child, '09b) that even in the œsophageal region the rapidity of tentacle-formation at the oral ends of pieces decreases with increasing distance of the level of section from the original oral end. Moreover, aboral tentacles appear much later than oral tentacles at the same level, as was noted above in the present paper. This retardation of aboral tentacles as compared with oral at the same level cannot be due to preëxisting and persisting quantitative axial differences, since it appears only in cases of heteromorphosis, but must be the result of some factor which is present only when heteromorphosis occurs. It is not then, properly speaking, a regional factor and therefore does not concern us at present; as a matter of fact it is undoubtedly a correlative effect, i. e., the presence or formation of oral structures at the oral end of a piece retards the formation of similar structures at the aboral end of the same piece.

The experiments do not afford the slightest evidence for assuming the existence of a directive polar organization in the œsophageal region of *Harenactis* such as Driesch and certain others have postulated, neither do they show any essential qualitative regional or axial differences in reaction; purely quantitative differences, i. e., differences in the rapidity of reaction, are the only differences which appear, and it is probable that they constitute the only polarity which exists in this region.

In the subœsophageal region, on the other hand, the two ends of the piece react differently, disc and tentacles appearing only at the oral end, while the aboral end redifferentiates more or less completely into the aboral structures removed. There can be no doubt that physiological differences exist at the two ends of the pieces in these cases, but such differences must be differences of correlation rather than of constitution, since any given level of the body in this region except the extreme aboral end gives rise to oral or aboral structures, according as it is in correlation with more proximal or more distal parts. Quantitative differences of con-

stitution do, however, exist in this region: the decreasing rapidity of disc and tentacle-formation and the increasing ability of the aboral end to function as a foot with approach to the original proximal end are indications of such quantitative differences.

The data of oral restitution in the preceding paper show only quantitative regional differences, except at the extreme proximal end of the body: the data of aboral restitution considered above show only quantitative differences, except in the distal, i. e., the œsophageal region. These results are, however, seemingly contradictory, for a given region of the body cannot be qualitatively like and different from other parts at the same time. Evidently some other factor besides the constitution of the body at different levels is involved in the phenomena of polarity. If we regard this factor as directive, as determining that oral structures shall arise in one direction, aboral in the other, we fall into new difficulties, for the phenomena of heteromorphosis then require a special hypothesis. I believe we must consider the physiological correlations between parts as an essential factor in determining the phenomena of polarity. In the following general consideration of polarity a brief analysis of the factors and the rôle played by each is attempted.

II POLARITY IN GENERAL

1 The Facts of Regulation and Their Significance

The most conspicuous fact among the data of regulation, so far as they concern polarity, and one might add, among the phenomena of development, is the appearance of characteristically different structure-complexes at the two ends of the principal axis. In regulation this apparent polarization can be well illustrated by the formation of structures typical of one end or the other from cells at exactly the same level of the body, according as these cells form one end or the other of the piece. Such polar differences occur throughout the middle region of *Harenactis*, *Cerianthus* and in many other forms. They are of course merely an expression in the isolated piece of what we find in the whole in normal development. These facts alone seem to point to the existence of a

directive organization along the polar axis as the basis of polarity, an organization of the ultimate particles or elements of the protoplasm, such as Driesch assumes. But I believe that these facts alone afford not only an inadequate, but an incorrect conception of the nature of physiological polarity so-called. In order to understand the organization with reference to the "polar" axis it is necessary to consider all the essential facts which indicate difference in capacity of any kind, quantitative or qualitative, along the axis. In addition to the qualitative differences which commonly occur at the two ends of the polar axis, there are three other groups of facts which must be considered before we can safely draw any conclusions with respect to the nature of polarity. These are as follows: First, in many forms the regulation of isolated pieces from regions near the oral or anterior end, and in some cases of pieces from the aboral or posterior regions, does not show the characteristic qualitative differences at the two ends of the axis. In such pieces the structures formed at the two ends are alike, except perhaps in size and time of appearance. These phenomena are commonly termed axial heteromorphosis. In the œsophageal region of *Harenactis*, for example, the formation of tentacles at the aboral end of the piece is just as characteristic as is the formation of tentacles at one end and a foot at the other in pieces from the subœsophageal region. Similar axial heteromorphosis has been observed in various other coelenterates: in *Planaria maculata* and *P. dorotocephala* heads frequently appear at both ends of short pieces from the region near the old head and the region of fission, where the head of the new zoöid is at least physiologically specified, and in *P. simplicissima*, which does not undergo fission, heteromorphic heads appear in short pieces from near the anterior end (Morgan '04). Numerous other cases have been noted.

In some species we find also that in regions posterior to a given level aboral or posterior structures are formed from the oral or anterior as well as from the aboral or posterior end. The formation of tails at the anterior ends of pieces from the posterior half of the earthworm (Morgan '99), and of short posterior pieces of *Planaria simplicissima* (Morgan '04) will serve as examples.

Evidently then the heteromorphic formation of the structures

characteristic of either pole of the axis may occur, but heteromorphic development of oral or anterior structures is probably of more frequent occurrence than aboral or posterior heteromorphosis; but this is probably due, however, to the fact that the oral or anterior region is a region of greater physiological activity than the other, i. e., negative results in aboral or posterior pieces are often due rather to lack of energy than to anything else.

In general heteromorphosis of oral or anterior structures occurs in regions near the oral or anterior end, heteromorphosis of aboral or posterior structures nearer the opposite end. In certain cases, however, as in *Tubularia*, axial heteromorphosis of oral structures may be a frequent or characteristic result at most or all levels of the body. Here and in all cases of this kind the external conditions after isolation are a factor in determining the result, consequently such cases do not afford data which can be used directly for the analysis of polarity (Child '07). They tell us nothing about an original polarity except that, if it ever existed, it is no longer present. In fact, as I pointed out in my discussion of polarity in *Tubularia* (Child '07e) we must distinguish two kinds of axial heteromorphoses, primary and secondary. Primary heteromorphoses are the necessary result of the axial organization of certain regions which existed in the original organism. They occur in all cases where the piece is so short axially that axial differentiation or specification is almost or wholly absent. In the absence of the original organization the parts cannot be correlated with each other as are the parts of the whole. The two terminal regions, being physiologically alike or nearly so, react similarly to the existing conditions, with little or no relation to each other, consequently new specifications are established with reference to these two regions instead of one of them, and we say that the polarity of one end has been reversed. The heteromorphic discs and tentacles in œsophageal pieces of *Harenactis* are undoubtedly primary heteromorphoses, i. e., there are no marked axial or polar physiological differences in this region in the original animal, and when a piece is isolated new polarities arise between each end and the middle, since conditions must necessarily be different in these two regions. Similarly the posterior heads in short pieces of

Planaria are primary heteromorphoses, also the double hydranths or partial structures in short pieces of Tubularia (Child '07c). Theoretically primary heteromorphosis may occur at any region of the body if sufficiently short pieces are isolated; whether it will actually occur or not will depend upon whether the pieces possess sufficient energy to produce morphogenic results.

Secondary heteromorphoses occur when the original axial specification of the organism is present in the piece at the time of isolation, but cannot persist under the conditions of the experiment. Under certain conditions secondary heteromorphoses occur in *Harenactis*, but these will be considered in a following paper. In *Tubularia* the formation of aboral hydranths in long pieces of the stem is, as I have shown (Child '07a, '07c, '07e), a secondary heteromorphosis.

In the case of primary heteromorphosis, then, we obliterate or almost obliterate the differentiation or specification in the axial direction by isolating a piece so short that its two ends are almost or quite similar physiologically: in secondary heteromorphosis the original organization persisting in the isolated piece at first is more or less completely obliterated by conditions arising after isolation of the piece. In *Harenactis*, for example, the union of the oral with the aboral end is apparently a factor, probably the chief factor, in obliterating the original polarity, and thus, so to speak, clearing the way for the establishment of a new polarity.

But the important point for the present consideration is that the phenomena of primary axial heteromorphosis indicate that the polar specification is not uniformly distributed along the axis. In the whole œsophageal region of *Harenactis*, for example, there is, according to this view, nothing more than a slight quantitative difference at the two ends of the axis of any piece, i. e., polarity in the usual sense of qualitative polar differences is absent or practically absent from this region. If my position is correct the same must be true for any region of any species in which primary heteromorphosis occurs. And finally, in forms like *Planaria simplicissima* where short pieces from regions near the old head, form heteromorphic heads and short posterior pieces form heteromorphic tails, these two regions must be so widely different in their

physiological specification and capacities that we may call the differences qualitative and not quantitative. In other words the extreme anterior region is capable of reacting only in a particular manner, i. e., so as to produce heads at either or both ends, while the extreme posterior region can produce only tails. In both cases the production of the characteristic structures fails to show any indication of a directive organization: the organization, specification, or whatever we may call the reactive capacity is, so far as the facts go, very clearly regional and direction is determined merely by the relations between the cut surface and other parts. I believe then that the facts justify the conclusion that the terminal regions of the body may differ so widely from each other in their constitution as to be incapable of reacting similarly at any point; consequently when pieces from these regions are isolated they produce similar structures at both ends if they produce anything, and the structures produced are those characteristic of that end of the parent body from which the piece is taken. Very commonly, as in *Harenactis*, primary heteromorphosis occurs only in the anterior or oral region and short pieces from the extreme proterior or aboral region form nothing. This difference is probably due, however, as was noted above, rather to a difference in energy or available material than to any fundamental difference in organization. There is abundant evidence to support the conclusion that in at least a very large number of forms the anterior or oral pole is primarily the region of greatest formative energy or activity, or of greatest rapidity of reaction.

We cannot then, I believe, escape the conclusion, that qualitative regional differences in the terminal portions of the body constitute in at least certain forms a feature of organic polarity, as well as the qualitative differences which usually appear at the two ends of the axis of the piece. In short the terminal regions of the body may be respectively wholly oral or anterior and wholly aboral or posterior as regards their "potences" and primary heteromorphosis is the necessary consequence of this extreme specification, provided sufficient energy for morphogenic reactions is present.

In addition to these two features of axial specification which we

may call qualitative, certain quantitative features exist. Usually, for example, the rapidity of development or the size of oral or anterior structures decreases as the distance between the level from which they arise and the original oral or anterior end increases, and the same is true, *mutatis mutandis*, for aboral or posterior structures. As was shown in the first paper of this series, the rapidity of tentacle-formation in *Harenactis* decreases with increasing distance of the level of restitution from the original oral end: in *Tubularia* (Child '07c, '07e) and in *Planaria maculata* and *P. dorotocephala* (Child '06) similar differences exist, though in these planarians a complicating factor exists in the presence at the posterior end of a region physiologically specified as a new zoöid.

And finally, in cases of primary heteromorphosis quantitative differences between the two ends of the axis often exist, as in *Harenactis*, where the aboral tentacles always appear later than oral tentacles in an oesophageal piece, and not only that, but later than oral tentacles at the same level. Similar differences often appear in *Tubularia* and *Planaria*.

Summing up what has been said, we find that the restitutional reactions show four distinct characteristics with respect to the principal axis: first, different reactions may occur at the two ends of the axis of a piece (qualitative polar differences or heteropolar phenomena); second, in cases of primary heteromorphosis the heteromorphic reaction very commonly occurs more slowly than the "normal" one (quantitative polar differences); third, the character of the reactions in primary heteromorphoses may differ completely according as the pieces are taken from one or the other end of the axis (qualitative regional differences); and fourth, in most cases the rapidity or energy of the reaction characteristic of either pole decreases as the distance between the level from which it occurs in a given case and the pole where it originally occurred increases (quantitative regional differences). In considering the problem of what we call polarity we cannot neglect any of these phenomena, for all of them have to do with the axis. If we consider polarity with Driesch as a directive organization we cannot account for primary heteromorphoses, in which the two ends of the axis are alike except perhaps quantitatively. If, on the other

hand, we accept Morgan's hypothesis that polarity is a gradation of substances along the axis, another hypothesis is necessary to account for the most conspicuous feature of polarity, viz: the fact that the same tissues may produce totally different structures according as they constitute one end or the other of the axis.

In short, neither the hypothesis of directive organization nor that of regional gradation alone will account for the characteristic phenomena of polarity in animals, for the very simple reason that polarity possesses both regional and directive features. In other words there are two internal factors in polarity, constitution and correlation. In *Harenactis* or in *Planaria* the cells at a given level form tentacles or a foot, a head or a tail, according to the character of their relation with other parts of the organism, i. e., their correlations. This factor of correlation and the part which it plays in polarity have been recognized by the botanists, and it is certainly no less important in animals than in plants. Whether a given cell complex gives rise to an anterior or posterior, an oral or aboral structure, cannot possibly depend upon itself alone, since it is originally the same in both cases, but nevertheless gives rise to different results.

Morgan's hypothesis can account only for regional, never for polar phenomena. According to his latest statement of the hypothesis (Morgan '07, pp. 378 to 380), a head forms at one end of a piece because there is more head-forming substance there, and a tail at the other end because that contains more tail-forming substance. This amounts exactly to the assertion that heads and tails appear where we find them because they do. Moreover, it affords us absolutely no basis for understanding how either a head or a tail may arise from the same cells according as they form one end or the other of the piece.

On the other hand, Driesch's hypothesis accounts for these differences at the two ends of the axis, but cannot account for the phenomena of primary heteromorphosis. Moreover, the evidence in favor of the hypothesis of a directive organization seems at least unsatisfactory.

I believe that no conceivable hypothesis which concerns constitution alone, or correlation alone, can account for the phe-

nomena of polarity in organisms, for both constitution and correlation, or in other words, both structure and function are factors in determining the character of the phenomena.

I use the term "correlation" in its physiological sense as including all effects of conditions and processes in one part upon another part. It is only within recent years that correlations have become in any real sense objects of investigation. Concerning their nature we learn but slowly: we know that some of them are chemical, others physical, and still others complex, but there seems to be no general recognition among zoölogists such as exists among botanists of their great importance in morphogenesis. I might cite in this connection various misconceptions and misinterpretations of my own work on regulation, for they furnish abundant proof of this fact, but time and changed conceptions of the problems of morphogenesis will perhaps accomplish what discussion cannot.

2 Constitution and Correlation in the Phenomena of Polarity

We may say in general that so far as internal factors are concerned, the constitution of a part at any given time determines what reactions are possible in it at that time, and its correlations determine what reactions actually occur. In *Harenactis*, in *Planaria* and many other forms the cells of a given level, e. g., the middle of the body, possess a constitution which is capable of giving rise to the structures characteristic of either pole. But whether they actually form tentacles or a foot, a head or a tail in any particular case is very evidently determined by their physiological relations with other parts, i. e., their correlations. Manifestly the cells of a given level must be in a different physiological state when they are in correlation only with parts aboral or posterior to them, from that which exists when they are in correlation only with parts oral or anterior to them. The nature of the differences between these two states we do not at present know, but we cannot doubt their existence. Moreover, both of them are different from the original state when the cells were correlated with both regions of the body.

Formative substances, so-called, do not assist us to explain these facts, they merely state the facts. It is self-evident that where a head is formed there must be "head-forming substances": the real problems lie in the questions of how they come to be there, and why in the same cells "head-forming substances" are active at one time and "tail-forming substances" at another.

My analysis of these qualitative polar differences or heteropolar phenomena in restitution is then as follows: first the tissues involved possess at the time of operation a constitution capable of either reaction; second, their constitution and consequently their reaction is altered in one direction or the other according to the character of their physiological correlations with other parts. These correlations may be either chemical or physical or both; in all probability they are exceedingly complex, as they are known to be in plants.

In the primary heteromorphoses, i. e., in those cases of heteromorphosis where the isolated piece is so short that polar differences are almost or quite absent at its two ends, we have another characteristic restitutional phenomenon. In such pieces the two ends are physiologically almost identical, consequently the correlations between them can have little or no effect in producing a difference between them and any effect must be slight. It follows then necessarily that if morphogenic reactions occur at the two ends of the piece they will be almost or quite similar in character. But the constitution of such pieces is different according as they are taken from one or the other terminal region of the original individual and consequently such pieces may give rise either to heteromorphic heads or tails, oral or aboral structures according to their position in the body. Sometimes, as in the case of *Tubularia* (Child '07d), the conditions of experiment, in this case the formation of free terminal regions, play a part in determining the character of the reaction, and in various other cases, as in *Harenactis*, pieces from the extreme aboral or posterior region apparently have not sufficient energy, when isolated, to produce anything. Under these conditions only primary oral heteromorphosis may appear, and this may be limited to the more oral region as in *Harenactis*, or may occur at any level of the body if the pieces are sufficiently small, as in *Tubularia*.

But the essential point for our present purposes is that the phenomena of heteromorphosis in short pieces—primary heteromorphosis—are the necessary consequence of the constitution of the material, when the length of the piece is so short that its axial differentiation is reduced practically to zero, and the correlations between parts consequently almost or quite eliminated. But, as pointed out above, the physiological state at the two ends of such pieces must after isolation become different from that at the middle, consequently the two opposed polarities result.

These cases of primary heteromorphosis show us, according to this view, something of the differences of constitution along the axis. In such a case as that of *Planaria simplicissima* (Morgan, '04), where short pieces from near the old head form double heads and those from the posterior region double tails, it is evident that the two terminal regions of the body are qualitatively different in constitution. Moreover, these phenomena afford in my opinion the strongest evidence against the hypothesis that polarity consists in a directive organization or orientation.

But correlations between the two terminal regions are not entirely absent in cases of primary heteromorphosis. In *Harenactis*, for example, the aboral tentacles in the œsophageal region always appear, not only later than the oral tentacles, at the opposite end of the piece, but later than oral tentacles at their own level. Evidently there is some slight physiological difference, at least a quantitative one, between the two ends of the piece, for the processes at the oral end retard those at the aboral end. Similar differences between the two ends occur sometimes or always in various other forms. In primary heteromorphosis in *Tubularia* I found that at least very commonly the aboral primordium or partial primordium was considerably delayed in the earlier stages (Child '07d), though after emergence the two were usually more nearly alike. In *Planaria* the two heads are often different in size and one may appear before the other.

Here again in the retarding influence of the oral or anterior end upon the aboral or posterior end in short pieces we find a correlative factor of polarity. The fact that the development of the aboral structures is slower than that of oral structures at the same

level, i. e., composed of the same cells, shows very clearly that the factor involved is correlative, not constitutional.

Finally we have to consider the quantitative regional differences which appear along the axis in restitution. *Harenactis* affords a fairly good illustration of such differences. Here the rapidity of tentacle development and to some extent also the size of the tentacles decrease as the distance between the level from which they arise and the original oral end increases: in the extreme proximal region tentacles do not appear at all. Similarly, though less clearly, the ability to form a foot decreases toward the oral end until in the oesophageal region it does not occur at all. Similar differences appear in all animals in which the phenomena of restitution are not confined to appendages and peripheral parts, except where they are complicated and modified by various other factors, e. g., the intensity of the correlative stimulus, unsymmetrical organization along the axis, cephalization of the nervous system, etc. Discussion of these factors is not necessary here since they do not alter the fundamental fact that quantitative regional differences in restitution do occur at both poles of the axis, which is all that concerns us at present. These differences are very evidently expressions of the constitution of different regions. In *Harenactis*, for example, from a level just proximal to the oesophagus tentacles develop rapidly and attain a large size when this level forms the oral end of a piece, but a foot is rarely if ever formed when the same level lies at the aboral end of a piece. At a level near the proximal end of the body tentacles appear slowly and remain small, but a foot forms readily from the same level. Evidently the new correlations established after isolation of the pieces do not completely obliterate the previously existing differences of constitution. If these were the only phenomena of polarity Morgan's hypothesis of a graded constitution would account for the facts.

To sum up: The qualitative regional differences as exhibited in primary heteromorphoses and the quantitative regional differences which appear in the structures of either pole at different levels are determined by the constitution of the material which existed before isolation of the pieces: the qualitative axial or polar

differences, i. e., the heteropolar phenomena and the quantitative axial or polar differences, i. e., the differences between the two ends of the piece in primary heteromorphosis are determined by the correlations existing between parts after isolation. Preëxisting constitution and present correlation are then the two factors or factor-complexes which determine the phenomena of physiological polarity as they exist in regulation.

These two factors are in other words the morphological and physiological aspects of the problem of polarity. I believe that every problem of morphogenesis possesses these two aspects and that any attempt either at purely morphological or purely physiological interpretation must of necessity be incomplete. When we assume the structural basis as given we may say that all problems of morphogenesis are physiological or functional in character, as I have done in certain papers. When we assume the various processes as given morphogenesis becomes a morphological problem. But strictly speaking living structure without function and function without structure are alike inconceivable: changes in structure must accompany changes in function and changes in structure cannot occur without producing changes in function. Recent criticisms of some of my work remind me that it is perhaps necessary, to emphasize once more the fact that I am using the word function in its broadest sense as synonymous with process or activity.

III SUMMARY

1 In the œsophageal region of *Harenactis* tentacles and disc are always formed at the aboral as well as the oral ends of pieces, provided the pieces live long enough and become sufficiently distended. The aboral mouth in these cases is not a new formation but is the result of fusion of the cut end of the body-wall with the cut end of the œsophagus so that the latter remains open.

2 Complete or partial aboral discs develop in the œsophageal region according as the operation involves the whole cross-section of the body or only a part of it.

3 The formation of aboral tentacles is less rapid than that of

oral tentacles in the same piece and also less rapid than that of oral tentacles from the same level of the body.

4 In the subœsophageal region aboral tentacles never appear except under certain experimental conditions to be considered later.

5 When only the most proximal regions of the body are removed restitution of a foot region occurs in a short time, but as the portion removed becomes larger the restitution of missing parts becomes less rapid and less complete, until in cases where most of the subœsophageal region is removed, only a slight degree of restitution occurs. Absence or incompleteness of aboral restitution in these cases is undoubtedly due wholly or in large part to the environmental conditions. When the animals are kept in water without sand in which they can burrow a considerable amount of reduction and atrophy occurs and this is greatest in the proximal regions and decreases distally. Under conditions in which these parts undergo atrophy when they are present it is not to be expected that their complete restitution should occur in pieces from which they have been removed. The form and constitution of individuals living in burrows in the usual manner are different from those of individuals living in water without sand, and restitution of the form characteristic of the existing environment does occur in my experiments. If the short pieces could be kept in burrows it is probable that at least much more complete restitution of the form occurring in nature would take place.

6 Two groups of factors are involved in the phenomena of polarity as they appear in restitution: these are constitution and correlation. The regulatory phenomena of polarity may be grouped under four heads as follows:

a Qualitative axial or polar differences in restitution (heteropolar phenomena): the same cells may produce qualitatively different structures according to their position at one pole or the other of the piece.

b Qualitative regional differences (primary heteromorphosis): short pieces from near one pole or the other, or in some cases both, may produce at both ends structures like those present at the nearest pole of the original individual.

c Quantitative axial or polar differences: in heteromorphosis the heteromorphic structure is very often delayed in development.

d Quantitative regional differences: when axial phenomena are not complicated by other factors, the rapidity of restitution and often the size or completeness of the parts decreases as the distance between the level at which they form and the similar pole of the original individual increases.

These phenomena may be complicated and altered by various factors such as greater differentiation or specification of certain parts and consequent decreased power of restitution, the intensity of the restitutorial stimuli under different experimental conditions, cephalization of the nervous system, etc.

7 The regional differences, both qualitative and quantitative, are determined by the regional differences in constitution existing in the original individual at the time the pieces were isolated. They are the result of the structural polarity which is a regional difference in constitution along the axis.

8 The axial or polar differences, both qualitative and quantitative, are determined by the correlations existing between the parts of the piece after its isolation. They are the result of the physiological polarity.

NOTE

Since this paper was written the results of Lillie's recent centrifuge experiments on *Chætopterus* eggs have appeared.¹ Lillie's conclusions require a brief consideration in connection with what has been said above concerning polarity.

The persistence of the original polarity and symmetry in the "ground substance" after centrifuging, and irrespective of the position of the granules, has led Lillie to suggest that organic polarity and symmetry are molecular and essentially similar to the polarity and symmetry of crystals. According to this hypothesis polarity is directive, i. e., it is the result of molecular orientation.

I have endeavored to show above that such a hypothesis cannot account for the regional phenomena along the axis, which are observed in regulation both in young and adult forms. Lillie assumes that these differences are due to secondary factors. As

¹ Biol. Bull. xvi, 2, 1909.

a matter of fact, however, in almost all if not all observed cases the directive feature becomes less and less conspicuous in isolated pieces, with approach to one or both ends of the body, and with decrease in the size of the piece, while the regional differences become more conspicuous under these conditions. If the directive feature is the primary feature of polarity it seems strange that it should give place more or less completely to a regional feature under these conditions.

Moreover, Lillie finds various evidences of the existence of a molar structure in the ground substance, which he regards as concentric. It seems at least possible that such a structure may possess axial characteristics which have not yet been recognized. The apparent homogeneity of the ground substance is certainly no argument against the existence in it of a polar structure. In short, Lillie's conclusions do not seem to follow necessarily from the facts and his argument is therefore somewhat unconvincing. Morgan does not seem to have presented in his recent paper² any more cogent reasons for accepting this hypothesis. In so complex a mixture of colloids and other substances as protoplasm certainly is, the possible morphogenic factors are so numerous and varied that we are scarcely justified in turning at once to the molecule when direct observation fails us.

It seems to me that the hypothesis rests essentially on negative evidence, so far as the organism is concerned, i. e., in the absence of any visible basis for polarity it is assumed that the phenomena concerned are the result of molecular orientation. The phenomena of fluid crystals are undoubtedly of great interest, but it is by no means certain that there is anything more than a very remote analogy between them and the phenomena underlying organic polarity and symmetry. Such an assumption seems to neglect the fact that protoplasm is not a homogeneous chemical substance nor even a simple mixture. Moreover, it exists in cells and within the cells various localized differentiations may occur which may well be the result of a molar structure of the ground substance. Besides all this restitution may occur in isolated pieces after centrifuging.

² Biol. Bull., xvi, 5, 1909.

At present it is a far cry from visible differentiation to molecular orientation in protoplasm.

And finally the hypothesis is essentially speculative and the problems involved are practically removed from the field of investigation by its acceptance. Consequently we are justified in accepting it only when the facts leave no better alternative. To accept it on the basis of our present ignorance cannot serve to advance actual knowledge. As a stimulus to future research the hypothesis must affect the skeptic rather than the believer.

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