An Analysis of Form-Regulation in Tubularia.

III. Regional and Polar Differences in the Relation between Primordium and Hydranth.

By

C. M. Child.

Eingegangen am 30. Januar 1907.

The present paper is concerned with the changes in form and proportion which occur in the metamorphosis of the primordium into the hydranth. Other observers have of course noted that the form and proportions of the two structures differ to a considerable extent but so far as I am aware the existence of typical regional and polar differences in the character of the change from one to the other has not previously been recognized.

I. The Relation between the Proportions of the Primordium and those of the Hydranth.

1. Regional and Polar Differences in the Total Length of the Primordia.

As regards the regional and polar differences in the total length of the primordium my observations confirm those of DRIESCH ('99) and require only brief mention: for the individual cases the reader is referred to Tables I, II, III, V, VIII, X of the preceding paper (CHILD, '07b). In general both oral and aboral primordia decrease in length from distal to proximal regions. In a piece 10 mm. or more in length the oral primordium is always the longer and the difference in length between the oral and aboral primordia increases with the length of the piece. Where oral and aboral primordia arise at approximately the same level of the stem as for example at the aboral end of a distal piece and the oral end of an adjoining proximal

piece, the oral primordium is always the longer. From this fact it is evident that polarity is an important factor in determining the total length of the primordium.

It is well known that the total length of the primordium determines the size at the time of emergence of the hydranth arising from it. The size of the hydranth at the time of emergence is therefore to be regarded as determined by the same factors as the length of the primordium. After emergence the size of the hydranth may be altered by nutritive and other conditions.

Up to the present no very satisfactory conclusions have been reached regarding the nature of the factors involved in these regional and polar size-differences. DRIESCH ('99, etc.) attempted to correlate them with the amount of the red pigment present in different regions but later rejected this view in consequence of the work of MORGAN and his students which demonstrated that the red pigment had nothing to do with hydranth-formation.

All the facts seem to me to indicate that the size of the hydranth, i. e., the length of the primordium is determined at least in part by quantitative factors in the processes involved. The more intense the reaction to the existence of the new terminal region where the hydranth will appear, the longer the region of the stem involved (CHILD, '07b, Pt. II) and vice versa: if this reaction is the »formative« reaction the length of the primordium and so the size of the hydranth will vary according to the conditions in the stem. We should expect distal regions to react more strongly to what we may all »terminal« conditions since they have been more closely associated with such conditions in the past than other portions of the stem, i. e., these regions have become predisposed or physiologically differentiated in the direction of hydranth-formation because of their past relations. This predisposition or specification decreases from the distal toward the proximal end of the stem, hence a like decrease in intensity of reaction and so a decrease in length of the primordium exists.

But since aboral primordia are shorter than oral at the same level polar as well as regional factors must play a part. In an earlier paper (CHILD, '07a) it was shown that the formation of a hydranth at the aboral end of a piece is the result of secondary changes, not of the original condition of the stem. Aboral regions of a piece are in general specified in greater or less degree in the direction of stolon-formation. Before the aboral hydranth can appear this specification must be altered by the altered conditions. But since no predisposition

toward hydranth-formation existed the reaction will be weaker than an oral reaction at the same level and consequently its effects, i. e., the parts of the primordium will be localized nearer the end of the piece.

It is also possible that different regions offer different »resistance« to the transmission of effects from the terminal regions. We know that in certain tissues the passage of stimuli alters the condition of the tissues in such manner that similar stimuli are transmitted more readily or in greater intensity through the region. Since specialization in cells is essentially the further development of properties which unspecialized cells possess in some degree we are justified in believing that such functional adaptation may occur to some extent in *Tubularia*. If this is the case we should expect the distal regions of the stem to permit the passage of the effects of »terminal« conditions more readily or in greater intensity than proximal regions since the former have been subjected to such effects in the past to a greater extent than the proximal regions. If these effects play a part in the formation of hydranths, then longer primordia may be expected to appear in the distal than in proximal regions. It is quite possible furthermore that the stem presents different conditions to the passage of effects in different directions. If this is the case we should expect that passage in the oral-aboral direction would be less obstructed than in the aboral-oral direction and that therefore aboral primordia would be shorter than oral at the same level. Certain experiments of MORGAN and STEVENS ('04) which show that the formation of an aboral hydranth alters the polarity of the stem for only a short distance from the aboral end seem to indicate that such polar differences exist under certain conditions.

These suggestions concerning the factors involved in determining the length of the primordium are simply an application to the case in hand of well-established physiological principles and do the facts no violence.

2. The Length of the Hydranth in Relation to the Length of the Primordium.

Measurements of the length of the hydranth after emergence compared with measurements of the length of the primordium show that the relation between the two exhibits typical regional and polar differences.

Care is necessary in measuring the hydranths on account of the

changes in length with extension and contraction of the manubrium. In all cases the measurements are those of the fully extended condition and were made 12—24 hours after emergence.

In the following tables the results of these measurements are given. Each table gives for each series the number of pieces, the average total length of the primordium and of the hydranth in mm., the difference between the two, and finally this difference as a percentage of the length of the primordium. The minus sign preceding the difference and percentage-difference indicates that the hydranth is shorter than the primordium, the plus sign that it is longer. The numbers under »Series« are the series-numbers in my notes: the letter *a* following the series-number indicates the distal half of the stem; *b* the proximal half. The cases with corresponding series-number in different tables are different parts of the same series, i. e., are from the same stems.

Table I.

Oral primordia and hydranths from the extreme distal end of the stem.

Series	Number of cases	Average length of primordia	Average length of hydranths	Difference	Percentage-difference
30	15	2.21	1.36	— 0.85	— 38.5 %
31	20	2.05	1.42	— 0.63	— 30.7 %
68 _a	8	2.3	1.6	— 0.7	— 30.4 %
70 _a	(7) 8	2.4	1.5	— 0.9	— 37.5 %
35 _a	20	1.96	1.2	— 0.76	— 37.7 %
Averages		2.14	1.39	— 0.75	35 %

In series 70 of this table 7 primordia and 8 hydranths were measured. This is indicated in the second column by the (7) preceding the 8. In all other cases the number of primordia and hydranths was the same. The averages given in the tables are not the sums of the five sets of measurements divided by five but are the sum total of all individual measurements divided by 70 for the primordia and 71 for the hydranths. This method is more accurate than the other since the different series include different numbers of cases. As a matter of fact, however, both methods give the same percentage difference, — 35 %.

This percentage-difference — 35 % expresses the fact that the length of the hydranth after emergence is 35 % less than that of the

primordium at the measurement stage. Comparison of the different series in the table shows that the variation from this amount is not very great in any case.

Table II.

Oral primordia and hydranths from different levels of the stem.

Series	Number of cases	Distance from distal end of stem in mm.	Average length of primordia	Average length of hydranth	Difference	Percentage-difference
68 b	8	25	1.5	1.1	— 0.4	— 26.7 %
70 b	8	20	1.4	1.2	— 0.2	— 14.3 -
35 b	20	10	1.43	1	— 0.43	— 30.1 -

Unfortunately the number of measurements (36 cases) of oral hydranths at other levels than the distal end is not large enough for satisfactory comparison of different levels. In the table the cases 20 mm. from the distal end show only half the reduction in length of those 25 mm. from the distal end, while those 10 mm. from the distal end show greater reduction than the others. It is evident, however, by comparison with Table I that the reduction in length from oral primordium to hydranth is greater at the extreme distal end of the stem than elsewhere. I am inclined to believe, moreover, that a larger number of cases would show that, in general, the reduction in length from oral primordium to hydranth decreases with increasing distance from the distal end.

Table III.

Aboral primordia and hydranths from different levels.

Series	Number of cases	Distance from distal end of stem in mm.	Average length of primordia	Average length of hydranth	Difference	Percentage-difference
68 a	8	50	0.75	0.8	+ 0.05	+ 6.7 %
68 b	8	25	1.1	1	— 0.1	— 9.1 -
35 b	11	20	0.87	0.7	— 0.17	— 19.5 -
37 and 38	17	15	0.98	0.786	— 0.194	— 19.8 -
35 a	12	10	1.1	0.8	— 0.3	— 27.3 -

This table shows several points of interest; in the first place comparison with Table I shows that the decrease in length from primordium to hydranth is always less in aboral than in oral hydranths

from the extreme distal end: secondly the table shows that the greater the distance from the distal end of the stem the less the decrease in length, in fact in aboral hydranths 50 mm. from the distal end of the stem the difference is positive, i. e., the hydranth after emergence is 6.7 % longer than the primordium. Undoubtedly more or less variation from these figures will be found in individual cases, but the differences are large enough to establish the general result beyond doubt. As a matter of fact the differences which the figures indicate can be directly observed at least for the longer stem-distances, as I discovered before the measurements were undertaken.

Comparison of Table III with Table II indicates that except at levels 20 mm. from the distal end the reduction in length from primordium to hydranth is less in aboral than in oral cases at the same level.

Series 68 was composed of distal and proximal half stems each 25 mm. long. Series 35 consisted of distal and proximal pieces each 10 mm. in length each pair from a single stem. In these two series then we can compare oral and aboral cases at approximately the same level of the same stem, i. e., the aboral cases in distal pieces and the oral in proximal.

The percentage-difference for the oral cases in the proximal pieces of Series 68 (Table II) is —26.7%. That for the aboral cases in distal pieces of the same series (Table III second from top) —9.1%; i. e., in this case the reduction in length is nearly three times as great in oral structures as in aboral structures at the same level.

For Series 35 the oral percentage-difference in Table II is 30.1 and the aboral percentage-difference for Series 35 in Table III is 27.3. Here also the aboral is less than the oral reduction but only slightly less. In Series 68, however, the two sets of structures compared are 25 mm. from the distal end and in Series 35 only 10 mm. from the distal end. These cases indicate that the change in length from primordium to hydranth decreases with increasing distance from the distal end more rapidly in aboral than in oral structures.

To sum up: these measurements establish the fact that the relation
$$\frac{\text{length of primordium}}{\text{length of hydranth}}$$
 exhibits typical regional and polar differences. Considered as a fraction, the relation reaches its maximum value, about 1.5, in oral structures at the extreme distal end of the stem: its value is less in aboral than in oral structures and even decreases below unity in aboral structures at the proximal end of long stems.

Comparison of these results with the preceding section shows that

the regional and polar changes in the relation $\frac{\text{length of primordium}}{\text{length of hydranth}}$ run parallel to the changes in total length of the primordium and size of the hydranth. It follows that the smaller the hydranth which is produced in a given case the less the reduction in length from the primordium to the hydranth. In the case of very small hydranths (Series 68, Table III) the reduction may be changed to an increase in length. It becomes evident at once that these differences in the primordium-hydranth relation are due simply to the fact that hydranths of very different sizes go through their development enclosed in a cylinder — the perisarc — of nearly uniform diameter.

When the hydranth emerges from the perisarc it undergoes a greater or less change in shape. In every case where the diameter of the hydranth immediately after emergence is greater than the diameter of the stem this change consists in a decrease in length and an increase in diameter. But the diameter of all hydranths except very small ones is greater than that of the stem, and that of very large hydranths is several times the stem-diameter; therefore the reduction in length must be greatest in the case of large hydranths and must decrease with decreasing size of the hydranth until in cases where the diameter of the hydranth immediately after emergence is less than that of the stem. The fact that the hydranth develops in a cylindrical tube of almost uniform diameter determines that the primordium is »too long« in the case of large hydranths and »too short« in the case of very small ones.

The metamorphosis of the primordium into the hydranth may be regarded, at least in part, as essentially a regulation; the hydranth is not simply distorted so as to fit into the perisarc. The whole process of change in form is fundamentally functional in character; as the internal conditions change during development the form changes, but this change is not complete until some time after the hydranth has emerged from the perisarc and is functioning as a fully developed hydranth. The changes are due to the fact that the hydranth is a functional system of different character from the primordium.

II. The Proportions of the Hydranths after Emergence.

Measurements of the hydranths after emergence is more difficult than measurement of the primordia because of the changes in length of the various parts. In the measurements which form the basis of

the following tables great care was taken to measure the fully extended condition in every case. All hydranths were measured 12 to 24 hours after emergence.

The tables are based on the measurements of 163 hydranths from different regions. In each case the length of the proximal and distal tentacles the diameter of the hydranth and the length of the hydranth from the constriction where it joins the stem to the tip of the manubrium were measured. The absolute lengths of the different parts possess no special interest except as a basis for examining the proportions and are therefore not given. In order to determine whether typical differences in proportion exist among the hydranths the length of the hydranth was taken as the basis (100%) of calculation and the measurements of the other parts were reduced to percentages of the length. Tables IV, V, VI, VII give these percentages, i. e., relative lengths of the different parts for the various groups.

Table IV.
Original hydranths present when colonies collected.

Series	Number of hydranths	Proximal tentacles	Distal hydranths	Diameter	Length
28	7	159.3 %	51.8 %	70.4 %	100 %
41	10	183.3 -	45.7 -	58.3 -	100 -
42	9	186.4 -	45.4 -	63.6 -	100 -
Average = Totals of all absolute measurements divided by number of hydranths and reduced to % of average length		176 %	47.5 %	63.2 %	100 %

Table V.
Regulatory oral hydranths from extreme distal end of stem.

Series	Number of hydranths	Proximal tentacles	Distal tentacles	Diameter	Length
68 a	8	175 %	36.3 %	56.2 %	100 %
69 a	8	235.3 -	37.3 -	58.8 -	100 -
70 a	8	193.3 -	33.3 -	60 -	100 -
35 a	20	191.7 -	34 -	58.3 -	100 -
Average = Totals of all absolute measurements divided by number of hydranths and reduced to % of average length		197.2 %	35 %	58 %	100 %

Table VI.
Regulatory oral hydranths from other levels of the stem.

Series	Number of hydranths	Distance from distal end	Proximal tentacles	Distal tentacles	Diameter	Length
68 b	8	25 mm.	172.7 0/0	36.4 0/0	54.5 0/0	100 0/0
69 b	8	20 -	246.1 -	38.5 -	69.2 -	100 -
70 b	7	20 -	233.3 -	33 -	58.3 -	100 -
35 b	20	10 -	180 -	30 -	60 -	100 -

Table VII.
Regulatory aboral hydranths.

Series	Number of hydranths	Distance from distal end	Proximal tentacles	Distal tentacles	Diameter	Length
68 b	8	50 mm	175 0/0	25 0/0	62.5 0/0	100 0/0
68 a	5	25 -	200 -	30 -	60 -	100 -
35 b	10	20 -	157 -	28.6 -	71.4 -	100 -
37 and 38	17	15 -	162 -	24 -	59.5 -	100 -
35 a	10	10 -	137.5 -	25 -	62.5 -	100 -

From examination of the tables it is evident at once that the proportions of the hydranths and especially the proximal tentacles are highly variable. It is therefore unsafe to draw conclusions except from the most general and constant features of the tables. The most characteristic difference in the tables is that the distal tentacles of the original oral hydranths (Table IV) are relatively much longer than those in any of the regulatory hydranths. This difference may of course be merely a matter of age or may be due to other considerations, but in any case indicates a difference in functional condition.

Secondly, the distal tentacles are relatively much shorter in the aboral hydranths, whatever the level (Table VII), than in the oral hydranths (Tables V and VI); such differences do not, however, appear to be correlated with differences in level (Table VII). The proximal tentacles appear to be relatively shorter in aboral hydranths (Table VII) than in oral hydranths (Tables V and VI). The relation $\frac{\text{diameter}}{\text{length}}$ does not vary greatly in any case. If the tables can be trusted on this point it is slightly greater, i. e., the diameter is slightly greater relatively in aboral (Table VII) than in oral hydranths (Tables V and VI).

According to the tables then the differences in proportion in the hydranths appear to be polar rather than regional. But perhaps the most interesting point of all is the fact that the tables show no trace of the differences in relative length of the tentacles corresponding to the regional and polar differences in length of the tentacle-areas discussed in the preceding paper (CHILD, '07b). If these differences in proportion were transmitted to the hydranth, the tables should show relatively greater length of both sets of tentacles in aboral as compared with oral hydranths and in hydranths from more proximal levels as compared with those from the extreme distal end. No such differences appear, however, the tentacles being apparently relatively shorter in aboral than in oral hydranths. The tables certainly justify the conclusion that such regional or polar differences of proportion as exist in the hydranths differ from those in the primordium: they are in fact to a certain extent in the reverse direction. In short, the regional and polar differences in proportion in primordia and hydranths are not parallel.

How shall we interpret these facts? Teleological hypotheses afford little assistance here. On the other hand it is evident that the proportions of both primordia and hydranths are determined by the conditions under which each exists. The hydranth is functionally a different system from the primordium and with the change from primordium to hydranth a functional regulation occurs which is expressed not only in the different proportions of the one as compared with the other but also in the differences as regards change in proportions with change in position.

If these observations are correct, we must admit that oral and aboral hydranths, for example, differ typically in proportions: furthermore since they arise from primordia which also differ in proportions from each other and in different directions from the hydranths we must conclude that the process of hydranth-development is different in the two cases. In general then the process of hydranth-development as well as its result differs typically with regional and polar differences in position. In this fact we have the strongest indication that development of form and structure is essentially the activity of a dynamic system working in a given environment, or physiologically speaking the form and proportions of both primordium and hydranth are the functional products of a physiological system.

Summary.

1) In the metamorphosis of the primordium into the hydranth a change in length occurs. In oral hydranths from the extreme distal end of the stem the length is 35% less than that of the primordium. The reduction in length is less in aboral than in oral structures from the same level and decreases in both oral and aboral structures with increasing distance from the distal end, until in aboral structures from the extreme proximal ends of long stems the length of the hydranth may be greater than that of the primordium instead of less.

2) These changes of length between primordium and hydranth show regional and polar differences parallel to the differences in size of the hydranth and are due chiefly to the fact that hydranths of very different size arise from primordia which develop within a cylinder, the perisarc, which differs only slightly in diameter in different regions.

3) The proportions of the hydranths after emergence differ with polar differences in position and probably also to some extent with regional differences in position. These differences in proportion of the hydranths are not parallel to the regional and polar differences in proportions of the primordia but are in part in the reverse direction.

4) The absence of parallelism in the regional and polar differences in proportion of primordia and hydranths is due to the fact that the two are different functional systems and that the factors determining the proportions differ at least quantitatively in the two systems.

Hull Zoological Laboratory, University of Chicago,
January, 1907.

Zusammenfassung:

1) Bei der Verwandlung des Primordiums in die Hydrante tritt eine Längenänderung auf. Bei oralen Hydranten vom äußersten distalen Stammende beträgt die Länge 35% weniger als die des Primordiums. Die Längenreduktion ist bei aboralen Bildungen geringer als bei oralen aus demselben Niveau und nimmt bei beiden, oralen und aboralen Bildungen, mit der wachsenden Entfernung vom distalen Ende ab, bis schließlich bei aboralen Strukturen von den äußersten proximalen Enden langer Stämme die Hydrantenlänge möglicherweise größer ist als die des Primordiums, anstatt geringer.

2) Diese Längenänderungen zwischen Primordium und Hydrante zeigen regionäre und polare Unterschiede parallel mit den Verschiedenheiten der Hydrantengröße und beruhen wesentlich auf dem Umstand, daß Hydranten sehr

verschiedener Größe von Primordien sich erheben, welche sich im Bereiche eines Perisarkcyinders entwickeln, der in verschiedenen Bezirken nur unbedeutende Durchmesserunterschiede zeigt.

3) Die Proportionen der Hydranten nach ihrem Auftauchen unterscheiden sich durch polare Verschiedenheiten und wahrscheinlich auch in gewissem Grade durch regionäre Verschiedenheiten in ihrer Stellung. Diese Proportionsunterschiede der Hydranten gehen den entsprechenden der Primordia nicht parallel, sondern verlaufen zum Teil in umgekehrter Richtung.

4) Das Fehlen der Übereinstimmung in den regionären und polaren Proportionsunterschieden bei Primordien und Hydranten beruht auf dem Umstand, daß die beiden verschiedene funktionelle Systeme darstellen, und daß die die Proportionen bestimmenden Faktoren mindestens quantitativ bei den beiden Systemen verschieden sind.

Bibliography.

- CHILD, C. M. '07a. An Analysis of Form-Regulation in Tubularia. I. Stolon-Formation and Polarity. Arch. f. Entw.-Mech. Bd. XXIII. H. 3. 1907.
 — '07b. An Analysis of Form-Regulation in Tubularia. II. Differences in Proportion in the Primordia. Arch. f. Entw.-Mech. Bd. XXIII. H. 3. 1907.
 DRIESCH, H. '99. Studien über das Regulationsvermögen der Organismen. 2. Quantitative Regulationen bei der Reparation der Tubularia. Arch. f. Entw.-Mech. Bd. IX. H. 1. 1899.
 MORGAN, T. H., and N. M. STEVENS. '04. Experiments on Polarity in Tubularia. Journ. Exp. Zool. Vol. I. No. 4. 1904.
-