REGENERATION IN AN EARTHWORM, EISENIA FOETIDA (SAVIGNY) 1826. I. ANTERIOR REGENERATION

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These contributions present the results of an attempt to obtain for one particular species of earthworm complete characterization of regenerative capacity with reference to exact levels. In this part anterior regeneration, by posterior substrates only, is considered.

SUMMARY OF PREVIOUS WORK

Information available as to the morphological nature and segmental constitution of anterior regenerates on posterior substrates is summarized, with certain reservations, in Table I.

In earlier work on *E. foetida*, as well as other species of earthworms, determination of morphological nature of regenerates seemed unnecessary. Later, Michel (1898, p. 283), recalling Bonnet's heteromorphic tails in aquatic Oligochaeta, suggested that two of his own anterior regenerates, as well as some of those of Joest and Rievel, were caudal. Although anterior heteromorphosis was definitely confirmed by Morgan (1899) no attempt was made then or since to clarify the situation, and in particular to determine the limits of homomorphic head and heteromorphic tail regeneration.

The consequent uncertainty as to morphological nature of regenerates at a considerable number of levels and even as to the levels (because of postregeneration estimation), as well as absence of data for numbers of levels and paucity at other levels, indicated the advisability of a systematic investigation of regeneration at each level from ½ posteriorly.

MATERIALS AND METHODS

Material was first secured from a heap of decaying leaves, later from manure heaps. Worms were kept in moist filter paper or paper towelling until the gut was cleared. Individuals with any indication of damage by collecting, disease, abnormality, homoeosis or previous regeneration were rigorously rejected, and only those which were clitellate, or which had been clitellate when brought into the laboratory, were used. Animals were kept throughout at ordinary room temperature, which in winter probably was never above 68° F.

Anaesthesia was brought about in 0.2 per cent chloretone. Transections were made under a dissecting binocular microscope exactly across the animal on an intersegmental furrow.

After operation worms were placed in water until recovery from anaesthetic and were then transferred to filter paper, paper towelling, or cheesecloth. On several

TABLE I

Anterior regeneration in Eisenia foetida

Level	Regenerate — Cephalic Number of segments							*Uncertain	Caudal	None	Comments	Author	Date	Page
	2	3	4	5	6	7	?							
1/2											See note (a)	··		
2/3	6											Morgan	1895	447
3/4	5	9										Morgan	1895	447
	4	1										Michel	1898	261
4/5	1	8	5									Morgan	1895	448
		1										Hescheler	1896	228
	3	10	1									Michel	1898	262
5/6		2	3								See note (b)	Morgan	1895	448
	1	8	5									Hescheler	1896	228–31
			1	1								Michel	1898	268
EL		5	5	1							See notes (c) (d)	Morgan	1895	453
6/7		2	3									Hescheler	1896	228
EL	1	4	6	1								Morgan	1895	453–6
7/8		1										Hescheler	1896	228
							1				See note (e)	Michel	1898	262
EL		1	9									Morgan	1895	453
8/9			1	3	1							Michel	1898	262
EL	1	3	5	1								Morgan	1895	455
9/10 EL	1	1		3								Morgan	1895	453–6
10/11			3					1			U = "Imp"	Morgan	1895	451
			2	5	3							Carpenter	1948	625–6
EL					1							Morgan	1895	455
11/12			3	1								Michel	1898	263
EL			1	1				1			U = "2 (or three very imperfect)"	Morgan	1895	456
12/13		1		2	1							Morgan	1895	451–6
	1	1		1							U:S = indistinct	Michel	1898	263
							2	1	0	0	100–0–0%	Dimon	1904	350
EL		1										Morgan	1895	456
13/14 EL		1										Morgan	1895	456
14/15			1									Morgan	1895	451
							10		0	0	100–0–0%	Dimon	1904	350

TABLE I—*Continued*

Level	*2	3	4	5	6	7	?	* Uncertain	Caudal	None	Comments	Author	Date	Page
15/16 EL							22 3	 4	2# 1?	0 5	92-8-0% ?="possibly a new tail"	Dimon Morgan	1904 1902	350 579
16/17 EL							11	 2	1#	0	92-8-0% 3-4 S, "not regenerated (mouth present)" (See note (f))	Dimon Morgan	1904 1895	350 455
17/18							12		1#	0	92-8-0%	Dimon	1904	350
18/19							26		5#	2	79-15-6%	Dimon	1904	350
19/20							 3	1 ?#	 ?		U="4 or 5 S" See note (g)	Morgan Dimon	1895 1904	451 350
20/21 EL									1		17 S See note (h)	Morgan	1899	409
?							4		7#	12	17-30.5-52.5% See note (g)	Dimon	1904	350
22/23								2			Very imperfect	Morgan	1895	452
23/24 EL								1 1			Very imperfect 3 or 4 S, imperfect	Morgan Morgan	1895 1895	452 456
24/25								2			See note (h)	Morgan	1897	574
EL 25/26								1	1		T = 17 S See notes (h) and (i)	Morgan	1899	40
EL 30/31								1	1		H = 7 or 8 S See note (h) T = 21 S	Morgan	1899	408
EL 34/35			1									Morgan	1901	7, Fig. G
EL 35/36									1		(L 63 S) T = 15+S See notes (h) and (i)	Morgan	1895	455
L 75 S									1		35 S	Morgan	1899	409
EL 50/51			1					 2	 14	 15	 T = 5-25 S	Morgan Morgan	1901 1902	7, Fig. H 579

TABLE I—*Continued*

Level	Regenerate										Comments	Author	Date	Page
	Cephalic Number of segments							*Uncertain	Caudal	None				
	2	3	4	5	6	7	?							
L20S										5		Michel	1898	263
L10S										5		Michel	1898	263
L5S										5		Michel	1898	263
L12-7S										98		Morgan	1897	575-6

NOTES TO TABLE I

(a) "Attempts made to cut off 1 and 2 segments" (Morgan, 1895, p. 449). As a result of confusion re numbering of containers there was but one case in which it was thought "one segment must have been cut off" and that specimen could have been a posterior homoeotic.

(b) The last two specimens in Morgan's Table IV were homoeotic and are here excluded. The three specimens next above are assumed to have been normal. (Homoeotics are excluded here, as well as from author's operations, to obviate possibility of complications resulting from a previous regeneration and because gradients cannot be expected to be the same as in normal specimens.)

(c) Amputations, apparently as a result of operating without anaesthesia, were often diagonal (Morgan, 1895, p. 457, also Korschelt), or if transverse then at an intra- rather than intersegmental level. In each case a portion of a segment is treated as if a whole segment, i.e. if $10\frac{1}{4}$ or $10\frac{1}{2}$ segments were removed from the anterior end, the level of regeneration is still considered to be 10/11. In favor of this convention is Morgan's conclusion, after study of deliberately made very diagonal cuts, that simultaneous completion of missing parts of segments did not interfere with replacement of those metameres that had been completely amputated (1895, p. 457).

(d) EL estimated level. Level of amputation in many operations was estimated *after* regeneration and from one of the following landmarks (Morgan, 1895, pp. 450 and 452): (1) Position of vasa deferentia, i.e. location of male pores. Subject to variation of six segmental levels (Morgan, 1895, p. 403). (2) Location of seminal receptacles, apparently thought to be three pairs. *Eisenia foetida* has only two pairs of spermathecae but four pairs of seminal vesicles. These landmarks are doubtful. [If three pairs of spermathecae were present another species was involved, possibly *Dendrobaena octaedra* (Savigny) 1826 or *Allolobophora chlorotica* (Savigny) 1826, both of which are found in compost heaps and apparently have been confused with *foetida*.] (3) Location of clitellum. That may begin on any of segments xxiv-xxvii and end on xxxi-xxxiv, a variation of three to four levels. Pre-clitellar amputation was variously listed as at 20/21, 25/26, and postclitellar as at 25/26, 30/31, 35/36. (4) and (5) The middle and the end of the body, the former regarded as at 50/51 and the latter as the hundredth segment. Number of segments varies from 67-125.

Actual variations, when recognizable, were: for (3) of seven segmental levels, i.e. 19/20-26/27 and 31/32-38/39, for (4) and (5) to about 20 levels, 41/42-64/65, etc.

Postregeneration determination of level of amputation would probably render unlikely detection of reorganization of substrate segments. Such reorganization, in some species, could affect the determination by one to three segmental levels.

In certain of Morgan's cases it is not clear whether levels mentioned were determined or estimated.

(e) Number of segments of other regenerates at this level "très variable."

(f) The regenerate segments were "very irregular." The characterization "not regenerated

occasions when the supply of cloth had been exhausted, worms were kept in large crystallizing dishes in water just sufficient to cover the bottom and keep the animals moist. Although *E. foetida* appeared to do as well in water, in cool weather, as in moist cloth, the method is not recommended, for in later work several long series of operated animals were completely lost over night. To prevent accumulation of metabolic wastes, water or paper was changed (or cloth washed) daily, except on Sunday when the museum was closed.

Specimens were killed so as to insure uniform contraction and were then preserved in formalin.

The experiments were carried out mainly during a sabbatical leave in the States in 1926–27. Shortly before Japan entered the war, a summary of the results obtained was prepared and sent home from Burma. Original records, as well as specimens, were lost in the sack of Rangoon.

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NOMENCLATURE

In one and the same article, an author once used "posterior end" to refer to: a posterior regenerate regardless of size; an anterior regenerate (heteromorphic); the anal region of an adult worm; and long posterior portions of varying lengths up to a half or more of adult size. Similarly "anterior end" has had various meanings, including even that of tail (heteromorphic). Most confusing, however, has been a failure to distinguish adequately in discussions between the regeneration taking place at a single surface of amputation and that taking place at exactly the same level when there are two cut surfaces. In an attempt to avoid further complications, an effort has been made to restrict terms and phrases consistently to the meanings given herewith.

(mouth present)" may refer to an anally sculptured cicatrix. Such sculpturing may be preliminary to growth of a tail regenerate.

(g) Results of all operations behind 18/19, were lumped together. Mention was, however, made of three "B" heads at 19/20 which have also been listed above at that level.

(h) No data as to number of segments in 1897 regenerates (Morgan, pp. 573–574) and no clues to warrant guesses as to nature of regenerates.

(i) Results of 30 operations (Morgan, 1902, pp. 578–579) omitted because of uncertainty: (1) as to level of operation, said to have been "just behind the girdle (about the 25th segment)," i.e. either at 25/26 or 34/35; (2) as to nature of substrate, i.e. whether posterior or a two-surfaced fragment. Three months after operation, four specimens having died, the container had 36 specimens which were not examined for autotomy. *Nevertheless*, presence of one distinct new head and 14 doubtful regenerates, of which "probably more were heads than tails" may be of considerable importance.

Presence of extra worms in containers may have another explanation than autotomy. Just hatched juveniles are exceedingly difficult to find in either manure or soil. In absence of sterilization of the manure used for culture medium, there was time, during the months allowed for regeneration, for young to attain adult size. In this connection a belief that regenerates became indistinguishable from substrates is perhaps important (Morgan, 1895, p. 424).

⧧ Regenerates referred to this class by Dimon were not characterized in any way. *Some "doubtful" regenerates of other authors are also included here. Others, that appear also to be doubtful, have been included in part.

In place of regenerant and regenerate, which are easily confused, *substrate* and *regenerate* are used respectively, to designate the portion of the original worm on which the new growth is formed and the new growth thus formed at the cut surface. This is in continuation of previous practice (Gates, 1941).

Posterior substrate refers to any posterior portion of the body, regardless of size, extending forward from the anal region to a single anterior cut surface.

Healing after amputation may be *cicatricial* or *enteroparietal*. In the first, a cicatrix is formed across the cut surface, while in the second, cut edges of gut and body wall apparently heal together without definitely recognizable cicatricial tissue.

A regenerate with no externally recognizable differentiation is a *bud* (indeterminate). As indications of buccal or anal sculpturing become recognizable, further characterization as cephalic or caudal is possible. With appearance of metameric differentiation the regenerate is a head or a tail.

A considerable degree of deviation from normal structure may be possible in a regenerate without affecting its caudal or cephalic nature. Such variant regenerates are abnormal. A regenerate without cephalic or caudal characteristics, or with a mixture of cephalic and caudal characteristics, or with bifurcations, is a *monstrosity*. A growth without indication of caudal or cephalic nature is an indeterminate monstrosity.

A metamerically normal regenerate may be *equimeric, hypermeric,* or *hypomeric,* depending on whether it has the same number of segments, more than, or fewer than the excised portion.

Heteromorphosis indicates a more or less normal structure in a reversed or abnormal direction. A head at a posterior amputation and a tail at an anterior amputation is heteromorphic. Homomorphic distinguishes the head or tail in normal position or direction.

Levels are designated in two ways, by reference to the segments, as xxvi, and to the furrows bounding the segment as 25/26 and 26/27. The Roman numeral in lower case means the twenty-sixth segment beginning with the buccal as i; the prostomium of the Oligochaeta is not counted as a segment. The fractions refer to the intersegmental furrow at the anterior and posterior margin of segment xxvi, and make possible, with shorthand brevity, exact designation of level. Indication of level of amputation merely by reference to the segment, as "at the twenty-sixth segment," may be inadequate unless the context indicates which of the two possible levels, anterior or posterior, is involved. EL before the fraction means *estimated level,* the estimate usually that of the original author, otherwise made in accordance with his custom so far as is possible.

The anal region of the body forward to the first complete intersegmental furrow is not regarded as an ordinary metamere but for purposes of segmental enumeration is taken as one segment (see Gates, 1948). Posterior substrates of unknown location with reference to the antero-posterior axis are characterized by a designation such as L14S, in that case meaning the last fourteen segments.

Homoeosis, as ordinarily used in connection with earthworms, means: presence of an organ or pair of organs, or a series of organs, in a segment or series of segments, other than that, or those, in which usually or normally found. It refers primarily to individual variation within a species; secondarily, to phylogenetic variation, for a species or a genus may be homoeotic with reference to other species in the genus, or other genera in the family. In case of individual homoeosis, the dislocation may involve one or both organs of a pair in a segment. The former is asymmetrical homoeosis, the latter symmetrical.

Summary of Results

Healing at cuts in an anterior portion of the body was cicatricial, the cicatrix a low, flat-surfaced, circular disc without recognizable sculpturing. In some specimens no further development was recognizable. In others the cicatricial disc gradually was protruded as a small, rather conical bud at first apparently unmarked by any sculpturing. In several cases the growth of the bud was inhibited at that stage. In the remainder the distal portion became sculptured to indicate a prostomium and mouth. Intersegmental furrows, setae, and finally pigment usually became recognizable in that order.

Regenerates always remained distinguishable from substrates by differences in pigmentation, segment size, setal intervals, etc.

Several months' starvation resulted in reduction of size of substrates but no macroscopically recognizable reorganization was noted, either externally or internally, behind the level of amputation.

Reproductive organs were not found, in regenerate or (as result of reorganization) in substrate.

A. After a single cut

All substrates with cut surfaces at levels from 8/9 anteriorly, with one exception, regenerated. At each level behind 8/9 one or more of the substrates did not survive operation long enough to regenerate or else failed to regenerate if surviving. Highest percentages of failure to regenerate were in the region around 25/26. Further posteriorly, survival was better and percentages of successful regeneration higher. Results just mentioned were, however, minimal, as inhibited buds, rare monstrosities (indeterminate) and certain conditions to be considered later on were recorded as failures (to produce a more or less normal head or tail).

Head regenerates were obtained at levels 1/2–23/24 only. Equimeric heads were obtained at levels 1/2–8/9 inclusive. Three regenerates at 4/5 were hypermeric (+ 1). All head regenerates at levels 9/10–23/24 were hypomeric, the maximum number of segments obtained being six. In a later series of operations, E43, of three head regenerates at 8/9, one had five, another had six, and a third had nine and a half segments, the half segment wedge-shaped and on the right side (+ 1½).

Heteromorphic tail regenerates were obtained, once each at levels 20/21 and 23/24, and from 24/25 to 54/55. The largest number of setigerous segments differentiated in such heteromorphic tails was 25 at 40/41, the evidence available indicating increase in number of segments posteriorly to 40/41 and then a decrease.

At levels behind 54/55 no regeneration whatever, including even buds and monstrosities, was obtained though numbers of substrates were under observation three to four months.

B. After a previous regeneration

In attempts to test for the effects of previous regeneration on anterior regeneration, several series of operations were made of which the following are mentioned.

In series E41 posterior portions were removed at 34/35 and 35/36 and the substrates (anterior) were allowed to regenerate for twenty-three days. At that time the anterior eight segments were removed and discarded. Of the surviving substrates (8/9–34/35 or 35/36 + a tail regenerate), four regenerated heads anteriorly. Three were hypomeric with six segments each, and one was hypermeric with nine segments (+ 1).

In series E58 the last ten segments were removed from specimens having one hundred or more segments. At the end of twenty-two days' regeneration, anterior portions were removed so as to leave ten or fifteen segments of the original substrates along with the tail regenerates. One of these small substrates had already produced a bud at the anterior cut surface by the seventh day, at which time circumstances compelled termination of the experiment. Anterior regeneration in

this series, would, if completed, have taken place at levels behind 75/76, while normal posterior substrates, unconditioned by a previous regeneration, failed to regenerate at levels behind 54/55.

In series E49 the posterior portion of the body was removed at 70/71. The anterior substrates were allowed to regenerate posteriorly for eighty days. At that time the tail regenerates were removed at the level of regeneration. One such tail regenerate, then acting as substrate, produced in twenty-seven days, at the anterior cut surface (level 70/71 with reference to location on axis of original worm), a heteromorphic tail, unpigmented but with six setigerous segments and a small anal region without indication of production of further segments. Final substrates in this series were 7 to 10 mm. long and of 30–41 setigerous segments.

C. After starvation

To test for the effect of starvation, the following experiment was run (see also series E49 above for regeneration after 80 days' starvation). From worms that had been starved for seventy days or longer, the anterior five or six segments were removed. Each surviving substrate regenerated a hypomeric head $(-1$ to $-3)$ with metameric differentiation complete and normal.

DISCUSSION

A first step towards obtaining a complete characterization of regenerative capacity in $E.$ foetida is determination of the morphological nature of the regenerate produced anteriorly, at each intersegmental level along the axis, by posterior substrates, as well as the number of segments in such regenerates. The latter, often neglected in the past apparently as of little importance, is of some interest with regard to morphogenesis in the Lumbricidae.

Hypermery in head regenerates has now been recorded for the first time in $E.$ foetida, and at two different levels, one of which, 8/9, is fairly well back. Hescheler (1896, p. 93) once secured a regenerate with more segments than had been removed but in a series of successive regenerations by a single individual, the worm even then still hypomeric by two segments (removal of $6\frac{1}{2}$ segments, regeneration of $5\frac{1}{2}$; removal of 4, regeneration of 2; removal of 2, regeneration of 3). One hitherto unnoticed case of hypermery in the Lumbricidae has been found—regeneration of four segments after removal of three by a specimen from which the nerve cord had been removed from the next two metameres behind the level of amputation (species unidentified, Goldfarb, 1909, p. 703, Table 4, No. 1.41).

Hypermeric regenerates are of especial interest in connection with the problem of the origin of posterior homoeosis. In $E.$ foetida posterior homoeosis of one segment only has been recorded and now in regenerates hypermery of one segment only. As all cases of symmetrical homoeosis in the species can now be considered to have resulted from hypomeric or hypermeric regeneration, postulation of some unknown embryonic cause is no longer necessary.

The new data as to segment number in homomorphic anterior regenerates provides confirmation of the cephalic nature of Michel's and Hescheler's regenerates of seven segments and of Morgan's regenerate of "7 or 8" segments, all of which seem to have been overlooked hitherto.

Presence in a head regenerate of nine segments may indicate a possibility of equimeric regeneration back to 9/10 but is of especial interest in connection with the problem of the constitution of the "head." In the Oligochaeta homomorphic anterior regeneration is generally thought to be restricted to replacement of the "head." The latter, in the Lumbricidae, has been thought to comprise five segments only. Six, seven, and eight (?)-segment head regenerates obtained by Michel and Morgan in *E. foetida* (Table I), and a six-segment regenerate at 9/10, as well as a seven-segment regenerate at 12/13 in *Allolobophora terrestris* (Hescheler, 1896), should have been taken into consideration in this connection. Carpenter's (1948) regenerates of six segments (Table I), and the author's of six to nine, show that regeneration of heads with more than five segments is not exceptionally rare. Smaller numbers in previous work may have been due to less favorable conditions.[1]

The maximum number of segments now recorded for head regenerates in the family Lumbricidae is nine. With the exception of one pair of seminal vesicles and of spermathecae, both of which develop in connection with septum 9/10, reproductive organs in the Lumbricidae are in the region from x posteriorly. All of the evidence available still indicates that Lumbricids regenerate anteriorly only a pregonadal portion of the body. Regeneration, after amputation of the gonadal region, accordingly, is not sufficiently "complete" to enable an individual to reproduce. Although this has often been thought to be characteristic of earthworms generally, at present it appears to be applicable only to the Lumbricidae. In those representatives of other families that have been studied, regeneration of the gonadal region not only is possible but even usual (see Janda, 1926, for the Glossoscolecid *Criodrilus lacuum*, and Gates, 1941, for the Megascolecid *Perionyx excavatus*). The pattern of regenerative capacity, even with regard to this one matter, accordingly, is not uniform throughout the earthworms.

Such data as are now available with regard to segment number, and in particular "7 or 8" segments in a head regenerate at EL 30/31 (Table I), do not appear to support current ideas as to decline in number of head segments regenerated as level of amputation recedes posteriorly (Hyman, 1940, p. 519) and gradient of head regeneration (Liebmann, 1943, p. 601, Fig. 12).

New data given above as to the morphological nature of anterior regenerates agree with some hitherto overlooked in showing a region of definite bipotential regenerative capacity. On amputation within that region a worm may regenerate either a head or a tail. The individual variation in response to the same stimulus suggests a possibility of experimental modification of the nature of regenerates.

The region of bipotential capacity, according to the author's results, is small and bounded by 20/21 and 23/24. Previous work indicates the possibility of considerable extension of those boundaries. Involved in estimation of the posterior limit of cephalic regeneration are two regenerates at EL 30/31 and EL 50/51 (Morgan, 1899 and 1901). Both, it is important to note, were obtained after rediscovery of heteromorphosis. The cephalic nature of the first was proved from sections. The second, having five metamerically normal segments, presumably was large enough to be easily and correctly identified. Level of the first amputation could have been from 31/32 to 38/39 (see note d, Table I), but was probably in re-

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[1] Carpenter now reports obtaining in one series, seven six-segment, two seven-segment, and one eight-segment head regenerates at 10/11.

gion of 32/33–35/36. The other amputation, estimated to be at the middle of the body, could have been from 41/42–64/65 (see note d, Table I), but with probability of location at or even in front of 41/42. A level about midway between 30/31 and 40/41, i.e., 35/36, appears at present to be as good an estimate as is possible in the circumstances.

The anterior boundary for heteromorphic tails is extended to 18/19 by Dimon's results (Table I). However, some of her "uncertain" regenerates at 17/18–15/16 presumably had, in absence of all reference to monstrosity, similarities to caudal regenerates. Morgan also had a regenerate at 15/16 thought to be "possibly a new tail" (1902, p. 579). All this seems to warrant placing the anterior boundary provisionally at 15/16. It is also noteworthy that at several still more anterior levels, to 10/11, some regenerates were "imperfect" or "very imperfect," characterizations apparently applied also to regenerates later found to be caudal.

Gradient of segment number in heteromorphic tail regeneration appears, from the author's data, to be of an inverted V-shape rather than the even slope apparently anticipated by Morgan (1902, p. 577) from results obtained on small fragments.

Failure, in the author's experiments, of normal worms to regenerate at levels behind 54/55 was unexpected in view of the results obtained from substrates as small as L14S in *A. terrestris* (Korschelt, 1898, p. 80). Regeneration by tail regenerates from levels behind 54/55 (E49), and behind that level by substrates conditioned by a previous regeneration (E58), suggests a possibility that failures on normal specimens were due to unfavorable conditions.

Regeneration of heteromorphic tails anterior to 20/21 and of heads behind that level, and more important, of both heads and tails from the same levels, does not appear to be in accordance with Liebmann's hypothesis (1943) that specifically polarized, eleocytic aggregates in the coelomic cavities, a head aggregate in v-xx and tail aggregates behind 20/21, determine the nature of the regenerate.

SUMMARY

Posterior substrates of *E. foetida*, cut exactly at intersegmental furrows, regenerated homomorphic heads at levels 1/2–23/24, with equimery at 1/2–8/9 and hypermery (+ 1) at 4/5 and 8/9. Heteromorphic tails regenerated at 20/21 and from 23/24 to 54/55. Behind 54/55, regeneration of heteromorphic tails was obtained only from tail regenerates and substrates conditioned by a previous regeneration. Gradient of segment number in heteromorphic tails appears to be of an inverted V-shape.

Starvation for 70 + days did not inhibit regeneration at 5/6 and 6/7 but all regenerates were hypomeric.

Hypermery and hypomery provide an adequate explanation of the origin of symmetrical homoeosis.

Regenerative capacity in a region from 20/21 to 23/24 is characterized as bipotential since an anterior regenerate, in that region, may be a homomorphic head or a heteromorphic tail.

Review of previous work on *E. foetida* provides indications that the region of bipotential regenerative capacity is even more extensive, with anterior limit of heteromorphosis possibly at or even in front of 15/16 and posterior limit of homomorphosis in region of 35/36.

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