(From the Marine Biological Laboratory at Plymouth, England.)

REGENERATION AND FRAGMENTATION IN THE SYLLIDIAN POLYCHAETES[1].

(STUDIES ON THE SYLLIDAE II).

By

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With 34 figures in the text.

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Contents.

Regeneration.

Regeneration takes place easily at the posterior end of divided Syllids, and the faculty for this regeneration is generally complete, i. e. it reconstructs all the missing parts, including the pygidium and the setigerous segments.

The external morphology of the growing tail is well illustrated in some of the papers already published, the figures in ALLEN's 1921 memoir (*Procerastea Halleziana*) being excellent. The chronological order of the regenerated segments can be followed easily in *Autolytus pictus*, as the regeneration cone of this species is darkly pigmented, and the subsequently

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[1] I take here the opportunity of expressing my gratitude to two gentlemen, Dr. E. J. ALLEN, the director of the Plymouth Laboratory and Prof. E. KORSCHELT of the University of Marburg, for their kind treatment during my visit to these two places of Europe, where I commenced and completed the work.

formed segments are without pigment. The first one of these segments to appear is in front of the pigmented tail cone, which is now the pygidium. It divides into two, a larger anterior and a smaller posterior portion. The anterior piece develops into the first setigerous segment of the regeneration, while the posterior piece elongates, and divides again into two. From the anterior of these two comes the second setigerous segment, and from the posterior the future third setigerous segment and the growth zone. Segmentation is repeated in the latter, and new formation of the segments is continued theoretically until all the number missing are restored. If this number be x, the prospective caudal regeneration can be expressed thus: $R_p = S_2 + S_3 + S_4 \ldots + S_{x-1} + S_x + S_1$, where S_x represents the last segment to be formed, which is always immediately anterior to the pygidium (S_1), the first segment of regeneration.

§ 1. *Problem of the Ectodermal Origin of the Regeneration Cells.*

In 1898 A. Michel published the results of his extensive "recherches sur la régénération chez les Annélides", including species belonging both to the Polychaetes and Oligochaetes. According to this work all the organs and tissues, except the endodermal derivatives, are re-established, at the time of regeneration, from those cells which have migrated secondarliy into the body cavity from the ectoderm, that is to say, reconstitution of new organs and tissues in the Annelids is entirely independent of their original differentiation from the three layers of the embryo. The value of this account seems, however, gradually to diminish in proportion to the increase of the same kind of work. W. R. Weitzmann's (1927) paper is, as far as I have seen, the latest, and the original view of metaplasia is, at the present time, only concerned with the caudal end of divided Polychaetes, the new septa and muscles of which according to E. Schultz (1899), P. Ivanov (1907 and 1908), T. Nusbaum (1905 and 1908) etc. are still found to be due to an activity of the ectodermal cells. H. Langhammer (1928) seems to hold the same opinion for the tail regeneration of *Procerastea Halleziana*. These organs and other mesodermal tissues in Oligochaetes are always, Weitzmann holds, regenerated from mesodermal elements, and here the secondary histogenesis does not disregard the primary differentiation from the three layers of embryonic development.

With such contradiction as to the process of regeneration between two groups of the same annulated animals, the Polychaetes and the Oligochaetes, it is worth while to describe some further precise observations upon the first phase of regeneration in Syllids, which I made in the course of the summer of 1927 in the Marine Biological Laboratory at Plymouth, England.

When a Syllid is divided, the wound closes almost instantly, except on cutting the most anterior part, when the chitinous tube and the massive proventriculus of the pharynx hinder the process of closing the wound, and subsequent regeneration in most cases fails, especially in the caudal direction (but not the head regeneration as will be shown later). However, the mechanism of wound-closure is not so simple as it looks on external examination. There is certainly a displacement of cells, as well as the approximation of the cut-edges due to the muscular contraction round the wound. Fusion takes place in the body wall and in the intestine respectively, but very often there is no real joining in the somatopleura and in the peritoneum. In the fused part, a number of the cells are evidently comparatively small and rich in protoplasm; vacuoles, secretion granules, and other metabolic products having entirely disappeared. Division figures become visible afterwards among them, but at the first phase of their appearance there is no trace of these. I am inclined, therefore, to regard these cells as displaced into the new site from the edges of the cut surface, rather than produced by the division of those of the edges. In relation to this movement, it is my opinion (Okada 1927, p. 531) that the cells become younger again, or in other words come back to their embryonic state. They are thus "rejuvenated", and the term embryonic is here employed in the sense that the cells become more vigorous than before. It is not claimed that they regain all the potential faculties of true embryonic development. There may be a different method or methods for the new-formation of the organs or tissues in regeneration, other than those which occur in the course of normal embryonic development, but it must be rare that organs or tissues of a different cell-nature, in such highly differentiated organism as the Annelids, are also produced.

The initial condition of a divided *Autolytus Edwarsi,* at 20 hours after the operation, is shown in Fig. 1, which represents a median longitudinal section. Based on this section, the length of the bridge-like tissue of the cicatrix measures as 0.06 mm in the wound of the ectoderm, and 0.08 mm in that of the endoderm, the former being made up of about 15 cells in a line and the latter of 10 cells. These cells are easily distinguished from those of the original tissue by the absence of the cuticular layer on the body wall, and the peritoneal membrane on the intestine. Moreover they are, as mentioned above, small and more deeply stained, and there are no metabolic products in them. Such a picture of the initial phase of regeneration could be observed in this species of *Autolytus* after from 20 to 30 hours, in the summer, when the room temperature was 12^0 to 19^0 C, but after that the segment showing kinesis (it is generally confined in the last segment, or at the most, extends to the posterior part of the last but one) was in a chaotic state, the freely wandering cells filling up its coelómic cavity. It beomes almost impossible to say from where these cells come, whether from the old septa or from the body wall. At the same time the intestine elongates backwards, and becomes closely applied to the inner surface of the body wall, the cells of which are also actively proliferating. In Fig. 3 we observe the cell-masses actually spreading out from the inner surface of the body wall towards the middle of the segmental cavity, as if their origin were in the ectoderm. Is not the proposed claim for an ectodermal origin of the new septa and segmental muscles of Polychaetes based upon this false view of the second phase of regeneration?

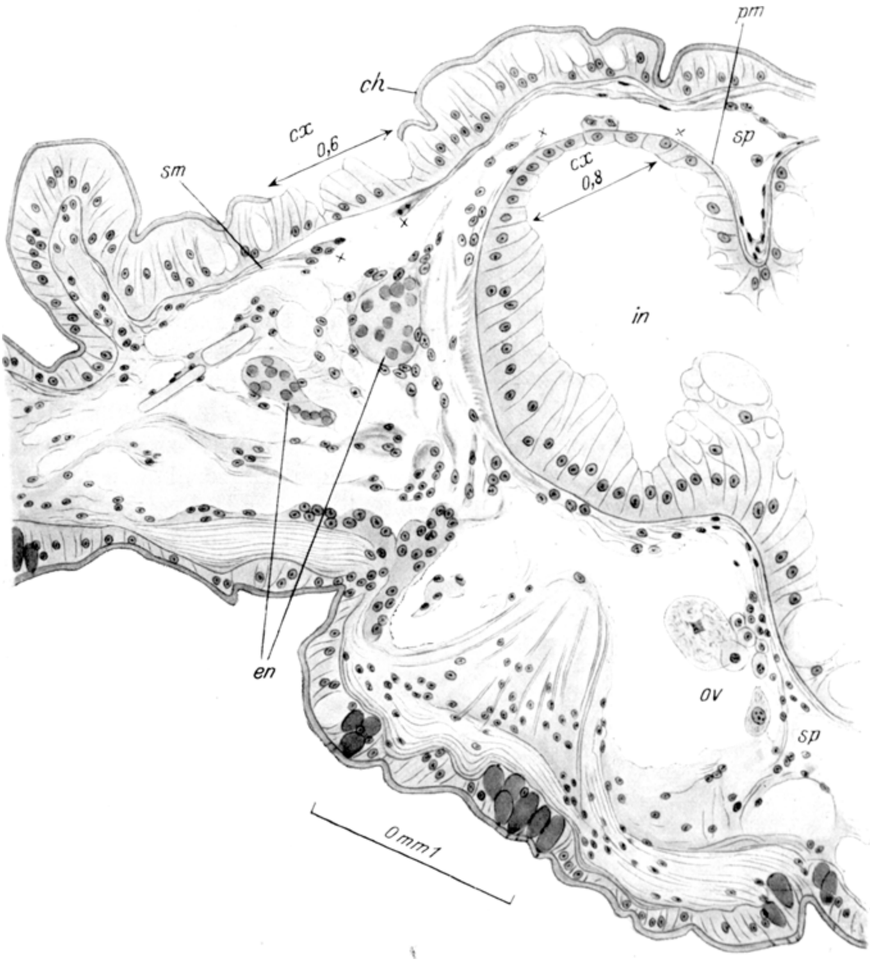

Fig. 1. Median longitudinal section of a segment, showing kinesis of regeneration (*Autolytus Edwarsi* DE ST. JOSEPH); condition 20 hours after the operation (August 10th — cut).

In the Syllid, there is also an ingrowth of the ectoderm cells on the ventral aspect of the regeneration-bud (fig. 3 and 4 b). These cells are, however, exclusively for the re-establishment of the nervous system of the new segments, while the mesodermal bands, which are already quite distinct on each side of the alimentary tract, show no trace of having any share in them. P. Ivanov, for exemple (1907, p. 6), states that "auf den darauf folgenden Stadien in der Entwicklung des Regenerates, beginnen von diesen Zellen aus einzelne Muskelfasern in die Leibeshöhle hineinzuwachsen, während einige der Zellen längs dieser Fasern selbst allmählich in die Leibeshöhle hineinwandern, was auf Querschnitten durch in der Entwicklung bereits etwas fortgeschrittene Segmente besonders deutlich zu sehen ist". But I wonder why he, and the other authors named above, do not regard the problematical muscle-fibres as being in a state of histolysis, instead of being in the histogenetic phase, as this process is frequently observed in such a case. As to this problem and the subsequent phenomena of Polychaet-regeneration, one of my friends, Prof. J. Morita of Ohsaka (Japan), has worked upon the same species of *Autolytus*, in the same Laboratory at Plymouth, during the summer of 1926, and is preparing a paper. A detailed description will, it is hoped, be given by him. Here, in the following, only an explanation of some figures is attempted.

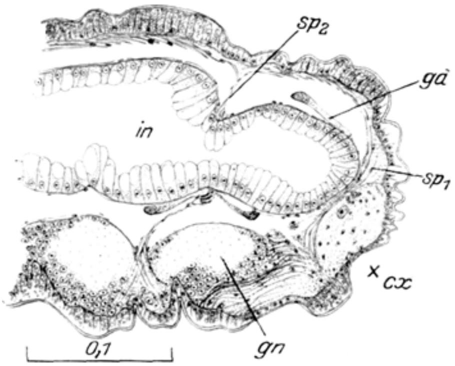

Fig. 2. Similer section to the preceding in a little wider range (*Autolytus Edwarsi* de St. Joseph); stage the same as before.

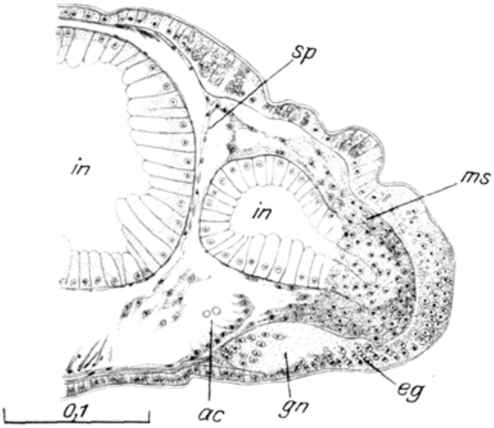

Fig. 3. Posterior end of a regeneration piece, 3 day old, shown in longitudinal section (*Autolytus Edwarsi* de St. Joseph); the mesodermal bands are forming.

Fig. 2 is a median longitudinal section of the last two segments of a divided *Autolytus*. It belongs to the same stage of regeneration as that of fig. 1. The plane of cutting in this example is believed to have passed immediately behind the septum of the last segment of the piece, because this organ is still distinctly seen, closely applied to the inner surface of the closed part of the wound, while fusion is complete at the end of the intestine, as well as in the body-wall. The free cells in question are just forming, and are seen inside the last septum. They do not arise between the septum and the body wall. In this case it would be almost impossible to suppose that the cells in question have migrated from the ectoderm, passing through the thickness of the septum.

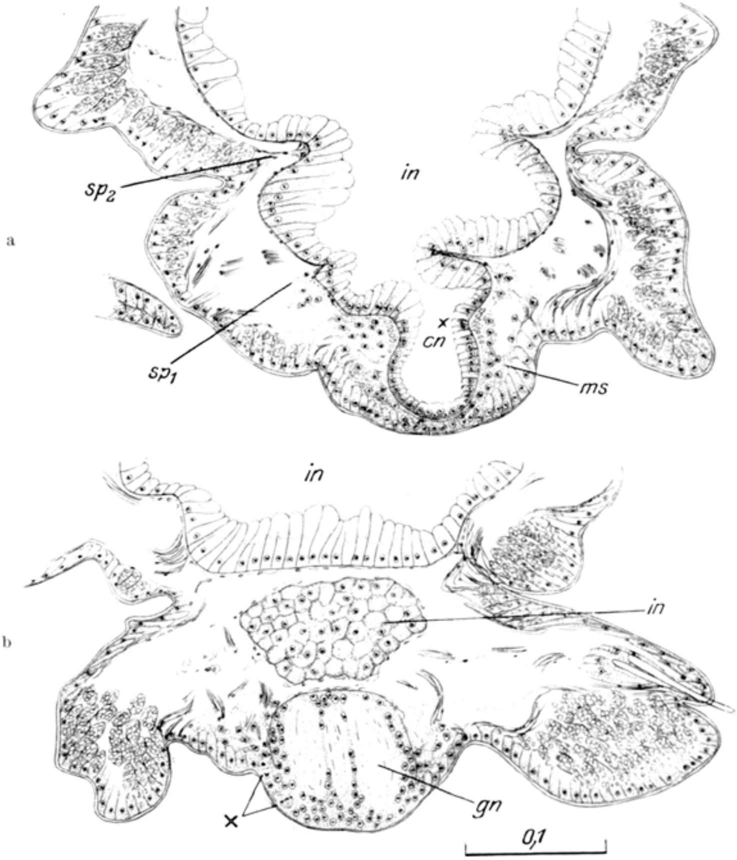

Fig. 4. Two horizontal views of the same stage of regeneration as in the preceding figure: a being upper, b lower in the position of the microscope slide.

Fig. 3 is a similiar section, but in an advanced stage (70 hour old), and at this stage we have already a pigment-free outgrowth from the closed surface of the wound. The embryonic mesodermal bands are established on each side of the intestine, spreading from the posterior extremity towards the middle of the segment, an additional number of the same sort of cells still being produced in front of them. Here we observe distinctly a hystolysis, which is taking place in the old septum, somatopleura and peritoneum of the last segment.

Fig. 4 shows two horizontal views of the same stage of regeneration as before, a, being upper, and b, the lower in the position of the microscope slide. In this example the cut seems to have been executed in the front part of the last segment, and the process of mesenchymatosis proceeds into the penultimate segment, but it is confined to the posterior part of that segment. There are no free cells in the anterior half of this same segment. The intestine, found in the last segment, is constricted in the middle (this is one of the characteristics features in regeneration), and in its hinder section the cells are evidently small and dense with protoplasm; these are concerned with the elongation of the structure into the new segments. On the ventral aspect of this part of the intestine, the ectoderm of the body wall is especially thick, and its cells are proliferating and supplying the new cells inwards. The cut end of the nerve does not itself grow.

Fig. 5, b, will show the process of segmentation in the mesodermal bands to form new segments. It is drawn from a horizontal section of a 5-day-old specimen, the external morphalogy of which is represented in the same figure (a). The caudal cirri are seen, as a round protuberance on each side of the posterior extremity of the regeneration cone, which is scarcely segmented in the external view. The caudal cirri do not as yet contain any mesodermal element. The anus begins to open. There is no proctodeal invagination at all, the posterior end of the intestine (endoderm) passing directly thraugh from the inside to the outside. The most important change at this stage is without doubt the establishment of new segments. However, I think this requires no description, as the fact is an exact repetition of the normal embryonic process, and is also the same as in the regeneration of other Polychaetes, as well as of Oligochaetes. It needs only be mentioned that the gonads and nephridia do not have a separate origin from the septa and segmental muscles. They are all mesodermal and regenerated all from the same source of rejuvenarated cells.

Thus the caudal regeneration of Syllids is started from the bridge-like tissue of the cut-edges, and in this case the process is largely due to a further rejuvenscence of the cells around the wound; the subsequent outgrowth is brought about by their proliferation by division. There is at the same time an ingrowth or migration of the ectodermal cells from the body wall, but this ingrowth is only for the re-establishment of the nervous system. The intestine of the last segment is first constricted in the middle and afterwards in the hinder section, by the rejuvanated cells, and then elongates directly backwards and passes through the body wall, from the inside outwards. No proctodeal invagination, therefore, occurs here. All the mesodermic tissues can be mesenchymatized, and from these cells the mesodermal bands arise *de novo* on each side of the intestine, as in embryonic development. They spread out from behind forwards, and then divide from before backwards, thus providing new segments one after the other, in the same embryonic order. The bands, when forming, receive no contribution from the ectoderm, and the organs and tissues produced, the septa, the muscles, the nephridia etc., are exclusively mesodermal. There is no evidence of separate formation of the reproductive organs from the septa. As a whole there is no trace of metaplasia in the regeneration of Syllids — a result in entire accordance with the case of Oligochaetes. This account, however, does not agree with the facts described as to the regeneration of certain structures in other Polychaetes.

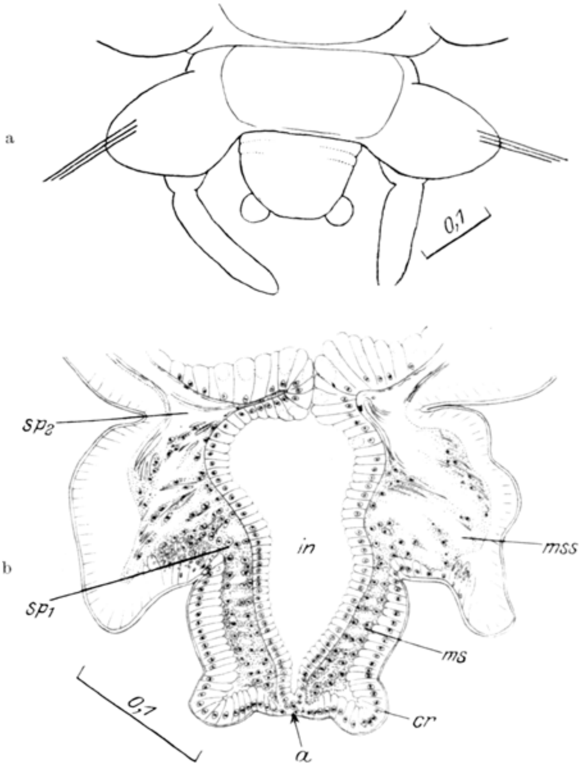

Fig. 5. a Ventral, external view of the new tail of 5 day old *Autolytus Edwarsi* DE ST. JOSEPH and b horizontal section of it; segmentation is going on, on each side of the elongated intestine in the new mesodermal bands, while mesenchymatosis is still taking place in front of them in the cavity of the old segment.

§ 2. Separated Formation of the Right and Left Side of the Segments.

In schizogamy, after the separation of the stolon, the posterior segments are restored with great rapidity. The process is generally the simple regeneration just considered. Sometimes a certain number of the new segments have been formed before the first stolon swims away. At other times two separate, half rudiments first grow out of the parent stock, and unite later to form a complete median tail rudiment. This remarkable process of regeneration was first described by MARION and BOBRETSKY, in 1875, in *Trypanosyllis Krohnii* of Marseilles. Doubt has been thrown upon this part of their account by G. PRUVOT (1890) and C. VIGUER (1902), but A. MICHEL (1909) not only confirms the observation in *Trypanosyllis zebra*, but demonstrates the occurance of the same phenomenon in *Syllis vittata*, *Syllis prolifera* and *Syllis cirropunctata*. A. MALAQUIN (1893) seems also to have observed the phenomenon in *Syllis variegata*, as he has drawn two pairs of tentacular cirri on the growing head of the *Chaetosyllis* "encore attaché à la mère" (see his pl. X, fig. 22).

Reconstitution of the hinder segments in these Syllids takes place before the first stolon separates off, and may proceed so far that its length, on the ventral surface, gives the appearance of a "*cauda bifida*" of the animal. The first phase of development of this second tail is represented by two semi-rudiments, lying transversely across the ventral surface, between the parapodia of the parent stock and those of the head-bearing segment of the stolon. They are joined at their bases to the parent stock, and terminated each by a short caudal cirrus, the two cirri being diametrically opposite each other, with their bases connected by a transverse band. When the band retracts, each rudiment comes as a consequence to lie completely underneath, and perpendicular to, the ventral surface of the last segment of the parent stock, and unites with its fellow to form the complete tail rudiment that follows. In *Syllis prolifera* for example, this union takes place only after the separation of the stolon, and the stage of two semi-rudiments remains for a relatively long time.

The semi-rudiments are due to the lateral outgrowths of the last segment of the parent stock, from its posterior border (fig. 6). They are club-shaped at first, but afterwards are rather retort-shaped, the bulbus being in the basal two thirds. This part consists posteriorly and upwards of a thin and unicellular layer, and anteriorly and downwards of a thick and multicellular layer, between which lies a mass of young mesodermal cells. The rudiments increase in length and in breadth, and segment synchronously but independently (fig. 7). There are on each side 3 half-segments, 3 parapodia, and a half-pygidium with a caudal cirrus, at the time of separation of the stolon.

When the stolon separates, the lateral semi-rudiments (fig. 8) are displaced obliquely, and then brought into the median position, each swinging through an angle of 90°. They approach nearer to each other,

Fig. 6. Left half of a horizontal section of *Syllis prolifera* **Krohn**, at the position joining two individuals, the parent stock in front and the stolon behind. (Male individual.)

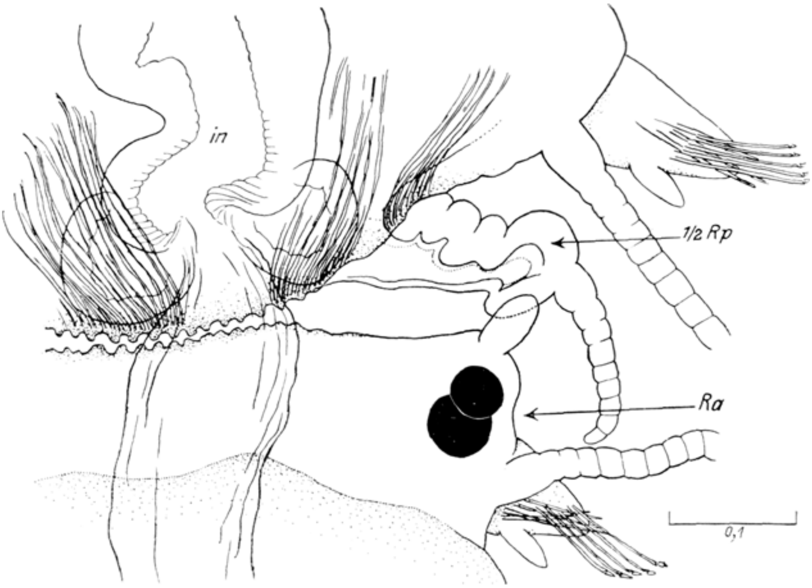

Fig. 7. Right side of *Syllis prolifera* **Krohn**, at the position joining two individuals at a more advanced stage than before; the half-rudiment of the tail has increased in length, in breadth and in segments, until there are 3 half-segments and a half pygidium, with a caudal cirrus already elongated and annulated.

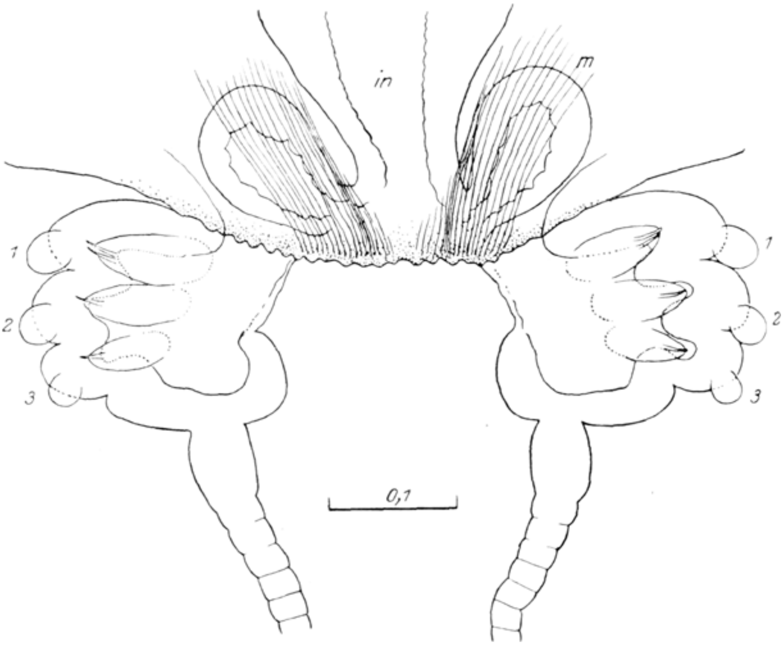

Fig. 8. The stolon is separated of and the lateral semi-rudiments of the tail are displaced toward the median posterior position. In each half segment a parapodium and a dorsal cirrus have appeared.

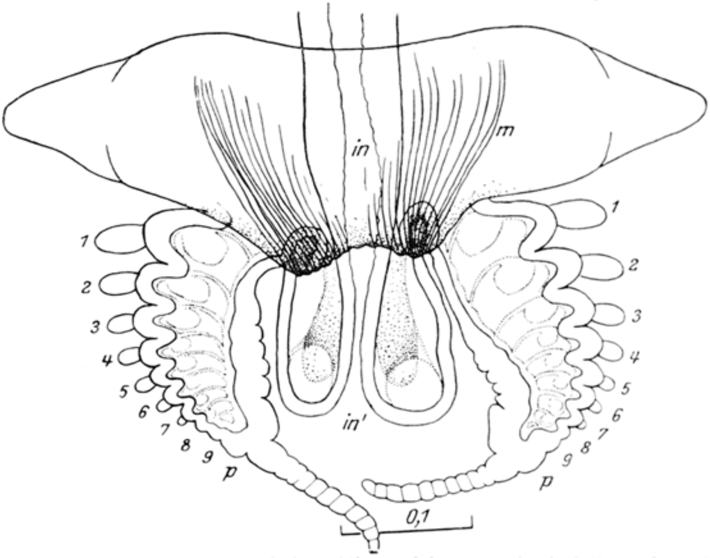

Fig. 9. More advanced condition than before of the caudal regeneration in *Syllis prolifera* KROHN; there are about 9 half segments and a half pygidium on each side. The end of the intestine is generally protruded to the exterior, between two semi-rudiments, as is shown in this figure.

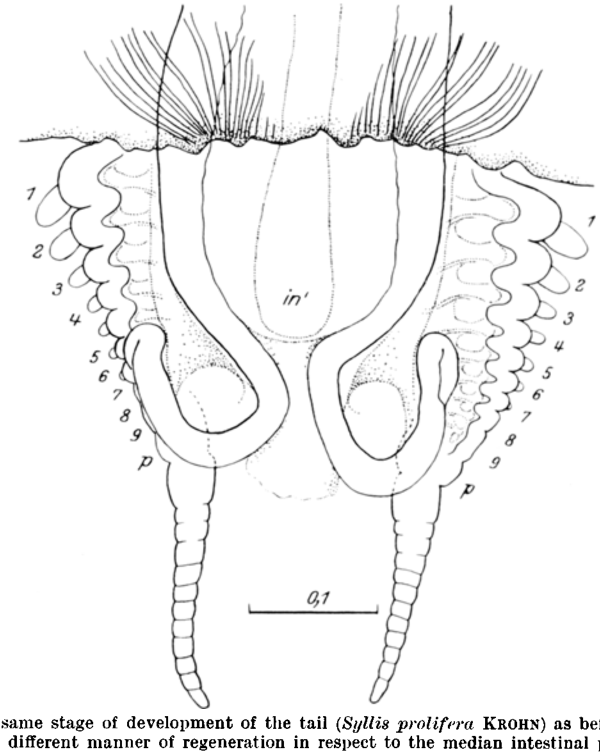

Fig. 10. The same stage of development of the tail (*Syllis prolifera* KROHN) as before, but in a somewhat different manner of regeneration in respect to the median intestinal protrusion.

fusion taking place by their ventral and by their dorsal borders, but there remains a dorsal fossa for the anus (from fig. 9 to 11). Some 10 half segments are formed on each side, and the complete tail rudiment receives, from the beginning, the same number of segments, as shown in fig. 11. Afterwards the tail elongates and multiplies its metameres, as in an ordinary case of regeneration, but we must bear in mind that the intestine of the new tail, or a part of it at least, is in this case composed of the ectodermal layer, instead of being a direct elongation of the posterior end of the original — the endodermal structure. This ectodermal part of alimentary tract may be compared to the proctodeal invagination of normal embryonic development.

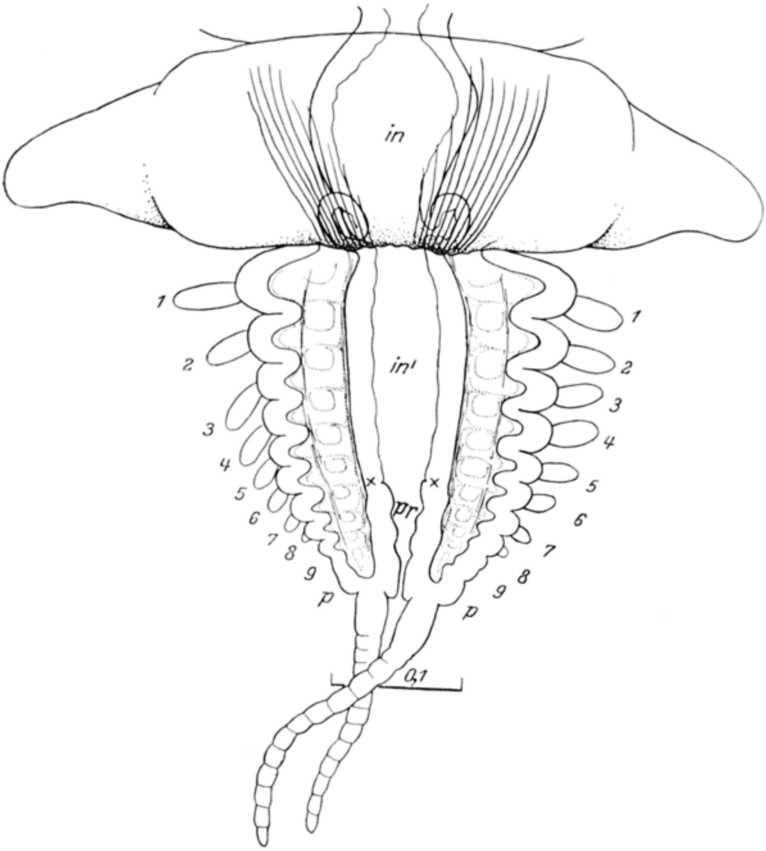

Fig. 11. The semi-rudiments have approached each other in the median line and fusion then takes place (*Syllis prolifera* KROHN).

It remains for us to consider whether the special method of caudal regeneration in certain species of *Syllis*, and in *Trypanosyllis*, is due to the primary character of the constitution of these worms themselves, or whether it is a case of the simple phenomena of regulation in tachygenesis. The problem will quite easily be settled when we artificially cut across one of the Syllids mentioned near the stolon (in front of the stolon head), and observe the caudal regeneration. Fig. 12 represents such a case, (*Syllis prolifera*) and is drawn from an example about a week from the time of operation. The tail rudiment is single and median; it bears a small cirrus on each posterior extremity, but still shows no trace of segmentation in its body.

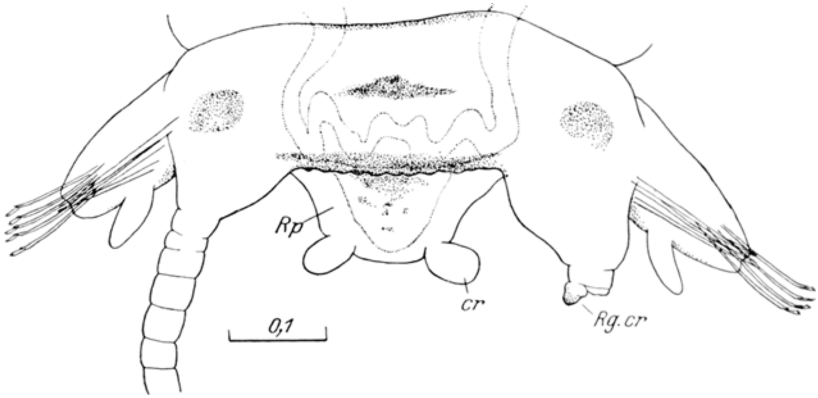

Fig. 12. Experimental case of tail regeneration following cutting of *Syllis prolifera* KROHN in front of the stolon-head; the tail rudiment is single and median with a small cirrus on each posterior extremity. There is no trace of its separate origin, as in the case of schizogamy. By chance, in the same figure, the regeneration of the tentacular cirrus is shown.

§ 3. *Faculty of the Anterior Regeneration.*

Regeneration occurs also at the anterior end of the posterior piece of a divided Polychaete. The extent of this regeneration is, according to the species experimented on, extremely variable. For example, there is almost no new formation of the head on an isolated segment of most Phyllodocids (*Phyllodoce*, *Eulalia*, etc.), while even a single segment of *Ctenodrilus* reconstructs an entire animal, by the method of a simple re-regneation. CH. GRAVIER (1909) has collected cases of anterior regeneration in Polychaetes, in his "contribution à l'étude de la régénération de la partie antérieure du corps chez les Annelides Polychètes". Perhaps we cannot here make any generalization as to the problem, beyond an enumeration of the names of those worms which can recover completely the missing part, and of those other species which do not show this property. Even confining our observations within the bounds of the single family of Syllids, we shall meet again with the same inconstancy of the anterior regeneration.

According to P. LANGERHANS (1879, *Syllis rosea*, *Opisthosyllis brunnea*), C. VIGUIER (1884, *Exogone gemmifera*), DE ST. JOSEPH (1887, *Syllis alternosetosa, Syllis prolifera, Syllis variegata*), G. PRUVOT (1890, *Syllis prolifera*), A. MALAQUIN (1893, *Syllis hyalina, Autolytus longeferiens*) etc. the anterior regeneration is only a recovery of one or two setigerous segments in addition to the individual head section (the prostomium and peristomium), in spite of the metameric number of the missing part, and there is absolutely no new formation of the pharyngeal organs, such as the pharynx, the proventriculus, etc. On the other hand, F. MESNIL (1901) found a fragment of *Syllis gracilis*, possibly detached from the 25th setigerous segment, regenerating at its anterior end 14 new segments, besides the prostomium, and a fairly long growth zone in front of the original segments. The pharynx and proventriculus are definitely restored, the former in the first two setigerous segments, and the latter extending from the 3rd to the 5th segment.

Complete regeneration of the anterior segments is more constantly met with in *Procerastea Halleziana* (E. J. ALLEN 1921; H. LANGHAMMER 1928). For example, a piece of 3 segments, probably corresponding to the original setigerous segments 17+18+19 (see ALLEN's 1921 memoire, pl. 13, fig. 6), regenerates the head and 16 setigerous segments in front, and 20 setigerous segments and the pygidium behind. With this number of segments, or even less than 3 original segments, ALLEN has experimentally demonstrated the capacity of the anterior regeneration of this Syllid.

So far as the facts described are concerned, *Syllis rosea, Opisthosyllis brunnea, Syllis variegata, Syllis prolifera, Exogone gemnifera* and *Autolytus longeferiens*, show an anterior regeneration, even when at its maximum, confined to the recovery of one or two setigerous segments in addition to the head section. *Syllis armillaris*[1] and *Odontosyllis fulgurans* regenerate a few more segments, but there is still no pharynx, no proventriculus and no ventriculus. In *Syllis gracilis* and *Procerastea Halleziana*, the regeneration capacity is limitless, and there is complete recovery of the missing segments, with a new formation of the entire system of pharyngeal apparatus. We must remember that these two species reproduce in nature by fragmentation, with accompaning regeneration of the missing parts (refer E. J. ALLEN 1921; F. MESNIL et M. CAULERY 1924).

My own observations show the same variation in the regeneration of the anterior segments; *Syllis spongicola, Syllis prolifera, Trypanosyllis zebra* and *Autolytus Edwarsi* do not form more than two setigerous segments in addition to the head, and very frequently only form the prostomium, peristomium and one setigerous segment, or simply two segments of the head. There is no stomodeal invagination and, of course no new formation of pharynx and proventriculus. The front end of the intestine elongates forwards, and passes directly from within outwards, as

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[1] = *Syllis alternosetosa* of de St. Joseph and *Syllis hyalina* of Malaquin.

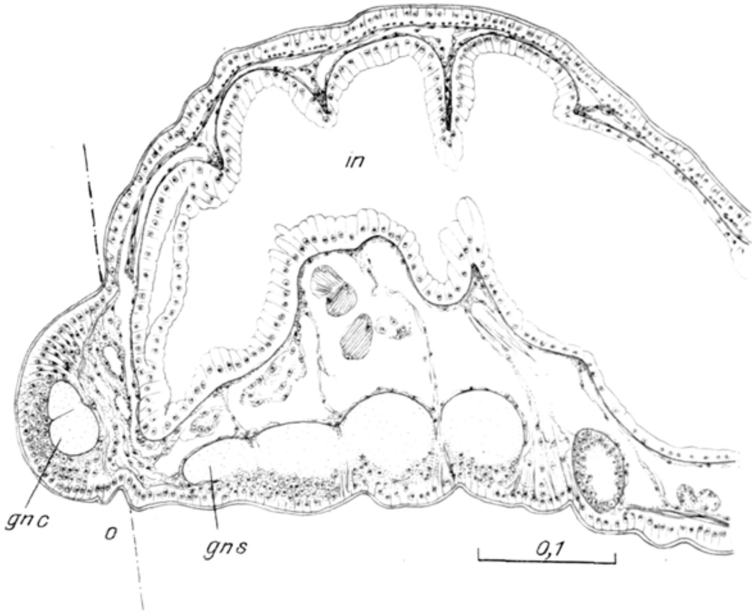

Fig. 13. Median longitudinal section of the anterior part of *Trypanosyllis zebra* GRUBE; there is distinctly a regeneration of the head section with its ganglia, and the position of the mouth is indicated by a small invagination of the ectoderm, but there is no stomodeal invagination.

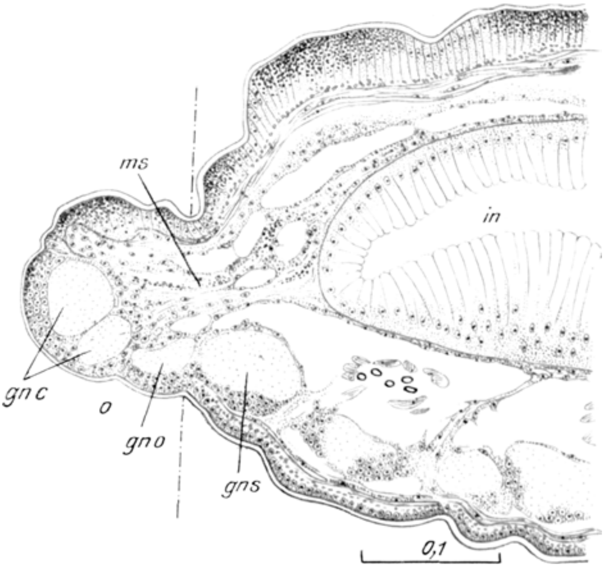

Fig. 14. Similar section to the last of *Syllis prolifera* KROHN. In this case there is one more segment (first setigerous one) regenerated in addition to the head section. The anterior end of the intestine remains undeveloped, and the ectoderm does not form the small invagination corresponding to the position of mouth.

in the regeneration of the posterior end (in *Trypanosyllis zebra*, fig. 13), or it remains undeveloped, without opening into the mouth, in *Syllis prolifera* (fig. 14). Sometimes a heteromorphic tail end, the pygidium, is produced in the place of the head of *Autolytus Edwarsi* (fig. 15).

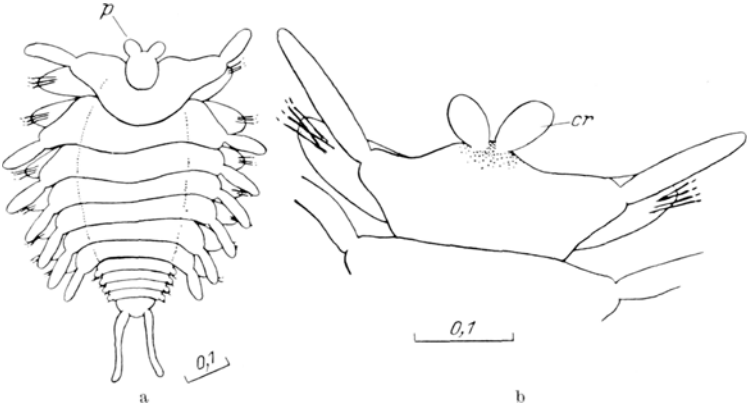

Fig. 15. Two different types of the heteromorphic tail regeneration in *Autolytus Edwarsi* DE ST. JOSEPH; in a the whole pygidium and in b the caudal cirri alone are produced.

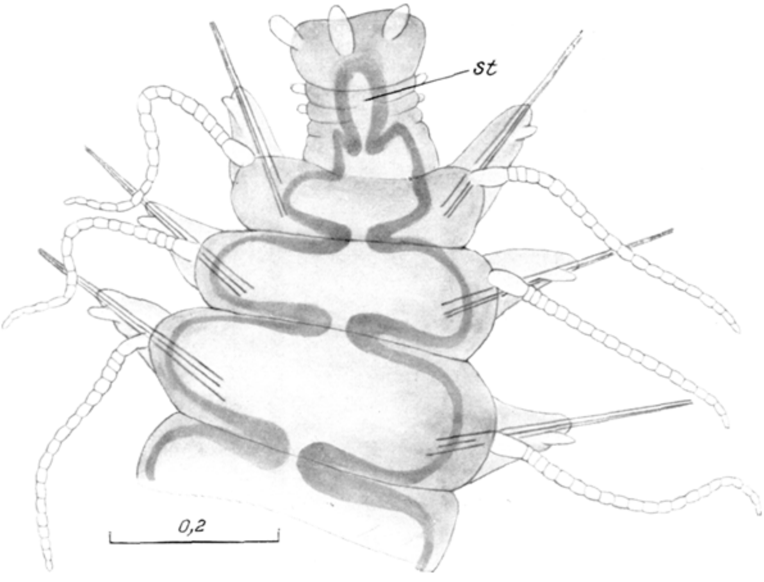

Fig. 16. Front part of a regenerating piece of *Syllis gracilis* GRUBE, the original segments being 9.

Syllis gracilis regenerates quite well. DE ST. JOSEPH (1887) states that there is no phyarnx and no proventriculus in the regenerated specimens, while F. MESNIL (1901) found both in his material. This is a great contradiction, but this kind of contradiction seems quite probably to depend upon the simple difference of the developmental stage of the organs when observed.

The front part of a young regenerating piece, the original segments being 9 setigerous, is figured in fig. 16. The new prostomium has the median and two lateral tentacles on the dorsal side, but there are no palps on the ventral. Of the following segments the two anterior are provided with a small dorsal cirrus on each side, while the rest are still very young, without cirri and without setae. Internally there is visible in front of the intestine an ovoid hollow structure, looking very much like a conducting canal from the original intestine to the new mouth opening. It would be quite natural, with this picture of the alimentary tract, to state that there is no pharynx, no proventriculus, and no ventriculus, while in place of them is a "conduit", like that of the sexual bud, whilst the moniliform intestine begins from its normal position. We should thus have DE ST. JOSEPH's description

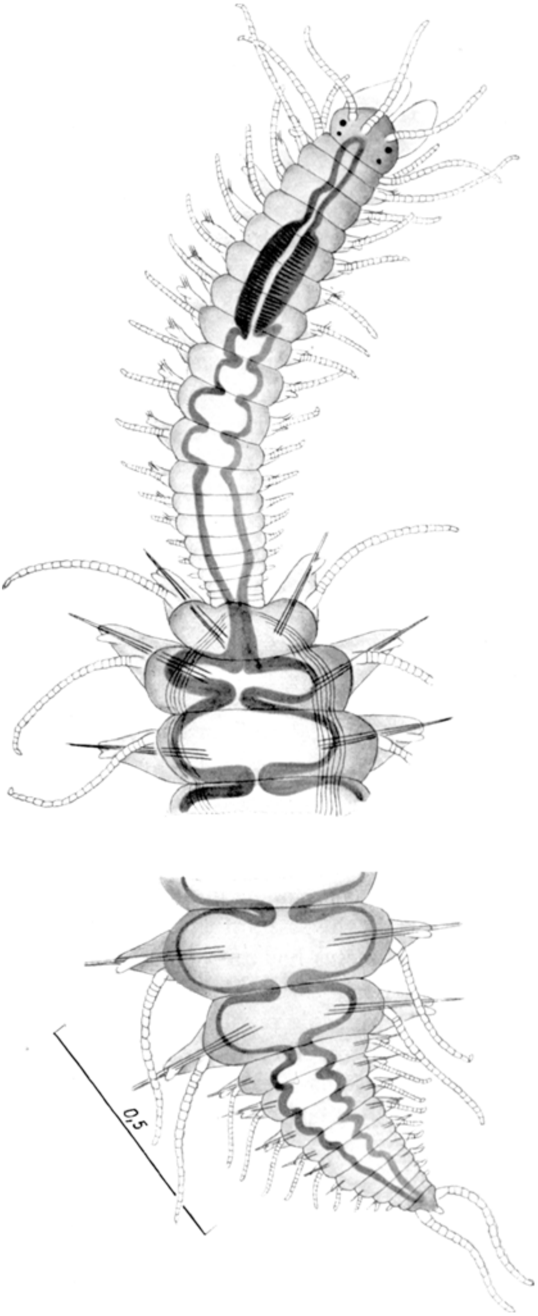

Fig. 17. Regeneration in *Syllis gracilis* GRUBE of 6 original segments.

of his specimens, the regenerating front part of which consists of the head, 5 setigerous and 2 embryonic segments. But this canal-like front organ is, in reality, a stomodeal invagination and not an anterior elongation of the old intestine. The pharynx and proventriculus become distinct afterwards, as represented in fig. 17, which is drawn from a piece of 6 original segments that produced, at its anterior end, more than 18 new segments and the head. The pharynx is distinctly visible as a tube, elongated up to the end of the 4th setigerous segment, and the proventriculus as an ovoid and striated mass in segments 4th to 6th. Some such view of the regenerated alimentary tract must have been observed by F. Mesnil. Indeed it is figured in one of the later publications (1924) with his brother-in-law, M. Caullery.

Regeneration follows fragmentation, and each fragment of *Procerastea Halleziana* gives rise again to a complete animal. The new segments are formed from the anterior end as well as from the posterior end, and this capacity of regeneration is little different — even if the velocity is not the same in different segments — between the fragments of the anterior region of the worm and those of the posterior. The regenerative faculty of the fragments seems to be equipotent, and each part of the body iso-potential. Or using Driesch's appropriate expression, the body of the Syllid may be said to represent an "equirotential harmonic system".

§ 4. Territories of Regeneration.

Standing between the two extremes of the regenerative faculty we are considering, *Autolytus pictus* forms a most interresting intermediate type, in which the position of cutting, becomes the most important factor determining the subsequent regeneration, especially in the anterior direction. This phenomenon is the same as that which I have tried to demonstrate in the stalk of the hydraid *Corymorpha* (Okada 1927).

Autolytus pictus has an avarage number of about 80 setigerous segments, and its dorsal surface is covered with a deep deposit of dark brown or deep purple pigment (see Mc Intosh's pl. XLIX, fig. 8, 1908), with the exception of a mid-dorsal line immediately over the alimentary tube, which is free of pigment and appears white. There is also a series of transverse bands free of pigment, which therefore appear white (see Allen's fig. 1, 1927). The white bands are especially marked after the 7th setigerous segment, and occur with great regularity, one to each between segment 9th and 10th, 11th and 12th, 13th and 14th, 19th and 20th, 22nd and 23rd, 26th and 27th, 30th and 31, 34th and 35th, 38th and 39th, 42nd and 43rd, 45th and 46th, 48th and 49th, 52nd and 53rd, 56th and 57th, 60th and 61st, 64th and 65th, 68th and 69th, 72nd and 73rd, and become gradually obscure towards the caudal end. When the body of the worm is divided according to these positions of the white bands, the result exactly coincides with the rule of fragmentation, which E. J. ALLEN (1927) formulates thus, H 9+2+2+3+3+3+4+4+4+4+4+3+3 +4+4+4+4+4+4+4 . . . . . . + x P. With the help of this regularity of grouping of the segments, we shall proceed to the investigation of the anterior regeneration in pieces cut from different levels of the body.

Starting from the head-end, when the prostomium is sectioned in any direction and at any position, but within the bounds of this segment, the missing parts are easily reconstituted; the new tentacles, eyes, and other cephalic structures are generally normal, as before the operation. Only once in the whole series of the experiments, a pair of separated palps appeared in front of the head, which had been cut across between the median and the lateral tentacles. We must remember that the palps of the Autolytinae are fused, and are usually not visible in a dorsal view of the animal.

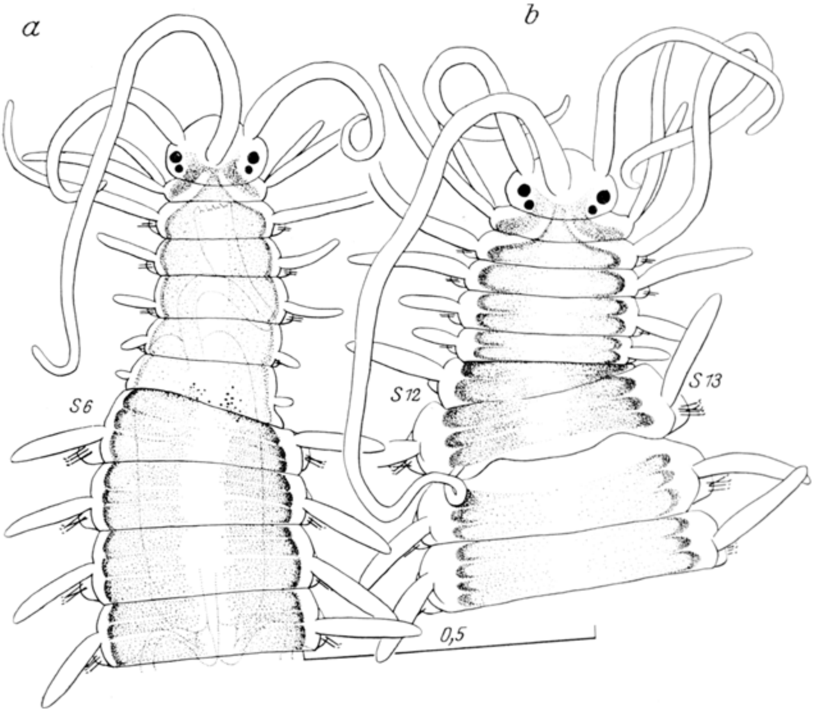

Fig. 18. a Regeneration of *Autolytus pictus* EHLERS in front of the 6th setigerous segment; b the same in front of the 12th setigerous segment. (The half segment, due to an oblique section, does not repair the other half.)

When the plane of section enters the second viz. the buccal segment, the whole prostomium and the missing front part of the same segment are reconstructed. In the same manner, after section of the third segment (the first setigerous one) the whole head regenerates, and from the second setigerous segment the head and the first setigerous segment are reformed. Such a complete recovery of the missing parts is observed almost invariably, down to the level of the sixth setigerous segment, and by the section of this segment the prostomium, peristomium and 5 setigerous segments, the first two of which having long cirri and on each side a special oblique band of pigment continous to the head[1], can be obtained (fig. 18 a). Behind this level, the regenerated segments are by no means always the same as the original number, being sometimes only 3 or 4, whatever the degree of injury; but when the conditions for regeneration are favourable, we have generally the same number as the missing segments produced from the eigth setigerous segment (fig. 19). The same maximum regeneration behind this segment, does not, as a rule, exceed 4 setigerous segments in addition to the head, as shown in fig. 18 b, a specimen which has been sectioned in front of the 12th setigerous segment. Only once have I got a case in which there is a regeneration of 5 setigerous segments from a section posterior to the eigth setigerous segment (fig. 24), but this can be regarded rather as an exception to the general maximum recovery of 4 setigerous segments in the region in question.

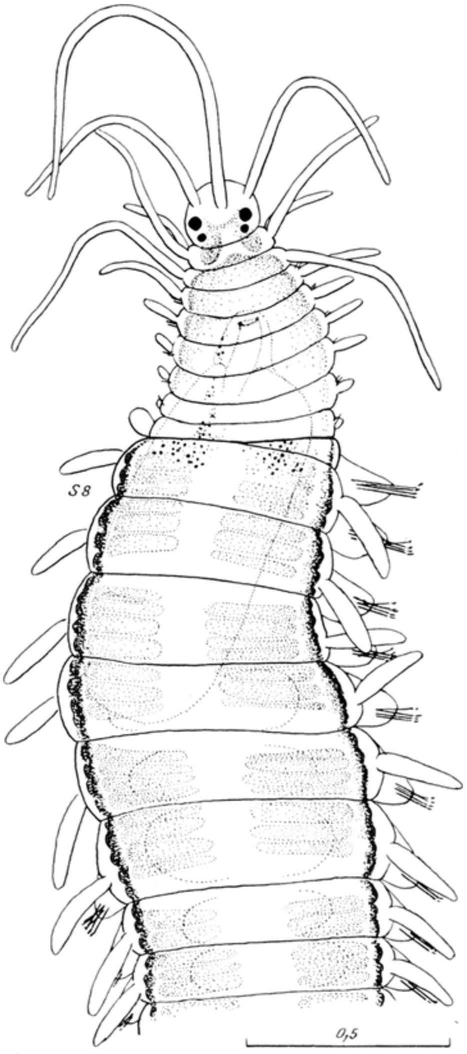

Fig. 19. Anterior regeneration of *Autolytus pictus* EHLERS in front of the 8th setigerous segment.

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[1] In the early stage of regeneration the oblique bands are only found on the prostomium and buccal segment.

The 6-meric regeneration, i. e. two head segments plus 4 setigerous ones, is continued down to the 13th setigerous segment but absolutely no further, so that when the cut edge is slipped down only slightly into the 14th segment, the anterior regeneration is suddenly reduced to the individual head section, and, at the most, one setigerous segment in addition, when young sexually immatured worms are employed. Fig. 20 represents a rather rare case, in which the asexual head appears in a quite advanced stage, the eggs becoming ripe at the end of regeneration.

There is, strictly speaking, no stomodeal invagination in the regeneration, after the 13th setigerous segment. The front end of the intestine elongates forwards, becoming closely applied to the ventral side of the segment, between the new head and the original piece, and then passes through the body wall, opening from within outwards, without any further differentiation in its structure, as we have seen in the anterior regeneration of *Trypanosyllis*. Another characteristic of the regeneration after the 13th setigerous segment, is that the new head has not always the same morphology as the original. In this case the regeneration is absolutely di-meric, consisting of the prostomium and peristomium, and there is no setigerous segment at all. The new head is sometimes that of the males individual (*Polybostricus*), sometimes that of the female (*Sacconereis*), as the case may be. There are however still plenty of instances in which the regenerated head is of the asexual type. The result is found to be entirely conditional on the state of sexual maturity of the subject employed, at the time of operation. It is simply that when the cut has been executed long before the maturity of the worm, the new head is generally asexual, while when the same experiment has been done with worms nearly mature, the head of the sexual stolon always results (see fig. 21).

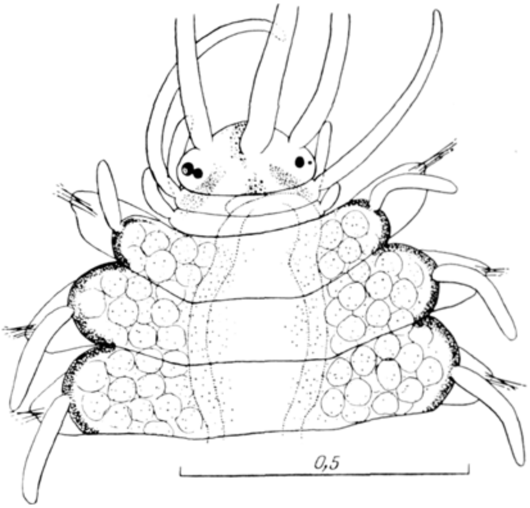

Fig. 20. Anterior maximum regeneration of *Autolytus pictus* EHLERS from a cut behind the 13th setigerous segment.

Comming back in front of the 14th setigerous segment, stomodeal invagination takes place in every case withaut exception. I shall not describe here the beginning of the invagination, since it seems not important for the present problem, but in a slightly advanced stage it is a solid, round mass, composed of one layer of cells, which, anteriorly and ventrally, is continous with the ectoderm of the ventral surface, between the prostomium and the buccal segment. Posteriorly and dorsally, it ascends obliquely backwards to meet the front end of the original pharynx when the comparatively anterior part is cut, as seen in fig. 22, or to meet the intestine in the case of cutting the posterior region, as seen in fig. 24. The latter structure, either the pharynx or the intestine, does not increase forwards at this time, and re-establishment of the new alimentary tract depends entirely upon the differentiation of the stomodeal invagination. Already, before

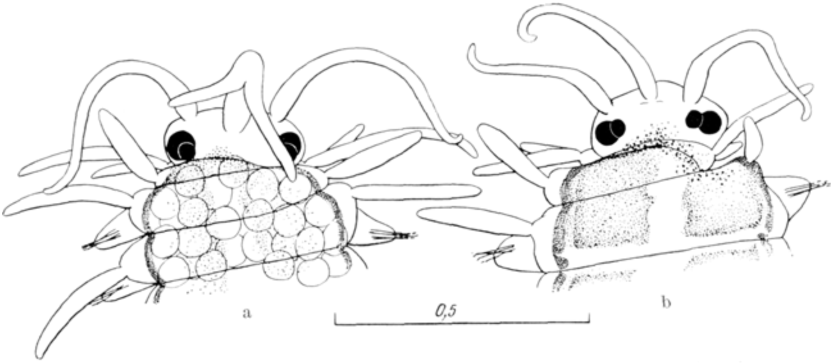

Fig. 21. Anterior regenerations of *Autolytus pictus* EHLERS from behind the 13th setigerous segment, with the head of a sexual individual (*Sacconereis*), a, cut at the front of the 18th setigerous segment, and b, at the 41st setigerous segment of the same worm. (Compare with the example in fig. 25a.)

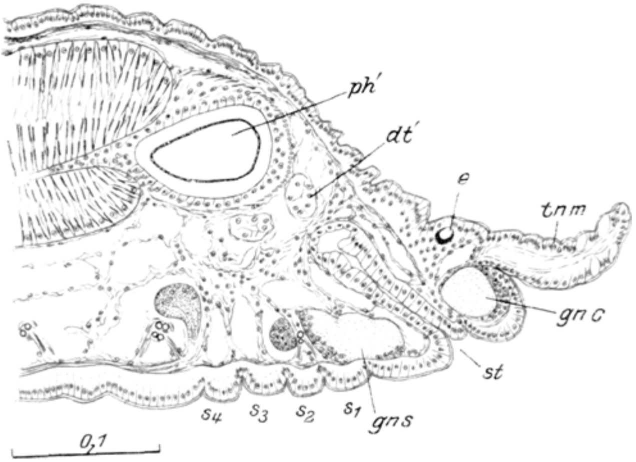

Fig. 22. Anterior regeneration of *Autolgtus pictus* EHLERS in front of the 5th setigerous segment viewed in a median longitudinal section. The stomodeal invagination is distinct.

the developing pharynx comes in contact with the old pharynx or with the intestine, it forms an ampulla-like structure in its hinder portion, a central space appearing. Later the bottom of the ampulla rises up gradually inwards, in its middle part, as in the gastrulation of some invertebrate eggs, and from this middle part comes afterwards (by a process of secondary backward elongation) the new pharynx, including the pharynx proper, proventriculus and ventriculus, while the lateral cavity of the ampulla is directly transformed into the buccal chamber, the pharyngeal glands being produced below it, on each side of the median pharyngeal structure. Without further description, it will easily be understood, that the degree of regeneration, i. e. the state of development of the middle raised part of the appulla, is dependent upon the degree of injury of the remaining part of the original pharynx, so that in sections

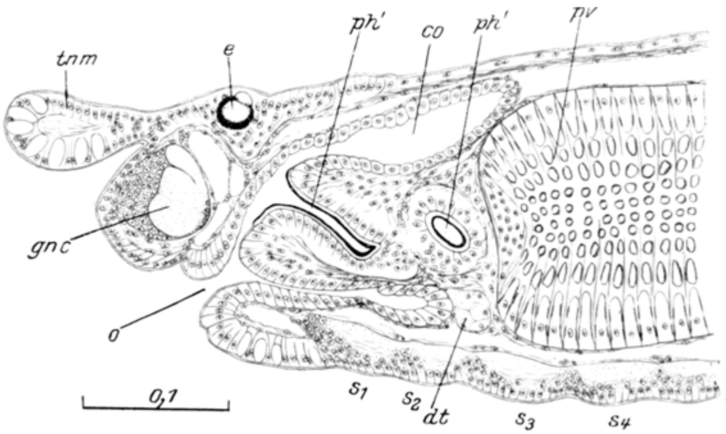

Fig. 23. The same as the preceding in a more advanced stage (from another example).

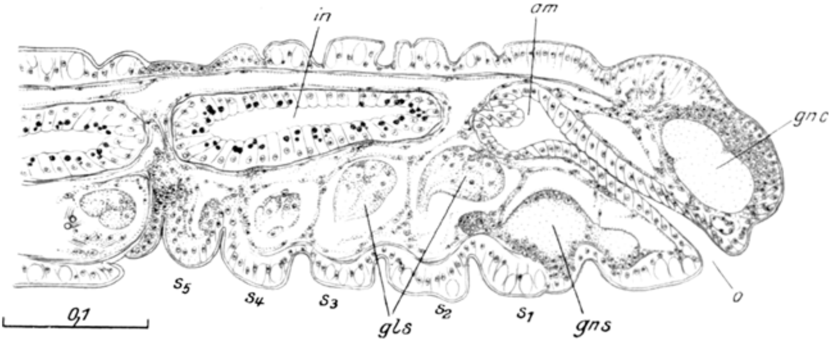

Fig. 24. Also a median longitudinal section of the anterior regenerating part of *Autolytus pictus* EHLERS cut posterior to the position of the ventriculus or at the beginning part of the intestine, but in front of the 13th setigerous segment.

made behind the ventriculus, the stomodeal invagination re-forms the entire system of the pharyngeal organs.

The potential faculty for anterior regeneration in *Autolytus pictus*, is not exhausted at the 14th setigerous segment. It is preserved in a still wider range in the posterior segments. There is however a hinder boundary for it. In fig. 25, a, the head is observed almost immediately in front of a white band. Behind this band, we count 3 segments to the next

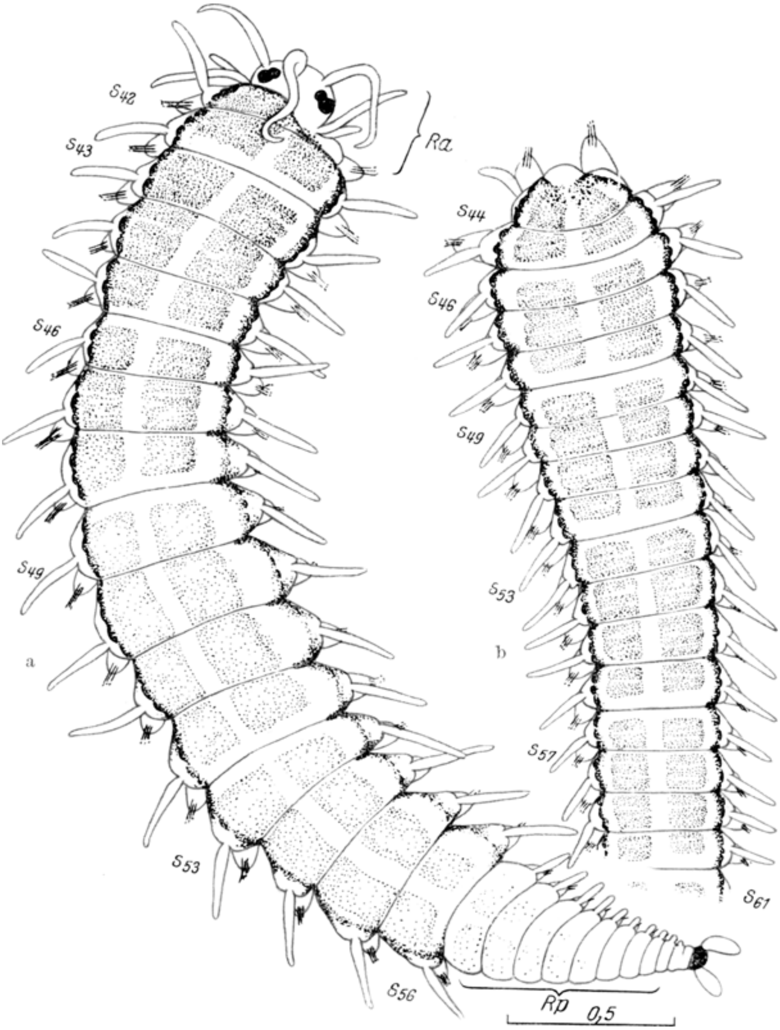

Fig. 25. a Piece of *Autolytus pictus* EHLERS consisting of 15 setigerous segments from the 42rd to 56th. This piece has regenerate the head in front, and some 10 new segments and the pygidium at the posterior end. b Posterior part of the same Syllid consisting of the whole number of segments behind the 43rd setigerous segment; this piece does not regenerate the head.

white band, and another 3 segments back to the third white band, but henceforth come groups of 4 segments only. This piece of regeneration cannot be in front of the 33rd setigerous segment, because there was, in front of it, another piece of some 20 segments, which was cut out after the 13th setigerous segment, at the same time, and from the same individual. From the known fact of the serial order in the metameric grouping, the groups of 3 segments after the 33rd setigerous segment in *Autolytus*, must be those of segments 43rd + 44th + 45th and segments 46th + 47th + 48th, and nothing more and nothing else. In the piece of regeneration in question, there are just two of these groups of 3 segments, and there seems practically no objection to regarding the new head as being formed on the 42nd setigerous segment.

Now let us glance at fig. 25 b, which represents a headless piece. This piece of regeneration was cut, also, on the same day as the previous operation, from nearly the same level of another individual i. e. after about the 35th setigerous segment, and was killed at an even later date than the preceding. The interval, during which regeneration took place in this instance, extented over three months, in late summer. The anterior group of segments consists of two segments, behind which is a white band, which is followed by a single group of 3 segments. The remaining segments are all in groups of 4 each. By the same deduction as before, the group of 3 segments can be identified as that of segment 46th + 47th + 48th, and as a consequence the two segments of the anterior group represent segments 44th and 45th. From the 44th segment, the head does not regenerate. In my experience, these segments of one and the same group, that is those between two white bands, show always the same physiological properties, including the regenerative faculty. Bearing this fact in mind, and considering all the cases of regeneration and non-regeneration, in addition to these two representative examples, I have come to the conclusion that the posterior limit of the anterior regeneration is, in *Autolytus pictus*, at the 42nd setigerous segment, or somewhere in the near vicinity of this segment. I must not, however, forget to mention, that this interesting result of the regional difference of regeneration cannot be extented and applied to the body of other Syllids, even within the bounds of the same genus; *A. Edwarsi* for example, as already mentioned, shows its faculty of anterior regeneration incomplete, even in front of the 14th setigerous segment.

§ 5. *Head of the Stolons and Double Head Regeneration.*

The anterior regeneration is closely connected with the formation of the head in stolons. The head, however, does not appear in the stolon of *Syllis spongicola*. In this Syllid the genital segments are quite mature and ready for reproduction, as soon as separation of the stolon takes place, the gonads being fully developed and the swimming setae elongated. Perhaps no time remains for regeneration in these circumstances. The similar, headless stolon detached from *Syllis armillaris* (refer also to A. MALAQUIN, 1893, his *Syllis hyalina*) has no swimming setae at the time of separation. A resting period of some days then elapses, the swimming setae elongate and the reproductive products ripen. Apparently separation of the stolon takes place before the segments arrive at the same state of maturity as in *Syllis spongicola*. Both potential capacity and time for regeneration are therefore present and a new growth actually appears on the anterior dorsal half of the first segment of the isolated stolon. The thickening gives rise to an upward and forward extension, beyond the anterior limit of the segment. A pair of eyes is associated with the thickening, which is now an acirrose *Tetraglene*-head, and a dicirrose *Chaetosyllis*-head soon follows. The head with three appendages is next established, and the pentacirrose (two of which belong to the buccal segment) *Ioda*-head appears as the final condition.

The whole series of these changes or a part of the series may take place in other Syllids before the stolon separates off, and the animal looks like two individuals joined together, one behind the other. The stolons of *Trypanosyllis* are generally *Tetraglene* and those of *Syllis* (*Typosyllis*) *Chaetosyllis*. The septa-cirrose *Sacconereis* and the noneca-cirrose[1] *Polybostricus* are found in the Autolytinae, the former for the female and the latter for the male respectively. The difference is so remarkable in this sub-family of Syllids between the heads of the two sexes and that of the parent stock, that had we not observed the development of them we could scarcely have credited their generic identity. Really in former times they are considered as representing three different groups of animal. Their generic identy was proved (by A. AGASSIZ 1862 and others), and the parent stock and the stolons were compared to the hydroids and their swimming bells, and regarded as "alternation of generations" among Polychaetes. This hypothesis is no longer accepted at the present time, the asexual condition of the parent stock being by no means constant but very variable. Moreover, the segments of such a posterior region, which is concered with the formation of the stolon, can regenerate the head and the anterior segments of the parent stock, a fact which is especially evident in *Procerastea Halleziana*.

We have just learned in the preceding experiments, that *Autolytus pictus* regenerates the head until about the 42nd setigerous segment, and between the 14th and 42nd segment the head section alone, or at most one setigerous segment in addition. The stolon of this Syllid separates

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[1] This number of nine tentacles is problematical, because the so called antero-lateral tentacles of the prostomium seem to be another kind of sense organ as well as being tactile.

almost without exception between the 13th and 14th segment, the male individual containing the spermatozoa in the first 6 segments i. e. from the 14th to 19th setigerous segment of the original worm, while there are a greater number of genital segments in the female individual. When the worm of either sex is cut in any position in those posterior segments near the time of its sexual maturity, but before the appearance of the anterior thickening upon the 14th setigerous segment, the regenerated head is almost invariably either that of a *Polybostricus* or a *Sacconereis*, but if the specimens employed are very young we may have a high percentage of the head of the parent stock. E. J. ALLEN (1921, pl. 13, fig. 7) has figured a *Sacconereis* of *Procerastea Halleziana*, which bears in front the head and a number of segment of the parent stock. Perhaps in this specimen the anterior regeneration had started long before the sexual maturity of the posterior egg-enclosing fragment. ALLEN (l. c. p. 165) mentions that "imnediately behind the 13th setigerous segment there has been formed what is evidently the commencement of a new head". This head will develop into that of the sexual individual — *Sacconereis* in this case—and the posterior segments will separate from the anterior regenerated part. Such a spontaneous regeneration of a head upon a certain posterior segment, if it belongs to a different type from that of the original, is itself mysterious and requires further investigation, though it must be due to a physiological isolation of the posterior segments behind the special one. Ligature of the body or isolation of a series of segments results always in a new head at the anterior end of the isolated part, or on the segment just immediately posterior to the ligature. In the case of *Autolytus pictus*, as in *Procerastea*, such a physiological isolation also occurs spontaneously between the segments in front of the 14th setigerous segment and those segments of the posterior part, the new head appearing at the anterior end of the special segment.

I know from my experience of regeneration in organisms where there are two different regions of regeneration, arranged one after the other in a line, that weakening the dominant power of the first region may revive a different morphological character or characters, which were subordinated in the second region, and that in the case of Coelenterates a simple process of diminishing the material in the first region may effect this purpose (refer OKADA 1927). Thus in *Autolytus pictus* if at the time of operation, we examine the material in respect to the degree of its sexual maturity, and properly control the position of cutting, we may easily induce even the asexual head on the 14th setigerous segment in addition to the normal regeneration at the front end of the served segment, the head of which is, it need not be said, that of the parent stock. Having this expectation in mind, I have cut *Autolytus pictus* in the 12th and in the 13th setigerous segments, and have got in this way plenty of double headed regenerations, both heads being of the asexual type and occuring one immediately in front of the other. Fig. 26 is one such example.

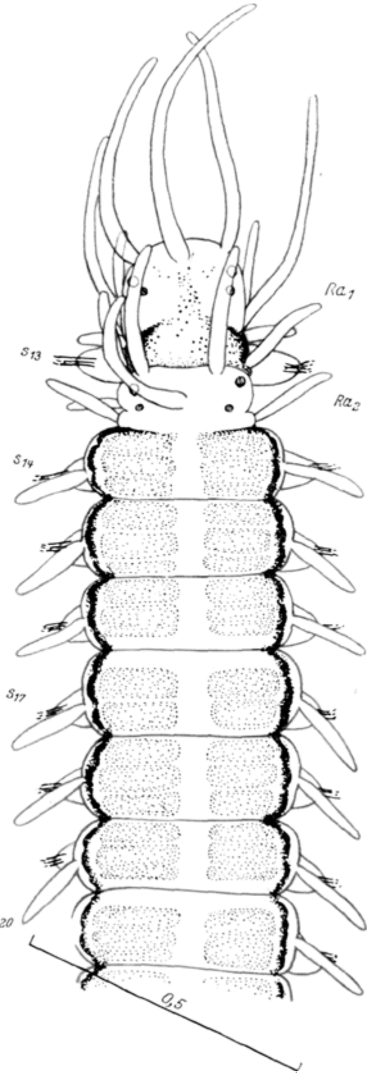

Fig. 26. Double head regeneration produced by cutting the front of the 13th setigerous segment. The second head has the same morphology as the first, and the following segments do not contain any sexual products.

When the experimental animal is divided between the 12th and 13th segment, the anterior regeneration of the posterior piece is naturally started first of all from the anterior end of the 13th segment, but this regeneration is especially interesting because when the second head appears at once on the 14th setigerous segment, it does not grow beyond the state of an individual head section, without setigerous segments, while, if the second head does not appear at all or if its appearance be very much retarded, the regeneration in question generally goes further, several setigerous segments being formed in addition to the head segments; this latter case of regeneration is however comparatively rare.

Even when the second head is distinctly developed, there are sometimes no reproductive products at all in the posterior segments, and there is in this respect no absolute reason for the phenomenon of stolonization in the sexual reproduction of Syllids. With its head of asexual character and with the segments without reproductive products, the experimental stolon in question reminds us of stolonisation of certain limicolous Oligochaetes.

Finally it must be confirmed that the inactivity of the stolon in respect to the regenerative faculty is due to the age or senescence of its segments. In my experience there is absolutely no regeneration in any stolon found in the plankton. The detached stolons of *Autolytus Ed-*

warsi, for example, show no power of regenerating a missing part, but young stolons still in the chain have been proved to have the property of regeneration, as will be seen in fig. 32.

§ 6. *Position of the Growth Zone in Regeneration.*

The initial process of the anterior regeneration is the same as that in the caudal direction, an outgrowth coming out first from the closed wound surface. This increases forwards and divides transversaly into two. From the anterior division comes the prostomium and from the posterior the following segments. In the caudal regeneration, the posterior extremity (pygidium) is first formed, and the other segments appear one after the other from in front backwards. Thus the growth zone, being always penultimate, is gradually separated from the original segment. In the anterior regeneration all the segments including the prostomium are in the same serial order from before backwards, and the growth zone is always just in front of the original segment; its position is stationary in respect to the old segments. ($Ra = S_1 + S_2 + S_2 \ldots\ldots + S_{x-1} + S_x$) But no difference will be found between the anterior and the posterior regeneration, if we just suppose the original piece, inspite of its length and metameric number, to represent an undivided section of the embryo, for the caudal direction the head and for the anterior direction the pygidium. The law of embryonic development of Polychaetes demands that the new segments shall be arranged from in front backwards, except the most postreior one, the pygidium, as the growth of the embryo or larva must take place in the penultimate zone. Since a posterior undivided section (the original segments) already exists for the anterior regeneration, there will be no necessity for the first segment of regeneration to be the most posterior. This fact explains simply why the growth zone in this case is stationary and is always placed immediately in front of the original segments. The process of posterior regeneration is, as already described, nothing more than a simple repetition of the normal embryonic development.

§ 7. *Anterior Differentiation.*

Comming back to where we began, I have stated that "regeneration takes place easily at the posterior end of divided Syllids" but "on cutting the most anterior part, the chitinous tube and the massive proventriculus of the pharynx hinder the process of closing the wound and subsequent regeneration in most cases fails, especially in the caudal direction". Isolated head pieces of several segments can live for some days and may close the wound. I have actually observed this process in some examples, though in no cases is there a caudal regeneration. Such anterior pieces die sooner or later and their segments disintegrate just as in those in which wound closure does not take place. The same phenomenon can be observed in experiments with other Polychaetes, as well as with Oligochaetes. Among the latter the smallest head piece from which the tail regeneration is still possible, is described in *Lumbriculus*, *Tubifex*, *Nais* etc. to be composed of 10 to 12 segments (M. ABEL 1902; F. v. WAGNER 1895, 1900, 1905, and others). According to A. MICHEL (1898) the similar piece of *Allolobophora* is of 13 segments. In *Criodrilus*, L. TIRALA (1913) obtained tail regeneration from a piece of 10 anterior segments. In *Ctenodrilus* the power of regeneration is especially strong, and E. KORSCHELT (1919) has observed a piece consisting of the head and 3 setigerous segments, i. e. 5 segments in all, forming a regeneration cone at its posterior end.

In *Procerastea Halleziana* the head and the following 7 segments easily separate from the posterior part of the body, and such a piece, according to E. J. ALLEN (1921), regenerates well the missing posterior segments. A similar head piece of the same metameric number does not, however, regenerate the tail in *Autolytus*. *Autolytus pictus*, regenerates the tail only after the 11th setigerous segment. In *Syllis spongicola* and *Syllis prolifera* it is found that a head piece, which is able to regenerate the tail, must comprise all the segments up to the 18th setigerous, and in *Trypanasyllis zebra* even more, 24 setigerous segments besides two of the head. Referring to this problem E. KORSCHELT (l. c. p. 611) suggests that "offenbar ist bei diesen Würmern eine so weitgehende Differenzierung der vorderen Körperpartie eingetreten, daß diese nicht mehr in der Lage ist, aus sich heraus das für die Neubildung der fehlenden Körperteile nötige Material zu schaffen. Anderseits erlaubt aber die hohe Differenzierung des Vorderkörpers nur eine teilweise und unvollkommene Ausbildung dieser Region oder verbietet ihre Neubildung vollständig."

In the Syllids those anterior segments which fail to show the caudal regeneration generally possess the faculty of regeneration. We may return again to the experiments already described of anterior regeneration in *Autolytus pictus*, and say that the anterior segments show positive regeneration, the capacity being however onesided. The defective regeneration of the head pieces seems rather to be due to the presence of some "higher differentiations in the anterior part of the body", than to the absence of the special material for regeneration in their segments. But what differentiation or differentiations we are concerned with here?

Syllids are Polychaete-worms with a narrow body, definitely segmented, and with articulated or non-articulated tentacles and cirri. The prostomium is rounded or quadrangular, has three tentacles and two palps, which are in various degrees of development and separation. The eyes are distinct and usually four or sometimes six in number, each two, right and left, forming a pair. The second segment is the buccal segment, or peristomium, so called because the mouth opens on its ventral side. It differs from the following body segments in structure, for there are on each side two tentacular cirri, a longer dorsal and a shorter ventral, but no parapodia. The third and the following segments are all provided with parapodia, and are arranged one after the other in succession, repeating one another in their structure, at least in their external morphology. An individual metamere is a short cylinder somewhat flattened dorso-ventrally, and has on each side a parapodium, which is uniramous, namely a neuropodium with a short ventral cirrus. (There are no ventral cirri in the Autolytinae.) The notopodium is absent, but its appendage (the dorsal cirrus) remains and is considerably developed. The dorsal cirri are elongated in the first setigerous segment of most Syllids, and in the Autolytinae elongation takes place also in those of the second setigerous segment, but from the third segment they are uniformely short or alternate with slightly longer ones. The anterior differentiation may thus be recognisable externally back to the second setigerous segment but no further.

The minimum metameric number of the so called head piece, which will give caudal regeneration, consists of the head and the following 7 setigerous segments in *Procerastea*, of 11 such segments in *Autolytus*, or of still more in other Syllids, so that the differentiation of the regenerative faculty in the anterior segments advances with the differentiation of the external morphological structures. Internally, however, the differentiation of the anterior segments has gone a step further.

The general arrangement or the various regions of the internal structures can be clearly seen, if the living worm be examined under the microscope, owing to the transparency of its body wall. If examined in this way, it will readily be seen that the septa are invisible or incomplete in a number of the anterior segments, and there appears instead a large chamber containing highly specialized organs, one following the other, until the first appearance of the moniliform intestine in a cavity which is separated from the former by a complete transverse septum. The length of this anterior chamber (the peripharyngeal chamber) varies in different species, the shortest being composed of cavities corresponding to 5 anterior segments in such examples as *Procerastea, Virchowia, Pterosyllis* and most Exogoninae. The peripharyngeal chamber of *Syllides longocirrata* is a little longer than this and comprises 7 segmental cavities. In most species of *Pionosyllis* and *Autolytus* the chamber extends back to the end of the 9th setigerous segment, in *Eusyllis* to the 13th segment and in *Syllis spongicola* and *Syllis prolifera* to the 16th segment. The same chamber in *Trypanosyllis zebra* is the longest which I have seen, and there are indeed 22 setigerous segments before the first complete septum. It is scarcely necessary to repeat here the whole anatomy of Syllids nor to enter into histological details. The only problem which remains is to determine the real end of the peripharyngeal chamber, which includes the organs of ectodermal origin i. e. the extent of the embryonic stomodeal invagination.

The front part of the pharynx can be protruded through the mouth opening at the time of feeding, the tip providing a chitinous spine or a crown of small teeth in the Autolytinae, with the single exception of *Autolytus inermis*. When the animal is at rest this part of the pharynx, i. e. the probocis, is drawn back into a special cavity called the buccal chamber, which is formed by a folded sheath coming down from the mouth opening. Just at the point at which the sheath is folded over upon the probocis, or, put in another way, at the bottom of the chamber, there is a compound gland on each side. The pharynx in then divided posteriorly into the pharynx proper, the proventriculus and the ventriculus. These organs, according to their special functions, have different shapes and show different degrees of development. However different their shape and their degree of development may be, they all agree in one histological point, namely, that the innermost cell layer is always chitinigerous. There is absolutely no chitin production on the intestinal epithelium. The posterior end of the stomodeal invagination and the anterior region of the intestine are, therefore, sharply marked off histolocically, and this boundary point is always found in front of the so called "ventricular coeca", instead of being behind them.

At the present time there will probably be no morphologists, who hold the opinion that the transverse striations or serial arrangement of small dots upon the surface of the proventriculus are glands. They are in reality the facets of attachment of the radial muscles of the proventricular wall to the outer membrane (see OKADA 1928). But the nature of the ventricular coeca is still generally misunderstood, as this term is very misleading.

A. MALAQUIN (1893) has figured a pair of ear-like appendages on each side of the middle of the ventriculus (his text figure p. 247). In his pl. IV, fig. 1, (*Syllis armillaris*), although the same coeca are drawn in the same position as in the text figure, the structure of the alimentary tract is sharply marked between the portion in front of and that behind them. MALAQUIN describes the former portion of the alimentary tract as the "anterior ventriculus" and the posterior portion as the "posterior ventriculus", in respect to their positions to the coeca. In the same figure the posterior ventriculus is observed to be posteriorly continous with the structure of the intestine, and anteriorly insensively spreads out on each side into the coecum in question, while the anterior ventriculus presents an entirely different view. A similar distinction also can be seen in

W. A. HASWELL's (1921), pl. 15, fig. 6 (*Syllis variegata*), between his "ventriculus" and "postventriculus" respectively. Doubt arises naturally from the figures of these authors as to the real nature of the ventricular appendages. I have studied *Syllis spongicola* and *Syllis prolifera*, and compared some representative species of other genera, *Trypanosyllis, Pterosyllis, Autolytus, Procerastea* etc.

Each coecum commences with a funnel-like chamber of entry (fig. 28 a), resembling the sieve of the intestinal glands of *Aphrodite*. Inside its cavity the epithelium is formed of elongated cells and clothed with dense cilia, especially long on the surface of the posterior arm, and at the bases this epithelium seems to be surronded by sphincters, probably formed by the circular muscles of the intestinal wall. The distal portion, which constitutes the principal length of the coecum, is made up of tall epithelial cells, in which, in *Syllis prolifera* at least, are enclosed comparatively large spherical granules of secretion, strongly stainable with iron-haematoxylin. Each cell-body is not vacuolated but dense, and has a nucleus towards the base. As a whole, with such structures, the coeca remind one strongly of certain glands of an excretory nature.

The so called "ventral coeca" are recognized as a separated chamber by H. EISIG (1881), who gives prominence to it as the second main division of the alimentary tract, the first being the whole pharyngeal part including the pharynx, proventriculus and ventriculus, and the third division the intestine behind the coeca. Of course his account of their function as "Schwimmblasen" cannot be accepted. DE ST. JOSEPH (1887) and A. MALAQUIN (1893) do not recognize the separation of the coeca from the structure of the ventriculus. According to W. A. HASWELL (1921), the epithelium of the latter "is ciliated and is loaded with unicellular glands". But so far as I can make out, such a histological appearance is never observed either in the proventriculus or in the ventriculus of Syllids, but is found only in the first part or the intestine, or speaking more strictly, in the portion corresponding to the so called ventricular coeca. I do not know exactly whether this part of the alimentary tract is employed for "absorption de l'eau" (MALAQUIN l. c. p. 247) at the time of feeding, but it is certain that the structure develops at the junction between the stomodeal invagination of the pharynx and the intestine. There are certainly many instances of the development of mid-gut glands in such a position in the Annelids, as well as in the Arthropods.

Pterosyllis formosa (=*Amblyosyllis lineata*) consists always of 17 segments, the first being the prostomium and the last the pygidium. In this worm, as already mentioned, the pharyngeal part comprises the first 5 setigerous segments, and the intestine commences at the 6th setigerous segment. There are therefore 9 swellings in the entire length of the intestine, and from each swelling, with the exception of the last one, comes out a pair of short lateral diverticula. The first pair of them, i. e. those of the 6th setigerous segment, is rather well developed and somewhat modified, but otherwise has the same structure as those that follow. This pair is figured by A. Malaquin in his pl. IV, fig. 5; "ce sont deux très petits sacs" (l. c. p. 241) and apparently possess no secretory function. In most Eusyllinae and in *Trypanosyllis*, the coeca are replaced by a forward outgrowth of the intestine (fig. 28 b), found ventrally to the

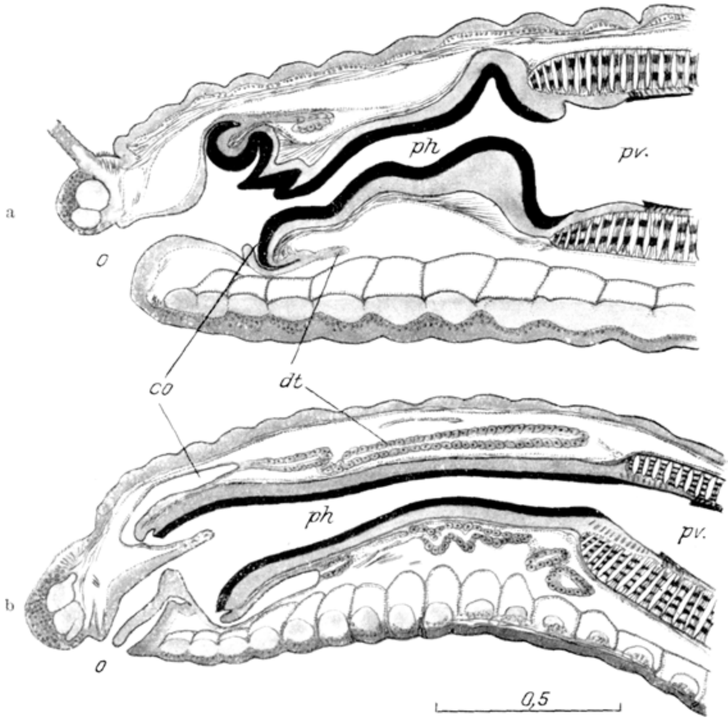

Fig. 27. Showing the anterior differentiation of Syllidian metameres, a representig a median longitudinal section of *Syllis prolifera* Krohn and b one of *Trypanosyllis zebra* Grube. (Notice the difference in the degree of development of the pharyngeal glands in the two species.)

posterior elongation of the stomodeal invagination, which constitutes the ventriculus. There is generally no development of the coeca in the Autolytinae, and the ventriculus pushes back into the anterior part of the intestine (see Okada 1928, fig. 7).

A further interesting point about the coeca in question is, that in those species of Syllids in which they are found to be especially developed and apparently function actively, as in *Sillys spongicola*, *Syllis prolifera* etc., the pharyngeal glands are generally rudimentary (see fig. 27 a). On the other hand the pharyngeal glands are enormously developed in the Autolytinae, in which there are, as already mentioned, no "ventricular appendages" at all. The two types of glands seem unable to exist together, and are not functional in one and the same individual Syllid. This relation is especially interesting between two genera among the Syllinae, *Syllis* and *Trypanosyllis,* as shown in the accompanying figures (fig. 27 and 28). Might this not be connected in some way with the kind of food on which the animal lives? Most *Syllis* feed upon sponges, while other Syllids eat hydroids or bryozoa. *Myrianida pinnigera* is found, however, always associated with Tunicates, such as *Ascidiella aspersa, Phallusia mammillata* etc. The problem remains for further investigation.

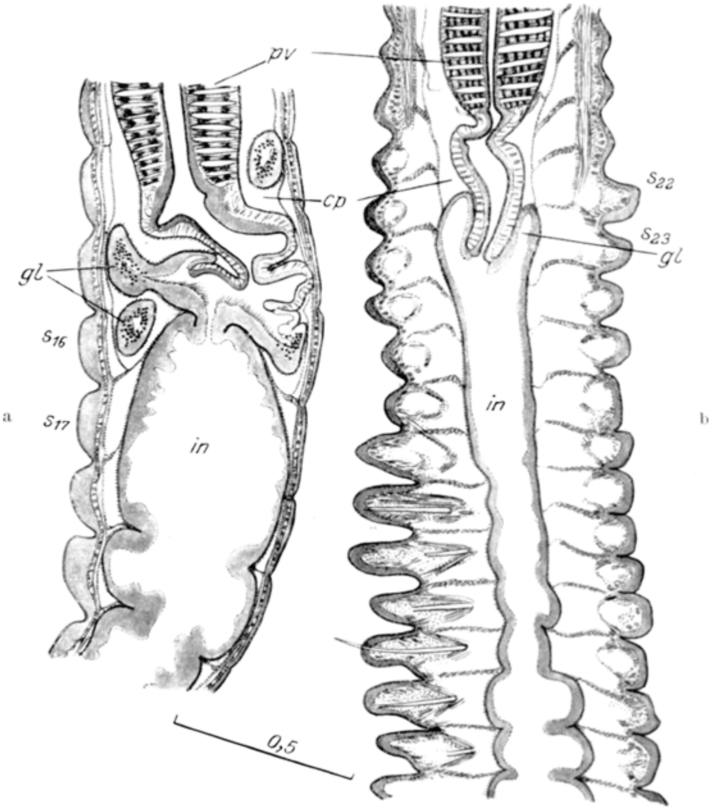

Fig. 28. Anterior differentiation of Syllidian metameres, following the part shown in the preceding figure. Drawings are horizontal a representing the segments of *Syllis prolifera* **Krohn** and b those of *Trypanosyllis zebra* **Grube**. The difference in the degree of development of the midgut glands, known as the "ventricular cocae" should be noticed in this case.

We have learned through the experiments on regeneration, that both *Syllis spongicola* and *Syllis prolifera* do not produce more than the head and one setigerous segment, when the anterior part of their body is cut off, and that there is absolutely no stomodeal invagination. It is also found that the anterior end of the intestine elongates forwards and passes directly from within outwards. *Syllis spongicola* regenerates very slowly. But at any rate when the anterior segments are re-established, we may find 3 lobes in front of the original intestine, instead of the single one of other Syllids (see fig. 29), consisting of two lateral ones on each side of a median one, the latter being always the largest and being in line with the original intestine. This median lobe can be regarded as representing the main tract of the regenerated digestive organs. But what then are the two lateral lobes? Are they not comparable to the so-called proventricular coeca? If so, they are evidently produced at the front end of the intestine and their formation has no connection with the stomodeal invagination.

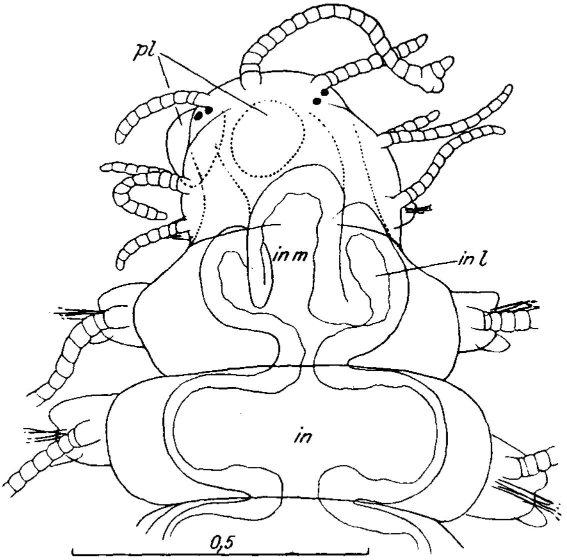

Fig. 29. Anterior regeneration of *Syllis spongicola* GRUBE consisting of the head and one new setigerous segment. There is no stomodeal invagination, but the front part of the intestine is trilobed, the median lobe being the largest.

The posterior end of the ectodermal structure is now determined; it is at the posterior end of the ventricule. On the other hand, we have already learned the difficulty of metaplasia in the regeneration of Syllids. Is the defective or one sided regeneration of the anterior segments brought about by these two main causes: 1) the ectodermal origin of the pharyngeal organs and 2) the fact that from these organs regeneration of the endodermal intestine is impossible? In reality, the minimum length of the head piece from which a tail regeneration is possible, comprises always a few more segments than those which constitute the length of the peripharyngeal cavity. It is interesting to notice that the head piece of fragmentation represents a close approximation to the minimum metameric number, found in the head of piece which is capable of caudal regeneration, for example, the head and 7 setigerous segments in *Procerastea,* the peripharyngeal cavity of which extends back to the end of the 5th setigerous segment. When the body of *Autolytus* fragments, the head piece separates between the 9th and 10th setigerous segments, but this fragment does not regenerate. The head piece which can produce a caudal regeneration must comprises at least 11 anterior segments in addition to the head, because the pharynx in this form extends back to the end of the 9th setigerous segment. The same relation hold true also in *Trypanosyllis*, in which the peripharyngeal cavity extends to the 22nd setigerous segment, and when this worm fragments the head piece separates with anterior 24 setigerous segments.

§ 8. From-recovery due to the Metamorphosis of the Segments.

In many Syllids, those segments which contain the generative products undergo more or less extensive changes, while the anterior ones remain unaltered. In the body of the ripe animal, an anterior non-sexual region and a posterior sexual region can be distinguished. The changes, which it undergoes in its transformation, affect chiefly the shape of the parapodia and the form of the chaetae of these parapodia. In addition to a comparatively small parapodium (the neuropodium in the strict sense) with a few compound setae, there appears a large and massive dorsal division or neuropodium, from which a bundle of large, flat, flexible swimming setae arises. Other organs may also be affected; thus the eyes are enlarged, the intestine may become so compressed by the generative products as to be functionless, and so on. These worms swimm generally near the surface of the sea.

In the Syllynae or Autolytinae the method of reproduction is further complicated, the modified posterior segments separating from the anterior part of the body and swimming away. The stolon of *Syllis spongicola* is, as has been mentioned, nothing more than a separated piece of these modified posterior segments; it has no head at all. The stolon of *Syllis armillaris* separates before its segments are modified, and the head is afterwards formed in the front. In other species, but within the boundary of the same subfamily, regeneration of the head takes place before the stolon separates, and the animal consists of two individuals joined together one after the other. The posterior individual is however quite different from the anterior on account of its incompletely developed head and its strongly modified segments.

In the Autolytinae, on the other hand, the head of the stolons consists of two segments, and their appendages are as well or even more developed than those in the asexual animal. And in these stolons there are always several unmodified segments immediately behind the new head, maintaining their original structures with small uniramous parapodia. The number of the unmodified segments is 2 or 3 in the female of *Myrianida* and of *Autolytus* with successive stolons (or gemmiparity), and almost always 3 in the male. In *Procea* of EHLERS, or *Autolytus* with a single stolon, and in *Procerastea* there are 6 or sometimes 7. Only the

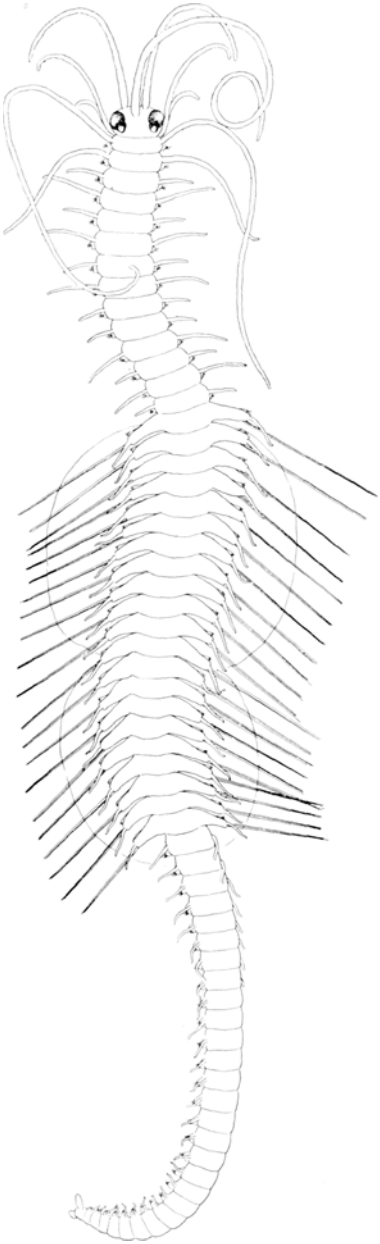

Fig. 30. Female stolon of *Autolytus longeferiens* DE ST. JOSEPH, known as "*Autolytus alexandri*" (MALMGREN). × 14.

stolon, either male or female, of *Autolytus longeferiens*, which is known under the name *Autolytus alexandri*, has the anterior region composed of 14 unmodified setigerous segments (fig. 30 and 31).

In those stolons with less than 3 unmodified anterior segments, the dorsal cirri of the buccal segment which is regenerated, are very massive, and in the male are thrown into a series of spiral coils. The following 3 segments are not modified in any way. On the other hand, in those stolons with more than 6 unmodified anterior segments, the tentacular cirri of the buccal segment are not so massive as in the previous case; they are present as rather slender structures, as in the head of the asexual form, the dorsal cirrus being of course longer than the ventral one. Behind this segment there is in this case a long and massive tentacular cirrus on each side. These two cirri are extraordinarily elongated, and in the male are carriend in special coils, resembling in this respect the pair of tentacular cirri of the buccal segment of the stolons of the former type. It should not be forgotten that these elongated cirri belong to the first segment of the 6 unmodified old setigerous segments, and that this first segment corresponds (generally) to the 14th setigerous segment of the original series of segments.

In *Autolytus alexandri* (fig. 30) the structure is further complicated, and a pair of elongated cirri occurs also in the second setigerous segment, though these cirri are not so long as those of the preceding segment, while the other 12 segments are provided only with short cirri, those of the 3rd, 5th, 7th, 9th, 10th, 12th and 14th segment being especially short and each regularly alternating with the slightly longer ones of the 4th, 6th, 8th, 11th and 13th segments. The fact should not be

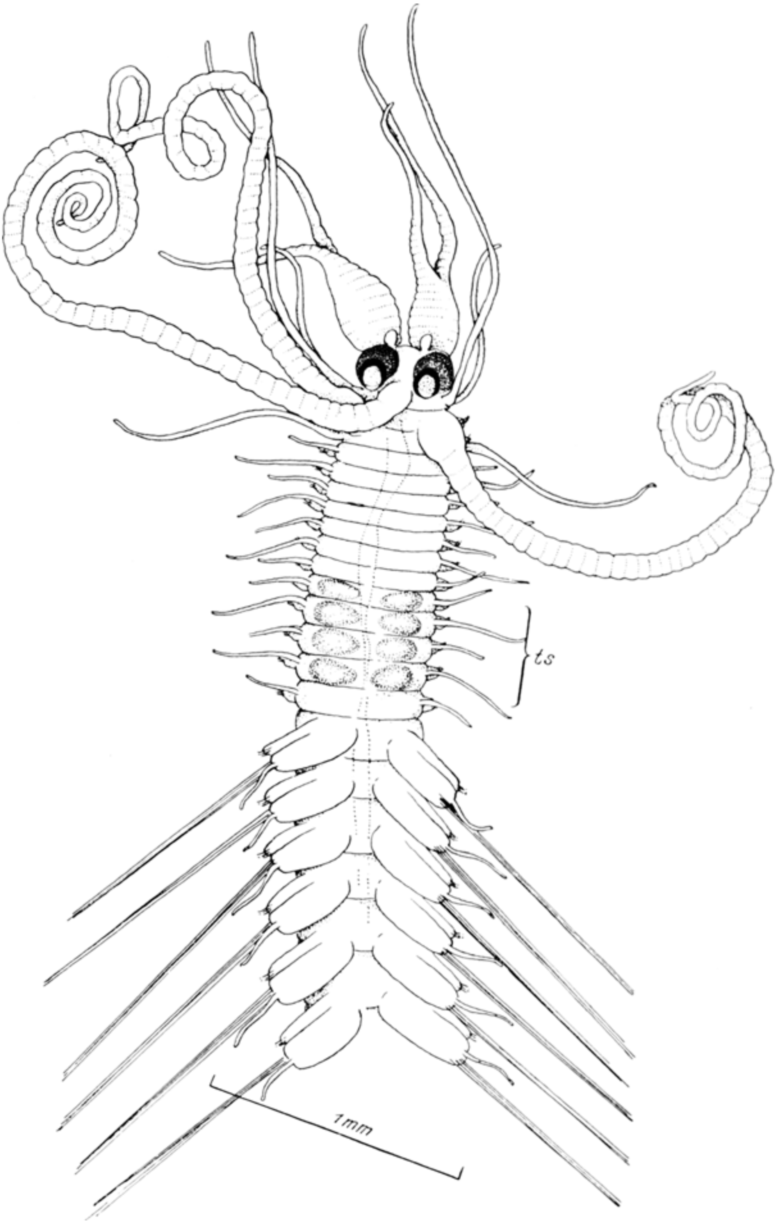

Fig. 31. Male stolon of *Autolytus longeferiens* DE ST. JOSEPH.

overlooked that, in the above scheme, there are especially short cirri, twice repeated, on the 9th and 10th segments, while in other parts the two types of the short cirri are absolutely in regular alternation.

An asexual form of *Autolytus longeferiens*, of about one centimetre, has about 72 setigerous segments. The head is, as in the other species of the genus, provided with 3 slender tentacles and 4 round eyes on the prostomium, and 2 tentacular cirri on each side of the buccal segment. The median tentacle measures 2,6 mm and the lateral 0,82 mm. The longer dorsal cirrus of the buccal segment is 0,94 mm long and the shorter ventral 0,47 mm. The dorsal cirri of the first setigerous segment are very long and attain even 2 mm. Those of the second segment are also fairly long and measure 1,2 mm, but with the third segment they are no longer conspicuous. The dorsal cirri of the third segment are but 0,3 mm, and those of the fourth segment are 0,5 mm. These two types of the short cirri occur afterwards in regular alternation, with the exception of the 10th setigerous segment, which like the 9th segment is provided with the shortest type of dorsal cirri.

As above described, the number and the relative length of the tentacles and dorsal cirri of these 14 anterior segments exactly correspond to those of the sexual individual, although the absolute measurements may be different. The head of the latter is due to regeneration, so that it is a new formation, but in this case no regeneration at all takes place in the setigerous segments. The stolon is produced always after the 13th setigerous segment of the parent stock. From this fact the presence of 14 unmodified segments in the first region of *Autolytus alexandri* would indicate a direct recovery of the anterior organisation of the parent stock, *Autolytus longeferiens*. Moreover, there appears always the special oblique band of pigment, from each side of the regenerated head of the stolon to the end of the second setigerous segment (original 15th segment), as in the head and following two segments of the parent stock.

That the first region of unmiodfied setigerous segment in the stolon represents a direct recovery of the anterior region of the animal may be more distinctly proved in *Procerastea*.

As in the allied genus *Autolytus*, the head tentacles and tentacular cirri of *Procerastea* are well developed. The tentacles are however club shaped and three in number, a median and two lateral. Immediately behind the head there arise on each side two tentacular cirri, a larger dorsal and a smaller ventral. Behind these cirri there is further on each side a single tentacular cirrus, which is inserted dorsally, and, from its position, as well as from the way in which it arises in relation to the head, belongs to the front part of the first setigerous segment. As it has already been pointed out by E. J. ALLEN (1921), the dorsal cirri of the body segments of *Procerastea* are in a state of great suppression as regards their length, and are represented by "a large round lobe or swelling of somewhat transparent tissue", which occupies the posterior dorso-lateral angle of the segment. This swelling of transparent tissue appears on and after the second setigerous segment, while the first segment is provided instead with a pair of tentacular cirri, which are shifted to the front part of the segment as just mentioned. The condition is especially well marked and is easily recognizable in the head of the *Sacconereis* (see ALLEN's pl. 12, fig. 5, for example).

Stolonization in *Procerastea* takes place by simple schizogamy with the production by each individual of a stolon, either male or female. And the position of separation is almost invariably between the 13th and 14th setigerous segments, as in most *Autolytus* the stolon of which has 6 or more unmodified anterior segments. The head of the stolon is, therefore, due to regeneration at the anterior end of the 14th setigerous segment, but this regeneration is limited, as in the general case of stolonization. To complete the morphology of the head, the dorsal cirri or the round swellings of transparent tissue at the posterior dorso-lateral angles of the 14th setigerous segment, disappear, while in the front part of the same segment there appears the third pair of tentacles (compare ALLEN's pl. II, fig. 2 and pl. 12, fig. 5). In the male these are extraordinarly massive and are carried in spiral coils (see ALLEN's pl. 12, fig. 4). Thus the head of the stolon is, in addition to being a simple regeneration at the anterior end of the 14th setigerous segment of the parent stock, due to a direct metamorphosis of the old structures of this segment to meet the new formation. Such an economy of labour in the anterior regeneration by changig the arrangement of certain old parts so as to complete the model of the original animal, is however not without parallel instances in the regeneration of Polychaetes.

C. VENEY and A. CONTE (1899) ligature *Spirographis Spallanzanii* and A. WATSON (1906) cuts a species of *Potamilla* near *P. reniformis*, both Sabellids, in the abdominal region, where the segments have the uncini on the dorsal side and the setae on the ventral side. (This condition of chaetal plan is just reversal in the thoracic region, being the uncini on the ventral side and the setae on the dorsal side.) The posterior piece, or the part which is physiologically isolated, regenerates always besides the cephalic plume-bearing segment, one new setigerous thoracic segment, as in the regeneration of *Autolytus pictus* behind the 13th setigerous segment, but no more, while the chaetel plan of the succeding 7 (in *Spirographis*) or 5—9 (in *Potamilla*) abdomial segments is changed, the dorsal uncini in these segments first disappearing give place to setae, and later the ventral setae being replaced by uncini into the segments of thoracic type, resembling in this respect the metamorphosis of the anterior segments in the Autolytid stolons just considered.

In the case of Sabellids, the metamorphosis takes place in any segment of the abdominal region only perhaps with the exception of the extremely posterior part. It remains for us to consider whether the "form recovery" in the stolons of the Autolytinae is also possible in any part of their body, as in the experimental case of *Potamilla* or *Spirographis*. I have cut a number of very young stolons of *Autolytus Edwarsi*, as well as those of *Autolytus pictus* in which regeneration is still possible. As we see in fig. 32, there is a certain degree of cephalic regeneration either in the male or in the femal individual, but in no case do the anterior segments behind the new head remain unmodified. The parapodia of all segments, including the first, are modified as if they constituted the second region of a normal stolon, appearing a large and massive dorsal division (notopodium), from which a bundle of large, flat, flexible, swimming setae arises. Rarely, the parapodia of the first segment remain less modified than the others, but this seems rather to be due to an incomplete metamorphosis of the segment, owing to the transformation of the energy which would normally be used in building up its own structure into energy required for regeneration. The direct recovery of the anterior region of the stolon seems thus to be impossible from segments, the character of which is determined. But what happens when the cha-

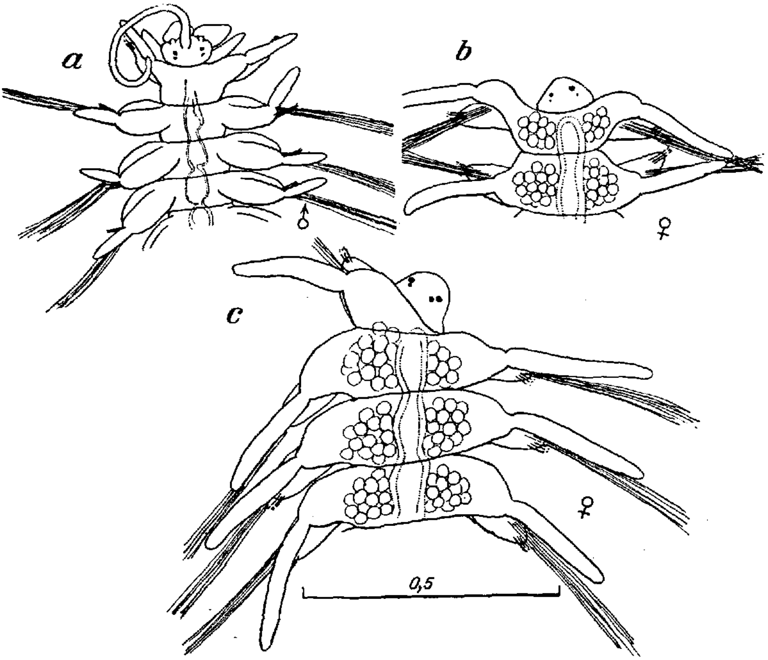

Fig. 32. Showing the regeneration capacity in stolons *Autolytus Edwarsi* (DE ST. JOSEPH), a the head regenerated from the middle segment of a male stolon, b and c the same from female stolons.

racter is not as yet determined as in a very early phase of stolonization, or in the course of embryonic development? To this question I can at present offer no reply.

Fragmentation.

Fragmentation is a phenomenon, as is well expressed by the term itself, of breaking up of the body of the worm, viz. the chain of segments, into a number of small blocks or unit groups, consisting of two, three or several segments. This phenomenon seems to be distributed quite widely through the different groups of both Polychaetes and Olygochaetes, being often employed as a method of asexual reproduction (see E. KORSCHELT and K. HEIDER 1910, p. 600 and E. KORSCHELT 1927, Chap. 6, p. 189). Within the family of Syllids F. MESNIL and M. CAULLERY (1919) have reported natural fragmentation followed by regeneration, and I have met with the same phenomenon taking place in a small luminous Polychaete, probably a Syllid, at Misaki (Japan). But *Procerastea Halleziana* is the most splendid object in which to observe this wonderful process of "achitomy".

By a chance observation, Mrs. SEXTON of the Plymouth Laboratory found "if the sea water in wihch a *Procerastea* was living on a microscope slide gradually evaporated, it tends break up in a constant and regular way". The same phenomenon is induced more readily by adding alternately distilled water and sea water, instead of relying on evaporation. E. J. ALLEN (1921) has in this way succeeded in finding a most regularly serial order, regulating the arrangement of the unit groups of segments, or fragments, in the body of the Syllid, the rule of fragmentation being expressed by the formula: $H\,7+2+2+2+3+3+3+4+4+4+4\,(+4)+3+3+3+3+3+3\,\ldots\ldots+x\,P$.

Six year later ALLEN (1927) wrote a second note on the same phenomenon of fragmentation in *Autolytus* and *Pionosyllis*. According to this paper, the genus *Autolytus* presents the same serial order of fragmentation as *Procerastea*, until the 15th fragment, or the 49th setigerous segment counted from the anterior end of the worm, is reached. Behind this point each fragment in *Autolytus* consists of 4 segments instead of 3 as found in *Procerastea*, so that the fragmentation formula is slightly modified, as follows: $H\,7+2+2+2+3+3+3+4+4+4+4+4+3+3+4+4+4+4\,\ldots\ldots+x\,P$.

The body of *Pionosyllis lamelligera* breaks up in such a way as $H\,9+2+2+3+3+3+4+3+4+2+2+6\,P$ and *Pionosyllis divaricata* as $H\,9+4+3+3+3+4+5+3+4+4+4+5\,P$. Comparing these facts of experiment (ALLEN) with the anatomical facts of fragmentation that will be later described the fragmentation formula of *Pionosyllis* (according to my view) may be expressed as $H\,(7+2)+2+2+3+3+3+4+4+4+4+4+4\,\ldots\ldots+x\,P$.

Trypanosyllis is described as showing no signs of fragmentation on addition of destilled water. But I have once observed a specimen of *Trypanosyllis zebra*, which carried a stolon after the 106th setigerous segment, also presenting the characteristic phenomenon, when it was transfered into distilled water. This fragmentation was by no means quite regular, but still suggested the existence of a certain definite serial order in the arrangements of its segments. *H* 24+4+4+4+6+8+4+6 +4+18+6+6+12+3+4+ (39 *P*, or a stolon).

So far as is known, artificial fragmentation of Syllids depends upon the change of salinity of the sea water in which the experimental animal is exposed, condensation through evaporation or dilution by the addition of distilled water. In the latter case, according to my observations, almost no effect is produced by dilution, until the degree of 6% of distilled water in sea water is reached. *Autolytus pictus* can live quite normally in such a medium. Lower than this concentration the worm first contracts and afterwards becomes restless. Constriction of the body at each white band becomes visible, when the worm is transfered into lower concentrations of sea water than half and half dilution. But breaking up of the body into pieces only takes place in a concentration lower than the mixture of x c.c. of sea water with 2 x c.c. of distilled water. In a concentration higher than the one and a half dilution, but lower than the half and half mixture of sea water and distilled water, a constriction which has appeard in the animal, disappears gradually when it is brought back again into the normal medium, that is into ordinary sea water.

The external change observed in this case of fragmentation is a separation of two consecutive unit groups of segments at each white band, the separation first appearing on the dorsal aspect as a transverse crack in the middle of the band. The greater the constriction, the wider is the separation of the anterior group of segments from the posterior, and the intestine, which is exceedingly swollen and is still swelling, protrudes at the same time through the gap. The swollen intestine is generally coloured brown, while in its normal condition it is almost without colour or at the most pale yellow. Fragmentation does not takes place in cane-sugar solution isotonic with sea water, but a series of the same processes and phenomena of fragmentation as observed in diluted sea water, can be repeated, by gradually diluting the sugar solution with distilled water. An appearance of strong convulsions, that accompanies the contractions of the body, should also not be overlooked.

Fragmentation can be induced more easily and more constantly when desired, by subjecting the animal to a medium having potassium excess. In a solution of KCl, isotonic with sea water, an *Autolytus pictus* of about 80 segments fragments somewhat in the following way: *H* 11+2+3+3 +3+4+4+4+4+4+3+3+4+4+4+4+4+4+4+(4 *P*).

The serial order of the arrangement of segments is the same as in the case of distilled water except in two regions i. e. in the anterior part in front of the 11th setigerous segment, and in the posterior part behind the 56th setigerous segment (this position is by no means fixed). When distilled water is employed the first fragment, including the head, separates nearly always between the 8th and the 9th setigerous segment, and the posterior fragment is more or less long, a number of unfragmented hinter segments being always attached to the pygidium. With KCl solution the separation of the head piece takes place almost constantly between the 11th and the 12th setigerous segment, i. e. at a position 2 segments posterior to that with distilled water. In the posterior region, on the other head, the individual groups of segments produced by KCl solution are carried further back, each group consisting of 4 segments, even back to the penultimate segment, though more often 4 to 7 posterior segments remain attached to the pygidium.

Solutions of NaCl, $CaCl_2$ and $MgCl_2$ do not provoke breaking up into series of segments. Anaesthetization with ether and chloroform, or with $MgCl_2$, either stops fragmentation altogether, or a worm in such a condition fragments very irregularly, and there is almost no regular serial order in its segmental groups. Fragmentation, therefore, seems to be in some way influenced by nervous stimulus, but a weak solution of strichnin nitrate is found to have no effect (the animal may perhaps be killed instantly).

It may be of passing interest here, to mention that a normal *Autolytus pictus* presents the homeing instinct, but a headless worm does not present this instinct. Again, the head plays an important rôle in nest formation by *Autolytus Edwarsi,* which lives inside a membranous tube, open at each end, with its body streched straightly within. When the head is cut off, the animal still preserves the power of nest formation, but the nest is no longer a stright tube, but is cocoon shaped. *Autolytus pictus,* on the other hand, builds a cocoon-like nest from the first, and lives within it bending and folding the body. In this case cutting off the head has no great effect upon the shape of the nest which is formed.

KCl solution is found to be a superb agent for producing fragmentation in Syllids, and by its use many of those species which we could not before get to fragment can be induced to break up into the same regularly serial order of segments as those just described. Among these is *Myrianida pinnigera,* the segmental arrangement of which, according to the method of fragmentation, can be represented thus: $H\ 13+3+3+3+4+4+4+3+3+4+4+4+4+4+4+3+3+3\ldots.+x\ P$, where the first $H\ 13$ can be resolved into $H\ 7+2+2+2$.

The chief feature of the body wall of Syllids is the proportionately large size of the dorsal longitudinal muscles, which form in transverse

Fragmentation in *Autolytus*

Medium	No.					Grouping of							
	order	*H*	S 1—7	8—9	10—11	12—13	14—16	17—19	20—22	23—26	27—30	31—34	35—38
	group	(*H* 7)		2	2	2	3	3	3	4	4	4	4
In distilled water	1	9[1]	....	..... ×	–	–	–	–	–	–	–	–	–
	2	9	....	..... ×	–	–	–	–	–	–	–	–	–
	3	9	....	..... ×	–	–	–	–	–	–	–	–	–
	4	9	....	..... ×	–	–	–	–	–	–	–	–	–
	5	9	....	..... ×	–	–	–	–	–	–	–	–	–
	6	9	....	..... ×	–	–	–	–	–	–	–	–	–
	7	9	....	..... ×	–	–	–	–	–	–	–	–	–
	8	9	....	..... ×	–	–	–	–	–	–	–	–	–
	9	9	....	..... ×	–	–	–	–	–	–	–	–	–
	10	9	....	..... ×	–	–	–	–	–	–	–	– ×	...
	11	9	....	..... ×	–	–	–	–	–	–	–	–	–
	12	9	....	..... ×	–	–	–	–	–	–	–	–	–
In KCl solution	1	11	....	....	..... ×	–	–	–	–	–	–	–	–
	2	11	....	....	..... ×	–	–	–	–	–	–	–	–
	3	11	....	....	..... ×	–	–	–	–	–	–	–	–
	4	11	....	....	..... ×	–	–	–	–	–	–	–	–
	5	11	....	....	..... ×	–	–	–	–	–	–	–	–

[1] Number of segments forming the head piece (*H x*).

[2] Number of unfragmented segments at the posterior end (*x P*).

× indicates the positions of the first and the last fragment. Number of segments of each animal is shown by numerical suffix of . . . S.

reg. means the regenerating tail.

sections a massive arch in the upper two thirds of the segment. A slight median raphe carries the mesentery from the alimentary tract, and separates the muscles symmetrically into a right and a left half. Externally are circular fibres, then hypodermis, and lastly the cuticular layer. The ventral longitudinal muscles are also composed of right and left bands. They are generally thinner than the dorsal longitudinal muscles, and more or less approach each other in the median line, where the nerve cords pass. There are oblique muscular strips passing through the intervals of the ventral muscles. As these strips from the base of the acicula pass dorsally along the inferior border of the dorsal longitudinal muscles and ventrally along the outer border of the ventral muscles, the movements of the parapodium with its setae are well provided for. There are however no special muscles in the middle of the segment. Very probably, therefore, the phenomenon of fragmentation is provoked by an unusually strong contraction of the longitudinal muscles, especially of the dorsal bundles, accompanied by the swelling mechanism of the intestine, but this explanation leaves us entirely ignorant as to why the chain of *pictus* EHLERS.

segments

39—42	43—45	46—48	49—52	53—56	57—60	61—64	65—68	69—72	73—76	77—80	*x*	*P*
4	3	3	4	4	4	4	4	4	4	4	(*x* *P*)	
–	–	–	–	– ×	…………	…………	…………	…………	S 76			20^2
–	–	(1+2)	–	– ×	…………	…………	…………	…………	…………	S 78		22
–	–	–	–	–	–	–	(2+2)	(3+1)	× ……	S 80		8
–	–	–	–	– ×	… reg.							
–	–	–	–	–	–	(3+1)	–	–	× ……	S 79		7
–	–	–	–	–	(3+1)	–	–	× ……	S 75			7
–	–	–	–	– ×	…………	…………	…………	S 70				14
–	–	–	–	– ×	…………	…………	…………	…………	S 73			17
–	–	–	–	–	–	–	–	× ……	…………	…………	S 85	17
…..reg.												
–	–	–	–	– ×	…………	…………	…………	S 70				14
	× ……	…………	S 50									8
–	–	–	–	–	–	–	–	–	–	× …..	S 81	5
–	–	–	–	–	–	–	–	–	× S 73			1
–	–	–	–	–	–	–	–	–	× ……	S 79		7
–	–	–	–	–	–	–	–	× ……	S 73			5
–	–	–	–	–	–	–	–	–	–	× …..	S 81	5

segments breaks up so regularly in definite positions, while the muscle bundles and the intestine, which are supposed to be either directly or indirectly concerned with the phenomenon, are repeated regularly with the other metameric structures, one after the other throughout the entire length of the body, except only in the anterior part and in the posterior extremity, where fragmentation does not take place. At length I found the reason. While I delayed to describe it H. LANGHAMMER (1928, p. 30) has mentioned the same fact in a somewhat different way.

"Auf Grund des gesetzmäßigen Beginnes der Stolonen in Verbindung mit den gesetzmäßig auftretenden Darmeinschnürungen, wie sie meine Beobachtung zeigten, läßt sich allein schon vermuten, daß die Proliferationszonen bei *Autolytus* schrittweise von hinten nach vorn verlagert werden." LANGHAMMER finds the "gesetzmäßig auftretenden" intestinal constrictions also in *Pionosyllis*.

"Von *P. pulligera* (KROHN, Südaustralien) fanden sich ein Kopfstück mit 9 Segmenten, das hinter dem 7. eine Einschnürung zeigte, zwei mit 11, ein weiteres mit 13 und ein vollständiges Tier mit 22 Segmenten und einer Einschnürung hinter dem 9. Ein stark beschädigtes Exemplar von *P. Weismannoides* (AUGENER, Shark Bay) weist hinter dem 13., 16. und 19. Segment Einschnürungen auf, während eine *P. spec?* (Uschnaia) hinter dem 16. und eine andere derselben Art hinter dem 19. Segment geteilt war. Von *P. Stylifera* (EHLERS, ohne Fundort), das durch ein Kopfende mit 11, zwei mit je 16 und ein weiteres mit 26 Segmenten vertreten war." It is interesting to notice that among Syllids fragmentation has only up to the present been experimently provoked in the genera Autolitinae and in *Pionosyllis* (refer E. J. ALLEN 1927).

The Polychaete body represents, it is almost unnecessary to say, a chain of segments, which are similarly constructed and only separated from one another by a septum. The septa are however incomplete, being absent on the dorsal side, in a certain number of the anterior segments, where in Syllids there occur the large pharynx and the massive proventriculus, enclosed in the peripharyngeal cavity. In this front part of the body fragmentation does not take place, and accordingly it does not further concern us. Proceeding backwards, the alimentary tract presents a moniliform appearance, swelling in the middle of each segment and narrowing between two swellings; this shape of the intestine is due to a constriction between two segments caused by the development of a septum, the hystological structure of which has been described by A. MALAQUIN (1893) and H. LANGHAMMER (1928, Taf. III, fig. 53 and 54).

The integument of Syllids, as already stated, is quite transparent in living or freshly killed specimens. Thanks to this transparency, we can easily observe every detail of internal structure from without. The septa are observed as thin screens hanging down between two intestinal swellings, being of the same thickness, length and state of development. But exceptions to this general structure of the septa are found in those species in which the phenomenon of fragmentation is pronounced. There are, in these, thick and long septa, that are developed more than usual. They are found to be interpolated among those of the usual size with great regularity, in positions which corresponding exactly to the "Darmeinschnürungen" of LANGHAMMER, in *Autolytus*, *Procerastea*, *Myrianida*, as well as in *Pionosyllis*. The term "mega-septa" is proposed for them and they are localized in *Autolytus pictus*, for example, in positions between two segments, namely between 11 and 12, 13 and 14, 16 and 17, 19 and 20, 22 and 23, 26 and 27, 30 and 31, 34 and 35, 38 and 39, 42 and 43, 45 and 46, 48 and 49, 52 and 53, 56 and 57, 60 and 61, 64 and 65, 68 and 69, 72 and 73, 76 and 77, etc. Now what do we learn from these positions of the mega-septa? Do they not exactly agree with the positions of the white bands, which in their turn indicate the breaking points in the fragmentation of the Syllid? In *Myrianida pinnigera* the positions of the mega-septa are found to be always just in front of the segments which bear the coloured bars, and these are also the points of fragmentation. Again in *Procerastea Halleziana*, the positions of the mega-septa and the points of fragmentation exactly coincide with one another. In fig. 33 the general arrangement of the septa in *Autolytus pictus* is illustrated in a rather diagrammatic way, and to assure it the microphotographe (a horizontal section) of the same animal is reproduced in fig. 34.

That the points of fragmentation can be recognized inan external view of the animal by the presence of special pigmentation is suggestive for the further study of this problem. E. F. ANDREWS (1891) has already made an interesting statement regarding the regular arrangement of the colour band of *Autolytus tardigrada*. "The female has a dark dorsal transverse band upon somites 3, 6, 8, 13, 17, 21, 25, 27, 29, 32, 35, 38, 42, 46, 49, 51, 53, 56, 57, 70, 71, 74, 77 . . . . . The nonsexual form has pigmented bands like those of the female, but arranged according to a definite law or general rule, to which the bands in

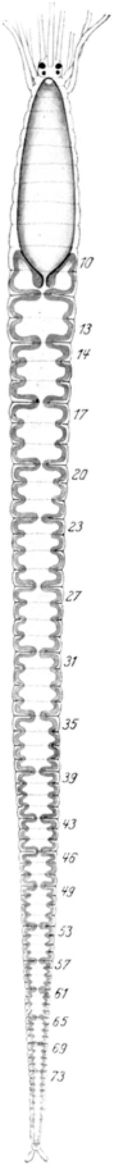

Fig. 33.

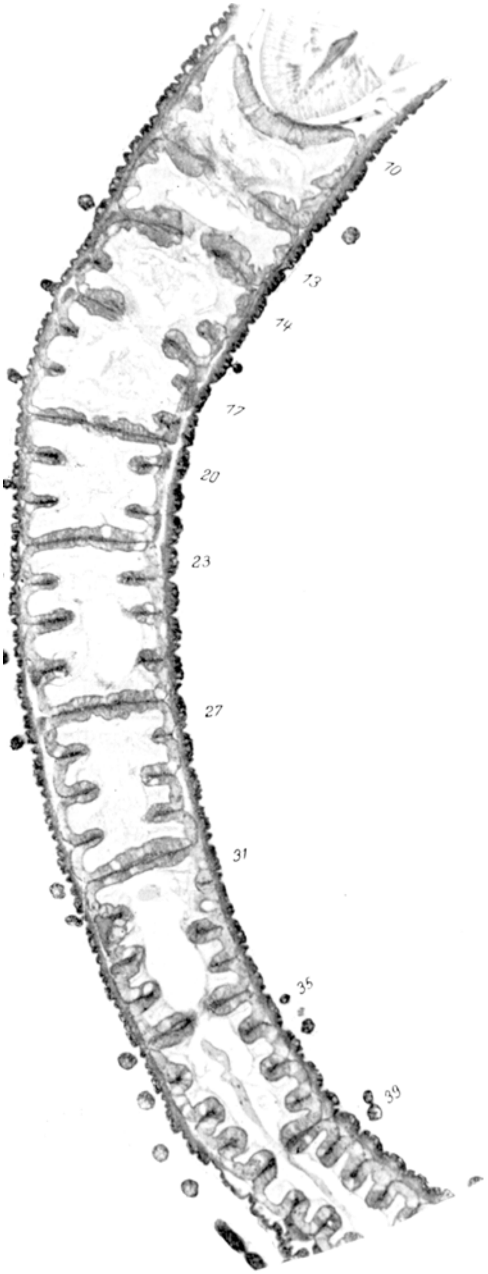

Fig. 34.

Fig. 33. Semi-diagramatic illustration of the positions of the mega-septa in *Autolytus pictus* EHLERS. × 15. — **Fig. 34.** Microphotograph to conform the preceding illustration of mega-septa (in horizontal section). × 53.

the female conform also; bearing in mind that the female is formed as a cut off part of the non-sexual stage, separating almost always just posterior to the 13th somite, and hence having 13 less somites than that stage." "Having tabulated the arrangement of the coloured band in these 110 individuals, there results the general rule that the bands occur upon the 3rd and 4th somites, then upon every other or alternate one up to and including the 12th, then (in the region of the bud) upon every fourth one up to and including the 25th, then upon every fifth one up to and including the 41st, after which the exceptions become so numerous that no rule is evident. The examination of so many cases shows a definite tendency to limitation in the bands to certain somites in the anterior region, and a greater and greater irregularity in the posterior region." Although the author seems not to have been aware of the significance of these positions of pigmentation, he however suggests that "these facts seem sufficient to indicate that we have in the Syllid a marked tendency to the acquirement of a regular metameric marking, which, however, does not coincide with the metamerisation of the somites, but tends to follow a special law best expressed in the oldest part of the body, in which certain alternating coloured and not-coloured somites are distinguishable—a series of groups or combinations of somites, thus following one another". It may be notices that in the above description the 25th and 41st of the coloured segments are, in reality, the 26th and 42nd segment respectively, as these two positions correspond to the 13th and 29th segment of the separated stolon. ANDREWS himself has indicated these two segments of the latter as colour bearing, and separations of the stolon as taking place between the 13th and 14th setigerous segment. The positions of the coloured segments in this case are always just behind each group of segments, at the anterior end of the first segment of the next group as in *Myrianidia*. In *Pionosyllis stylifera* the pigmentations, according to H. LANGHAMMER (1928, p. 30), is just on the boundary of two segmental groups, "die nach dem 13., 16., 19., 22. und 26. Segment auffallend stark gegenüber den übrigen ausgeprägt und somit ein ganz anders geartetes, rein anatomisches Merkmal für die Segmentgruppierung zutage treten lassen (fig.59)".

There is a strong development of muscles in the septa, the fibres of which strech diagonally and circularly around the central apenture, though which the alimentary tract passes from one segment to the other. The muscles are especially developed in the mega-septa and their function in connection with the phenomenon of fragmentation will now be understood, as well as their regular occurrence in the serial arrangement of segments. The function of the mega-septa is also interesting in relation to wound closure in the mutilated worm. When *Autolytus pictus* is cut across at any level of the body, but not anterior to the 14th setigerous segment, and if this level be not in one of the white bands, a deep constriction will almost invariably appear in the white band immediately in front of the group of segments in one of which the cut is made, and this hinder small piece is then droped off. For example, if the 25th setigerous segment be cut, a constriction appears between segments 22nd and 23rd and the group of segment 23rd + 24th is cast off. In the same way if the cut be made in any of segments from 27th to 30th, caudal regeneration in always started from the end of the 26th setigerous segment, instead of from the actual posterior end at the time of operation. However, this clever device of the wound closure is rarely seen in front of the 14th setigerous segment, where the mega-septa are incomplete, and the regeneration takes place at the actual hinder extremity, whether the operated segment bears the white band or not.

In the Autolytinae the positions of the mega-septa are intimately connected with the positions of stolonization, but this problem I shall postbone until another occasion, and I shall now close this second part of "Studies on the Syllidae" with the following summary.

Summary.

1. Regeneration takes place easily at the posterior end of divided Syllids, if the extremely anterior part be not cut, where the segmental cavities combine to from the common peripharyngeal chamber containing the ectodermal part of the alimentary tract. The faculty for this regeneration is generally complete.

2. The limit of the ectodermal structure in the alimentary tract is found at the posterior end of the ventricule, while the so-called "ventricular coeca" belong to the intestinal part. The front part of the alimentary tract which is derived from a stomodeal invagination runs through different number of anterior segments in different species. On cutting the animal in this region regeneration does not take place in the caudal direction. This seems to be due to the fact that the front piece is deficient in endodermal elements.

3. It is generally stated that in Polychaetes, all the mesodermal organs and tissues are re-established in regeneration from those cells which have migrated secondarily into the body-cavities from the ectoderm, that is to say reconstitution of the new organs and tissues is independent of their original embryonic differentiation. In Syllids this accout does not holds true. There is no evidence that the secondary "mesodermal bands" receive any contribution from such migrated ectodermal cells. All the mesodermal elements are mesenchymatized at the beginning of the regeneration process, and from these cells areise *de novo* the mesodermal bands. Ingrowth of ectodermal cells does, however, occur; it is observed on the ventral aspect of the regeneration bud, but these cells are exclusiv-

ely for the re-establishment of the nervous system in the new segments and play no other rôle in regeneration.

4. The intestine found in the last segment of an operated animal, is first constricted in the middle, and the hinder section, with the rejuvenated cells, then elongates directly backwards, and passes through the body-wall form inside outwards. Therefore, there is no proctodeal invagination in the new tail.

5. In schizogamy, after the separation of the stolon, the missing segments are restored with greath rapidity. There is generally a process of simple regeneration, but sometimes a certain number of new segments have been formed before the first stolon swims away. Again, in some species two separate half rudiments first grow out the parent stock and unite later to form a complete median tail rudiment (*Trypanosyllis*). Fusion takes place even after the separation of the stolon (*Syllis*). In these cases a part of the intestine, at least, is composed of the ectodermal layer, instead of being a direct elongation of the posterior end of the original intestine, as in the experimental case of regeneration.

6. The faculty of anterior regeneration is exceedingly variable in different Syllids. *Syllis spongicola*, *Syllis prolifera*, *Trypanosyllis zebra* and *Autolytus Edwarsi* do not generally form more than one setigerous segment, in addition to the head and there is absolutely no stomodeal invagination. There is of course no new formation of the pharynx at all, while the front end of the intestine elongates forwards and passes directly through form within outwards, as at the posterior end. Sometimes a heteromorphic tail-end is produced in place of the head.

7. On the other hand, the regenerative capacity of *Syllis gracilis* and *Procerastea Halleziana* is limitless and there is a complete recovery of the missing parts, including a new formation of the entire system of the pharyngeal apparatus. These Syllids reproduce in nature by a wonderful method of fragmentation with accompaning regeneration of the missing parts. The regenerative faculty of each fragment seems to be the same everywhere in the body.

8. The similar groups of segments are not equipotent in *Autolytus pictus*, in which the segments of the anterior, the middle and the posterior part of the body are quite different in respect to their faculties of regeneration. From the tip of the head to the end of the 5th setigerous segment the number of new segments always corresponds to that of missing ones. Behind this level the new setigerous segments are by no means always the same as the number missing, being sometimes only 3 or 4, however great the injury. But we can still have the same number of missing segments to the end of the 7th setigerous segment. The same maximum regeneration behind this segment cannot as a rule exceed 4 setigerous segments, in addition to the head, and this 6-meric recovery holds to the end

of the 13th setigerous segment, but absolutely no further. So that when cut is done in the 14th segment, the anterior regeneration is suddenly reduced to the head section and at the most one setigerous segment in addition, when a young sexually immatured worm is employed, otherwise only to the head. An anterior regenerration is found until about the 42nd setigerous segment, and behind this level the tail-pieces remain always headless.

9. Stomodeal invagination takes place in *Autolytus pictus* in every case without exception to the end of the 13th setigerous segment, and there is a complete recovery of the pharyngeal apparatus. However, there is absolutely no new formation of the pharynx after this segment. Further, there are three variations in the regenerated head after this critical level; the head may be that of an asexual individuel, of a *Polybostricus* or of a *Sacconereis*, according to the sexuality and the degree of sexual maturity of the material employed.

10. In *Autolytus pictus*, if we cut off the anterior segments at the front of the 12th or 13th setigerous segment, double head regeneration is often produced, with an appearance of a second head on the 14th segment. Sometimes, while the second head is distinctly developed, there are no reproductive products in the posterior segments at all. In such a case the second head has always the same morphology as that of the first, viz. the asexual type.

11. The peripharyngeal chamber seems to determine in Syllids the length of the head-pieces from which a caudal regeneration is first possible, and this length roughly corresponds also to the anterior pieces of fragmentation, including the head.

12. The rule of fragmentation is expressed by the following formulae, for the genus *Procerastea*: $H\,7+2+2+2+3+3+3+4+4+4+4(+4)+3+3+3+3+3+3+\ldots\ldots x\,P$; for the genus *Autolytus*: $(H\,7+2)+2+2+3+3+3+4+4+4+4+4+3+3+4+4+4+4+\ldots\ldots x\,P$; for the genus *Myrianida*: $(H\,7+2+2+2)+3+3+3+4+4+4+3+3+4+4+4+4+4+4+3+3+\ldots\ldots x\,P$; for the genus *Pionosyllis*: $(H\,7+2)+2+2+3+3+3+4+4+4+4+4+4+\ldots\ldots x\,P$; and somewhat $(H7+2+2+2+3+3+3+4+)+4+4+4+3+3+4+4+4+3+3+4+4+4+4+3+3+3+3+3+3+3+3+3+$ etc. in *Trypanosyllis zebra*.

13. The fragmentation would seem to be provoked by an unusually strong contraction of the longitudinal segmental muscles, but the positions of breaking are pre-destinated by the special arrangement of megasepta, the presence of which can be seen by external observation through the transparent integument, as particularly deep constriction in the alimentary tract. In some species, in which special pigmentation develops in certain segments, the pigmentation may be found sometimes in those segments just in front of (*Autolytus tardigrada*) or sometimes just behind

(*Myrianida pinnigera*) or at other time exactly upon (*Pionosyllis stilifera*) the mega-septa. In *Autolytus pictus* there are transverse bands free of pigment at the positions of mega-septa.

14. The regenerative faculty of the sexual animals is very limited, but certain stolons of the Autolytinae have the structure of their anterior segments more complex than if they were merely a simple separation of the posterior segments of the parent stock with a regeneration of the head. Several setigerous segments following the new head more or less resemble the original structure. Such an economy of labour in regeneration, by changing the arrangement of certain of the old parts so as to complete the model of the original animal, is evident in those stolons having large number of segments such as *Autolytus alexandri* or the stolons of *Procerastea*.

Deutsche Übersetzung der Zusammenfassung.

1. Eine Regeneration des Hinterendes tritt bei durchschnittenen Sylliden regelmäßig ein, wenn nicht die Durchtrennung in dem vordersten Körperabschnitt erfolgt, wo die aus mehreren Segmenten verschmolzenen Cölomabschnitte den ektodermalen Vorderdarm umschließen. Im allgemeinen tritt ein vollständiger Ersatz des abgeschnittenen Teiles ein.

2. Die Grenze des ektodermalen Teiles des Verdauungskanals befindet sich am hinteren Ende des Magens, während die Darmblindsäcke dem entodermalen Mitteldarm angehören. Der Vorderdarm, der embryonal von dem Stomodeum abzuleiten ist, erstreckt sich bei den einzelnen Arten durch eine verschiedene Anzahl von Segmenten. Daß bei einer Durchtrennung in diesem Körperabschnitt keine Regeneration erfolgt, läßt sich vielleicht darauf zurückführen, daß hier keine entodermalen Zellelemente vorhanden sind.

3. Man nimmt gewöhnlich an, daß bei Polychäten alle mesodermalen Organe und Gewebe bei der Regeneration von den ektodermalen Zellen ersetzt werden, nachdem diese zuvor in die Leibeshöhle gelangt sind, das heißt also, daß die Widerherstellung neuer Organe und Gewebe ganz unabhängig von der ursprünglichen embryonalen Differenzierung erfolgt. Das gilt aber nicht im vorliegenden Falle. Hier findet man keinen Anhaltspunkt dafür, daß die sekundären Mesodermanlagen sich aus solchen umgewandelten Ektodermzellen zusammensetzen. Alle mesodermalen Gewebe können sich zu Beginn des Regenerationsprozesses in Mesenchymzellen auflösen, und aus diesen Zellen entstehen dann die neuen Mesodermanlagen. Ein Hineinwachsen des Ektoderms geschieht an der ventralen Seite der Regenerationsknospe, aber diese Zellen werden nur zur Bildung des Nervensystems in den neuen Segmenten verwandt und spielen weiter keine Rolle bei der Regeneration.

4. Der Darmteil, der sich im letzen verbleibenden Segment des operierten Tieres befindet, wird zunächst in der Mitte zusammengeschnürt,

der hintere Teil verjüngt sich dann und durchbricht die durch Wundheilung gebildete Körperwand. Daher kommt es nicht zur Bildung eines ektodermalen Enddarmes.

5. Bei der Schizogamie werden nach der Abtrennung des Geschlechtstieres die verlorenen Segmente mit großer Schnelligkeit wieder ersetzt. Man beobachtet hierbei gewöhnlich eine einfache Regenerationsweise, aber zuweilen bildet sich schon vor Ablösung des Geschlechtstieres eine gewisse Zahl neuer Segmente an der Abtrennungsstelle. In anderen Fällen treten zunächst zwei Halbanlagen des Schwanzes seitlich an der Ablösungsstelle auf. Diese können sich noch vor der Ablösung des Geschlechtstieres vereinigen (*Trypanosyllis*-Arten) oder aber erst nach der Ablösung (*Syllis*-Arten). In diesen beiden letzgenannten Stellen besteht wenigstens ein Teil des neugebildeten Darmes aus Ektoderm, während bei der experimentalen Regeneration der neue Darmteil durch direkte Verlängerung des Mitteldarmes zustande kommt.

6. Die Regenerationsfähigkeit des Vorderdarmes ist sehr verschieden bei den Sylliden. *Syllis spongicola, Syllis prolifera, Trypanosyllis zebra* und *Autolytus Edwarsi* regenerieren nie mehr als ein borstentragendes Segment und einen Kopf ohne ektodermale Einstülpung, da, wie bei der Regeneration des Enddarmes, auch hier ein Durchwachsen des entodermalen Mitteldarmes nach vorn erfolgt. Zuweilen bildet sich ein heteromorphes Schwanzende an Stelle des Kopfes.

7. Dagegen tritt bei *Syllis gracilis* und *Procerastea Halleziana* eine vollständige Wiederherstellung der verlorenen Teile einschließlich der Neubildung des ganzen ektodermalen Vorderdarmes ein. Diese Syllidenarten vermehren sich in der Natur durch eine sonderbare Methode, sie zerfallen nämlich in kleine Teile. Hierauf erfolgt eine vollständige Regeneration bei allen Teilstücken.

8. Die entsprechenden Segmentgruppen bei *Autolytus pictus* sind nicht äquipotent, sondern die Segmente des Vorder-, Mittel- und Hinterkörperteils zeigen eine sehr verschiedene Regenerationsfähigkeit. Vom Kopfende bis zum hinteren Ende des 5. borstentragenden Segments entspricht die Zahl der neugebildeten Segmente immer derjenigen der verlorenen Segmente. Hinter dieser Grenze ist die Zahl der neugebildeten borstentragenden Segmente keineswegs immer dieselbe wie die der verlorenen; zuweilen beträgt sie nur 3 oder 4, je nachdem, wo die Durchschneidung erfolgt. Meistens aber erfolgt ein Ersatz aller verlorenen Segmente bis zum Ende des 7. Segmentes. Bei einer Durchtrennung zwischen dem 8. und 13. (einschließlich) Segment erfolgt im Maximum eine Regeneration von 4 borstentragenden Segmenten und einem Kopfteil. Wird der Schnitt durch das 14. Segment geführt, so werden nur bei jungen, noch nicht geschlechtsreifen Würmern ein borstentragendes Segment und der Kopfteil neu gebildet, sonst aber nur der Kopfteil. Eine Regenera-

tion des Kopfteiles erfolgt bis zum 42. borstentragenden Segment; hinter dieser Grenze bleiben die Schwanzstücke immer ohne Kopf.

9. Eine ektodermale Einstülpung und eine vollständige Wiederherstellung des Schlundapparates findet bei *Autolytus pictus* bis zum Ende des 13. borstentragenden Segments regelmäßig statt. Hinter diesem Segment tritt niemals eine Neubildung des Schlundes ein. Die Köpfe, die nach Durchschneiden hinter dieser Grenze (13. Segment) neu gebildet werden, weisen den Bau eines männlichen, weiblichen oder ungeschlechtlichen Individuums auf, je nach der Sexualität des verwendeten Tieres bzw. der sexuellen Reife.

10. Beim Durchschneiden in der Gegend des 12. oder 13. borstentragenden Segmentes bildet sich häufig außer dem normalen Kopf noch ein zweiter an der dorsalen Seite des 14. Segmentes. Gelegentlich erkennt man in den nachfolgenden Segmenten keine Geschlechtsprodukte. In diesem Falle weist der zweite Kopf den Bau des ungeschlechtlichen Tieres auf.

11. Die Länge der noch regenerationsfähigen Vorderenden (Kopfstücke) des Wurmes wird durch die Länge der den Vorderdarm umgebenden Leibeshöhle bedingt. Ebenso scheint hiervon die Länge des vordersten Teilstückes bei experimentell hervorgerufenen Zerfallserscheinungen bestimmt zu werden.

12. Die Regel des Zerfalls läßt sich mit folgenden Formeln ausdrücken, für die Gattung *Procerastea*: $K\,7+2+2+2+3+3+3+4+4+4+4(+4)+3+3+3+3+3+3\,\ldots\ldots\,x\,P$; für die Gattung *Autolytus*: $(K\,7+2)+2+2+3+3+3+4+4+4+4+4+3+3+4+4+4+4+4+4+\,\ldots\ldots\,x\,P$; für die Gattung *Myrianida*: $(K\,7+2+2+2)+3+3+3+4+4+4+3+3+4+4+4+4+4+4+3+3+\,\ldots\ldots\,x\,P$; für die Gattung *Pionosyllis*: $(K\,7+2)+2+2+3+3+3+4+4+4+4+4+\,\ldots\ldots\,x\,P$ und bei *Trypanosyllis zebra* etwa $(K\,7+2+2+2+3+3+3+4+)+4+4+4+3+3+4+4+4+3+3+4+4+4+4+3+3+3+3+3+3+3+3+3+$ usw.

13. Der Zerfall ist wohl auf eine ungewöhnlich starke Kontraktion der Längsmuskulatur der Körperwand zurückzuführen, aber die Lage der Durchschnürungsstelle ist durch eine besondere Einrichtung, die Riesendisseptimente, vorbestimmt, deren Vorhandensein sich von außen durch die durchsichtige Körperwand an den tiefen Einschnürungen des Verdauungskanals bemerkbar macht. Bei einigen Arten tritt eine besondere Pigmentation in bestimmten Segmenten auf, und zwar kann diese Pigmentation in dem Segment, welches dem Riesendisseptiment vorausgeht, auftreten (*Autolytus tardigrada*) oder in der dahinterliegenden (*Myrianida pinningera*), zuweilen auch gerade auf dem Riesendisseptiment (*Pionosyllis stylifera*). Bei *Autolytus pictus* finden sich an den Durchschnürungsstellen pigmentfreie Querstreifen.

14. Die Regenerationsfähigkeit des Geschlechtstieres ist sehr gering.

Bei gewissen Stolonen von Autolytinae tritt aber eine Komplikation im Bau der auf den neugebildeten Kopf folgenden und vom Muttertier übernommenen Segmente ein. Sie gleichen dann in ihrem Bau den auf den Kopf des Muttertieres folgenden Segmenten. Eine ähnliche Umbildung an alten Segmenten, die gewissermaßen eine Ersparnis an neugebildeten Segmenten darstellt, findet man besonders bei den aus einer großen Zahl von Segmenten bestehenden Stolonen, z. B. *Autolytus alexandri* und Stolonen von *Procerastea.*

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Key to the Abbreviated Terms used in the Figures.

a, anus, anal position; *anterior*;
ac, acicula;
ch, chitin, chitinous investment;
am, ampulla-like structure;
cn, intestinal constriction in regeneration;
co, buccal cavity;
cp, peripharyngeal cavity;
cr, cirrus;
cx, cicatrix;
dt, pharyngeal gland;
e, eye;
ec, ectoderm;
eg, ingrowth of the ectoderm;
en, endoderm; intestinal fragment;
gd, reproductive organ;
gn, nerve ganglion;
gnc, cephalic ganglion;
gn o, peristomial ganglion;
gns, segmental ganglion;
in, intestine;
l, *longitudinal* or *lateral*;
m, muscle; *median*;
ms, mesoderm, mesodermal band;
mss, mesenchyma;
o, mouth, oral position;
ov, ovary;
p, pygidium; *posterior*;
ph, pharynx;
pl, palp;
pm, peritoneum;
pr, proctodeum or corresponding part of the intestine;
Pv, proventriculus;
Ra, anterior regeneration or head of the stolon;
Rp, posterior regeneration;
$^{1}/_{2}Rp$, semi-rudiment of the tail;
S, segment, *segmental*;
sm, somatoplura;
sp, septum;
st, stomodeum, stomodeal invagination;
tn, tentacle,
ten l, lateral tentacle;
ten m, median tentacle;
ts, testicle.