

## Regeneration in the polychæt *Chætopterus variopedatus*.

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With 4 Figures in the Text.

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THE members of the family Chætopteridæ are the most highly differentiated and most truly tubicolous among polychæt worms. In view of the ability to autotomise developed in connection with the tubicular habitat and the great specialisation of the different segments, a study of the phenomena of regeneration in this group becomes of special interest. *Chætopterus variopedatus*, the species most abundant and readily obtained in European waters, has been examined from this aspect.

This worm inhabits parchment-like semicircular tubes, which may or may not be buried in mud save for the two open extremities. It occurs from the low-water level to at least thirty fathoms, and may be found in extraordinarily large numbers. The morphology of this form has been investigated very thoroughly by Joyeux-Laffuie (1890), while the habits, general physiology, and development have been described by Enders (1909), but it is necessary for the present purpose to give a brief account of its structure and behaviour.

The body may be divided into three parts: anterior, middle, and posterior, the homologies of which have been well made out by Laffuie.

The anterior part, or so-called head, has been shown by him to consist of eleven segments, of which only the last nine are setigerous, and the whole forms a massive trowel-like structure with a terminal funnel-shaped mouth.

The middle region shows by far the greatest diversity of structure and consists of segments twelve to sixteen (see Fig. 1). Segment 12 bears a pair of large aliform notopodia, each possessing a ciliated furrow which unites with a furrow from the anterior region (see Fig. 4, A). The neuropodia are fused to form a powerfully adhesive disc, as also are those of segment 13.

Segment 13 is much elongated and contains the more dilated part of the green intestine, which undergoes peristalsis. The mid-dorsal part of the segment is greatly modified to form what Laffuie describes as a sucker, but which is said by Enders to be an accessory feeding organ.

This latter view is confirmed here, and never in several hundred cases has it been observed to act as a sucker. It is in the form of a cowl opening antero-dorsally, and is lined with cilia continuous with the dorsal ciliated furrow running forwards to that joined by the furrows of the aliform notopodia mentioned above. Segments 14, 15, and 16 have their dorsal parts expanded to form circular fan-like structures, which beat rhythmically. The ventral parts of each form an adhesive disc, though not so powerful as those of segments 12 and 13.

The posterior region may consist of as many as fifty segments, according to the age of the worm, and contains the sexual elements, male or female as the case may be. The segments of this region are all alike.

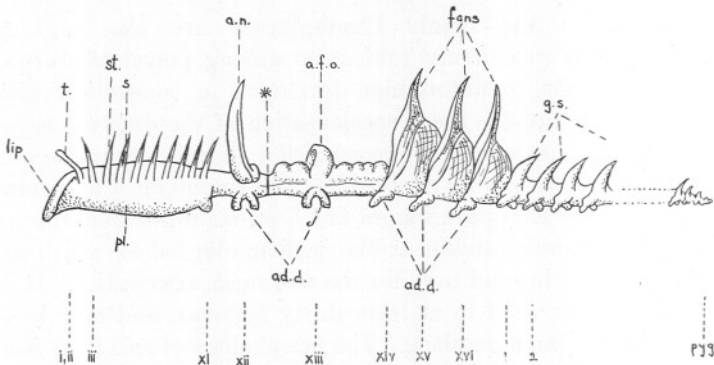


FIG. 1.—Diagram of *Chaetopterus* showing order and types of segments: i-xvi-1-2, etc., segment numbers; *pyg.*, pygidium; *t.*, tentacle; *pl.*, plastron; *st.*, setigerous segment; *s.*, stout setae; *g.s.*, genital segments; *a.n.*, aliform notopodia; *a.f.o.*, accessory feeding organ; \*, autotomy level.

The animal normally lives completely within its tube, and the various specialised segments just described have been evolved for such an existence.

When undisturbed it lies along the base of the tube, so that the trowel-like "head" is closely opposed to one side, reducing the effective bore of the tube by about one-sixth. It is fixed in position by the especially stout setae of the third setigerous segment. The rest of the body is held close to the side of the tube by the ventral suckers of the twelfth and thirteenth segments and to a less extent by those of the three succeeding segments. The large flattened notopodia of segment 12 extend dorsally along the side of the tube to meet above, thus forming an arch through which the water current produced by the rhythmically beating fan segments has to pass. The co-ordination of these fan segments has already been described (Berrill, 1927).

The animal feeds on planktonic and detrital matter brought in by the

water current. This current passes over the ciliated mouth, between the aliform notopodia, the inner sides of which are ciliated, and converges on to the accessory feeding organ on the thirteenth segment, and thus altogether is exposed to extensive ciliary fields which carry forward to the mouth any particles that may have been brought in with the water. According to Enders there is a ciliary sorting mechanism for such particles in the region of the mouth.

While normally the worm lives completely within its tube, it not infrequently protrudes its anterior end, the white or creamy colour of which becoming a very obvious mark to any passing fish. This must be of such frequent occurrence in nature that autotomy has been developed and has a survival value for the species. When any sudden pull is made on the anterior "head" region, a local but very strong contraction of circular muscles of the body wall occurs between segments 12 and 13, cutting through all the more internal tissues and dividing the animal into two parts. In this way the genital and current-producing segments would be saved at the expense of the less valuable head region. The ability to autotomise and of the posterior piece so formed to regenerate the missing twelve anterior segments has long been known.

In most cases where regeneration has occurred, the regenerated tissues may readily be distinguished by their white delicate nature from the coarser cream or brownish tissues of the original piece. On this basis 10-15 per cent of a *Chætopterus* community will be found in various stages of regeneration of the anterior part. After two or three months, however, it becomes impossible to distinguish by colour between regenerated and non-regenerated segments, and the total percentage of worms that have regenerated missing parts cannot be determined.

Fig. 2 shows anterior regeneration from an animal that autotomised. The regenerated tissue is about 2 mm. in length, and consists of the rudimentary head with terminal mouth and the beginnings of the tentacles and first two setigerous segments.

The animals used for experiment were divided between various adjacent segments and the pieces kept in finger-bowls into which water was allowed to drip or over which to flow, thus ensuring a plentiful supply of oxygen and the removal of waste products. The greatest difficulty was experienced in maintaining alive the pieces consisting of genital segments alone, the more muscular tissues of the anterior part, and the beating of the fans of the middle part rendering those regions relatively hardy. The results of the last two out of four different sets of experiments are summarised in the tables given below.

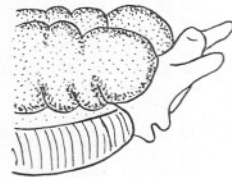


FIG. 2.—Anterior regeneration from segment 13 (autotomy) (see text).

TABLE I.

Large Roman numerals, e.g. XI, denote original segments.

Small Roman numerals, e.g. xi, denote regenerated segments.

Arabic numerals, e.g. 3, denote number of genital segments.

O, lack of regeneration.

+, junction between regenerated and regenerating segments.

-, junction between adjacent segments of like nature.

REGENERATION AFTER 95 DAYS AT 10-11° C.

| Type a. | Pieces consisting of segments I-XII. | Segments regenerated.                | No. of cases. |
|---------|--------------------------------------|--------------------------------------|---------------|
|         |                                      | I-XII + xiii-xiv-xv-xvi-5 genital.   | 1             |
|         |                                      | ” ” ” 6 ”                            | 1             |
|         |                                      | ” ” ” 7 ”                            | 3             |
|         |                                      | ” ” ” 8 ”                            | 1             |
|         |                                      | ” ” ” 9 ”                            | 1             |
| Type b. | ” I-XIV.                             | I-XIV + xv-xvi-4 genital.            | 2             |
|         |                                      | ” ” 6 ”                              | 1             |
|         |                                      | ” ” 8 ”                              | 1             |
| Type c. | ” I-XVI.                             | I-XVI + 5 genital.                   | 1             |
| Type d. | ” XIII.                              | i-xii + XIII + xiv-xv-xvi-8 genital. | 1             |
| Type e. | ” XIII-XIV.                          | i-xii + XIII-XIV + xv-xvi-5 genital. | 1             |
| Type f. | ” XIII-XV.                           | i-xii + XIII-XIV + xvi-8 genital.    | 2             |
| Type g. | ” XIII-XVI.                          | i-xii + XIII-XVI + 9 genital.        | 5             |
| Type h. | ” XIV.                               | i-x + XIV + xv-xvi-3 genital.        | 1             |
| Type j. | ” XV-XVI.                            | O + XV-XVI + 5 genital.              | 1             |
| Type k. | ” XV-XVI-Genital complete.           | O + XV-XVI-Genital complete.         | 3             |
| Type m. | ” XVI-Genital complete.              | O + XVI Genital complete.            | 3             |
| Type n. | ” Genital complete.                  | O + Genital complete.                | 2             |
| Type o. | ” 12 Posterior Genital.              | O + 12 Posterior Genital.            | 2             |

REGENERATION AFTER 45 DAYS AT 10-11° C.

| Type    | Pieces consisting of segments  | Segments regenerated.            | No. of cases. |
|---------|--|----------------------------------|---------------|
| Type d. | XIII.  | i-xii+XIII+xiv-xv-xvi-4 genital. | 2             |
| Type i. | XIV-XV.  | i-xiii+XIV-XV+xvi-6 genital.     | 1             |
|         |  | i-xi+XIV-XV+xvi-2 „              | 1             |
| Type k. | XV-XVI-Genital complete.   | O+XV-XVI-Genital complete.       | 2             |
| Type l. | XVI-3 Genital.   | O+XVI-3 genital+4 genital.       | 2             |
| Type o. | 12 Posterior Genital.  | O+12 Posterior Genital.          | 2             |
| Type p. | Numerous cases of regeneration of genital segments posteriorly from remaining genital regions. |                                  |               |

From these results two facts emerge. First, that while regeneration can take place posteriorly from any level, anterior regeneration is only possible from the fourteenth segment forwards; this level at which anterior regeneration ceases is very definite, for while regeneration may be completed from segment 14, there is none at all from segment 15 or any segment posterior to it. Secondly, where regeneration occurs at all, it is always complete, unless the original piece of tissue is too small to contain sufficient reserve food material. That is, since the majority of segments are perfectly recognisable by their peculiar structures, it appears very clearly that regeneration continues from any segment until that segment occupies in the new worm its original distinctive position (cf. Allen, 1921, p. 165). It is obvious, however, in the case of Chætopterus where regeneration occurs so commonly in nature, that had it been otherwise, striking diversities in structure of whole worms would long ago have been noted.

Fig. 3 shows the first fan segment

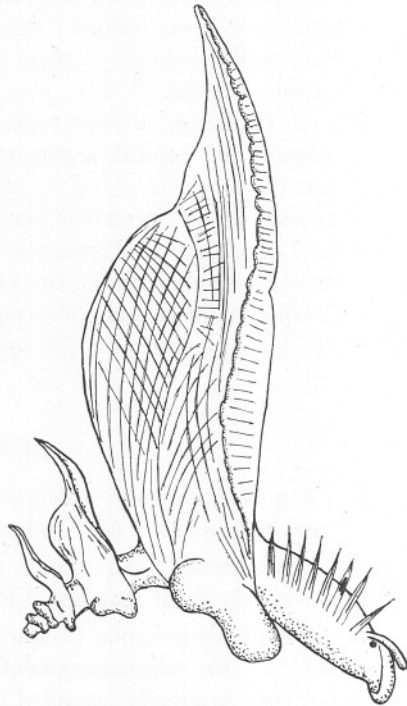


FIG. 3.—Anterior and posterior regeneration from (fan) segment 14.

(XIV) which was isolated ninety-five days before being drawn (see Type h in Table I). Posteriorly it has regenerated the remaining two fan segments and two to three genital segments, i.e. the zone of growth being terminal, the segments regenerated are already in their correct relative positions. Anteriorly, however, regeneration is not yet complete in that only the segments of the anterior part proper have been formed, segments xi, xii, and xiii being omitted. It may be noted that in this case the tissue comprising segment x merges directly with the muscular face of the fan segment and a zone of growth is ill-defined. That such a segment can regenerate forwards completely is shown by the first experiment recorded under Type b (Table I).

Fig. 4, A and B, shows regeneration posteriorly from the anterior piece resulting from autotomy, showing the characteristic flexure of the regenerated segments towards the ventral surface of the original part. Only in one instance was an autotomised "head" (Type a) found in a tube, which exhibited regeneration. This presumably had been kept healthy by the water current produced by the remainder of the animal in another region of the tube. Regeneration had occurred to a considerable extent, in that the thirteenth, fan segments, and twelve genital segments had been formed; moreover, the green pigment in the gut was very well developed, a stage not reached by experimental cases even after three months.

Fig. 4, C, shows anterior regeneration from the autotomy level, and regeneration of genital segments posteriorly from the hindmost fan segment (Type g).

The experiments recorded here, and others, were carried out at the Marine Laboratory at Plymouth during the last three years, and were only made possible through the kindness of Dr. E. J. Allen and the staff in affording facilities and collecting the material. Thanks are also due to Mrs. T. A. Stephenson for her care of experiments during my absence.

#### SUMMARY.

1. Regeneration from different levels in the polychaet worm *Chaetopterus vario pedatus* has been studied.
2. Regeneration can occur posteriorly from any segment, but anteriorly only from segment XIV forwards.
3. Where regeneration occurs at all, given sufficient time, it will be complete, i.e. the original segments occupy in the new worm the relative position they originally occupied in the old worm.

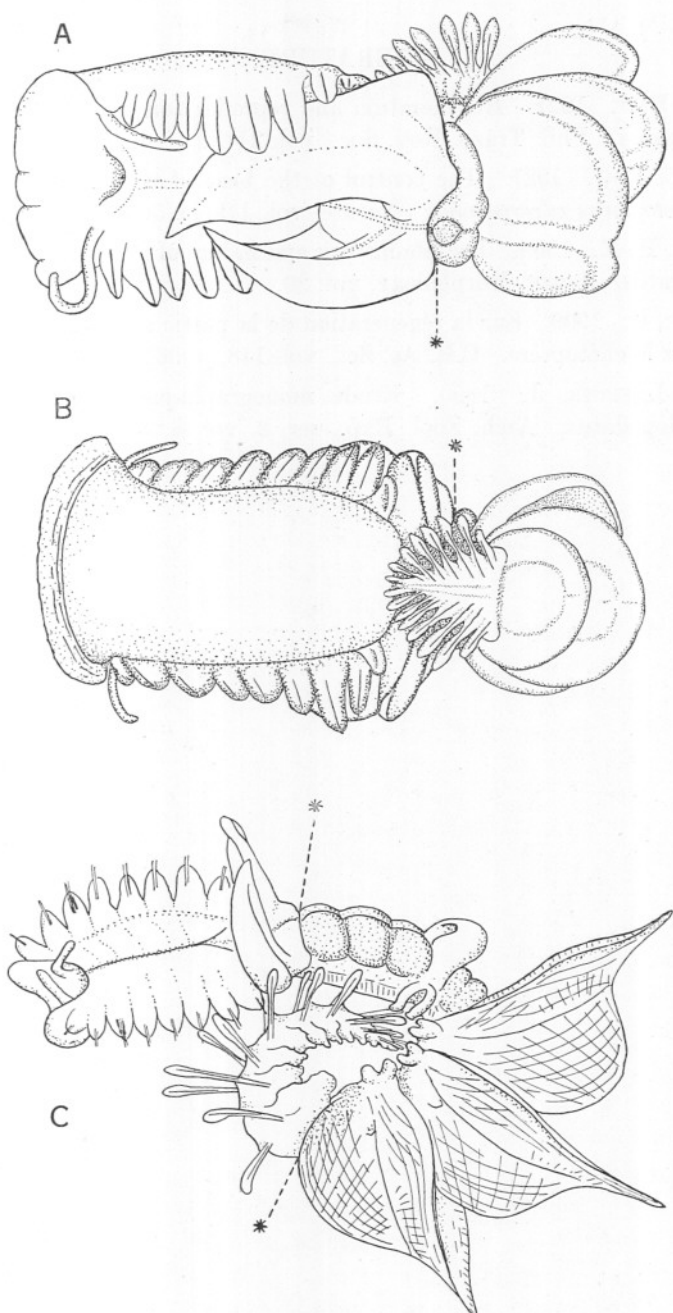


FIG. 4.—A, dorsal, B, ventral aspect of autotomised "head" showing posterior regeneration of fan and genital segments, reflected ventrally and anteriorly; C, segments XIII—XVI showing regeneration of "head" forwards from autotomy level and genital segments posteriorly from last fan segment.

\* Junction of old and new segments.

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