PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

# Regeneration and Reproduction of the Syllid Procerastea

E. J. Allen

*Phil. Trans. R. Soc. Lond. B* 1923 **211**, 131-177
doi: 10.1098/rstb.1923.0003

# III.—*Regeneration and Reproduction of the Syllid Procerastea.*

*By* E. J. Allen, *D.Sc., F.R.S., Director of the Plymouth Laboratory.*

(Received November 23, 1920,—Read February 24, 1921.)

[Plates 11–16.]

Contents.



## Introduction.

The family Syllidæ is divided into four sub-families, of which the sub-family Autolytea is characterised by the absence of ventral cirri on the setigerous segments. The genus Procerastea was established by Langerhans (1884) and is defined as an Autolytea in which the parent stock (souche) has dorsal cirri on the first setigerous segment only. Behind the first setigerous segment the parapodia consist simply of small lobes (neuropodia) from which a single bundle of setæ projects. Langerhans described under the name *Procerastea nematodes* a species he found in Madeira, which he states has a short pharynx provided with six indistinct teeth. Malaquin (1891, p. 175; 1893, p. 81) describes a second species of the genus found by him at Boulogne, characterised by a pharynx armed with a circle of 20 to 22 teeth and possessing a distinct loop, similar to that generally found in the genus Autolytus. Malaquin named his species *Procerastea Halleziana* and says (1893, p. 81) that the

 [Published, October 8, 1921.]

worm lives in the interior of the test of large Ascidians (Ciona) on hydroids and bryozoa.

Some specimens belonging to MALAQUIN's species were found at Plymouth in 1914 and recorded in the 'Journal of the Marine Biological Association' (ALLEN, 1915). These specimens were obtained from amongst Ascidians growing on a raft moored in Cawsand Bay.

In July, 1919, *Procerastea Halleziana* (Plate 11, figs. 1 and 2) was found living in large numbers on a species of the hydroid Syncoryne, which was growing luxuriantly on a floating pontoon in Millbay Dock, Plymouth, and it occurred in the same situation through the following winter and spring, though the hydroid colonies were greatly reduced in number during the cold weather.

The Syncoryne, with the Procerastea associated with it, was growing on the pontoon in a zone only 4 or 5 inches in depth, immediately below the surface of the water in the dock. Since the pontoon was floating the hydroid always remained in the same position relatively to the surface of the water, and was therefore unaffected by the rise and fall of the tide. The conditions, which seemed specially favourable for the growth of the species in question, were therefore such as do not often occur. In the spring of 1920 the pontoon was moved for repairs and since then it has not been possible to get more living specimens of the worm.

In consequence of the abundant supply of material, I have been able to make a more complete study of the habits and development of the worm than was possible to previous observers, and particularly to follow its rapid multiplication by fragmentation and regeneration.

I am greatly indebted to Mrs. SEXTON for the very faithful drawings which illustrate this paper, as well as for much assistance with the observations and experiments recorded in it.

## HABITS AND METHOD OF FEEDING.

The specimens of Procerastea upon which the present observations have been made seem under natural conditions all to have been living inside membranous tubes, which they had built along the stems of the hydroid Syncoryne. The tubes appear to be open at both ends and are sufficiently elastic for the worm to turn round on itself and travel either up or down the tube. The tubes are generally much longer than the worms which live in them and one of the openings is situated, certainly in a great many instances and probably always, just below the base of a hydranth.

When a colony of the hydroid is placed in a glass dish of clean sea water, some of the Procerastea leave their tubes almost at once, others in the course of a few hours and still others only after a few days. The majority creep up to the edge of the water, where they form fresh tubes which lie horizontally where the water meets the glass. A few form tubes, which they do not seem to leave, at any rate during daylight hours, on the bottom or sides of the dish. A few wander about the vessel without forming a tube at all for some considerable time. Under the conditions named the hydranths of Syncoryne generally drop off after a day or two, though fresh ones sometimes regenerate.

In connection with some experimental work on regeneration of the worm, it became important to find out exactly what its food was and this proved rather difficult. The Procerastea were always associated with the Syncoryne, but although the hydranths of the latter dropped off they never seemed to be eaten. The first hint of the real method of feeding was given by an observation made by Mrs. SEXTON who put one of the worms, which had been in a vessel of clean sea water and, therefore, without food for some days, in a watch glass with a few polyps of Syncoryne. After a time the Procerastea was seen to creep along a hydranth and to keep on applying its mouth to the mouth of the hydroid, and at one time she noticed what she thought must be a pumping action on the part of the worm. A similar observation was subsequently made on another specimen, but in this case although the animal was watched under the microscope for more than an hour repeatedly applying its mouth to that of the hydroid nothing that suggested a pumping action was seen, nor could it be seen, although carefully watched for, that the pharynx was extruded.

Eventually I was able to make an observation which made the whole matter quite clear. A specimen of Procerastea was selected in which the head and anterior segments had recently regenerated, so that this part of the worm was very transparent and a complete view of the long, looped pharynx and of the muscular proventriculus behind it (Plate 14, fig. 16) was obtained. The animal which had been for several days without the chance of feeding was put in a watch glass of sea water together with two stalks of Syncoryne bearing hydranths. It soon attached itself to the stem of the hydroid, lying along the stem in the position generally occupied by freshly-captured worms in their tubes, and moved up and down it, sometimes with the head towards the hydranth, at other times in the opposite direction. The experiment began at about 11·30 A.M. (Feb. 24, 1920) and the worm was watched at frequent intervals under a 1 inch power, but nothing in the nature of feeding was seen up to 1 P.M. On looking down the microscope at about 2 P.M. Procerastea was observed with its head just behind the last (basal) tentacle of the Syncoryne (Plate 14, fig. 12) a stream of moving granules was seen in the intestine and a kind of pumping action, which I did not then properly define, was going on in the fore part of the body. I realised that the worm was feeding, but almost immediately it drew back its head and I saw distinctly the protruded pharynx (*cf.* Plate 14, fig. 17). The worm withdrew some little distance down the stem.

It was then noticed that a streaming of granules in the gastral cavity of the Syncoryne and its stem, which had been noted on previous occasions, was very active from time to time, the stream flowing sometimes in one direction and sometimes in the other.

After a time the worm again crept up the stem and the head remained just behind the last tentacle of the polyp. Evidently the proboscis was protruded, for the coil of the pharynx straightened right out, and the pumping action previously noticed suddenly recommenced. I could see clearly a stream of granules passing along the pharynx, through the proventriculus and into the intestine. The cavity of the highly muscular proventriculus was enlarging and narrowing rapidly with a pulsating movement. The proventriculus clearly was functioning as a quick-acting pump, the pulsations, as estimated immediately afterwards from a memory of the rhythm, being at a rate of 150 to 200 per minute. The granules could be distinctly seen passing into the intestine where they continued in movement. They were of the same size and were certainly the same or similar granules to those seen in the gastral cavity of the Syncoryne. After the pumping process had continued for about a minute the head of the worm was withdrawn, but I did not this time catch sight of the protruded pharynx.

Watch was continued, but it was only after several hours that the feeding process was again seen, and then the view was not as good as that just described. The head of the worm was in the same position as before, granules in rapid motion were seen at the anterior end of the intestine and a general pumping movement in the anterior part of the body, but a clear view of the pharynx and proventriculus was not this time obtained. After about a minute the worm withdrew its head and I was fortunate in distinctly seeing the protruded proboscis withdrawn from the body wall of the hydroid.

The worm evidently on these occasions penetrated with the hard serrated edge of its proboscis the body wall of the hydroid just at the base of the hydranth, and pumped out the fluid from the gastral cavity.

That the proventriculus of Syllids functions as a pump has been clearly recognised by DE S. JOSEPH (1886, p. 152) and MALAQUIN (1893), amongst other authors, but their descriptions do not suggest that they have realised the rapidity of its action or the strong current which it can produce.

Sometimes, in a semi-moribund Procerastea, one can see the pharynx protruded (Plate 14, fig. 17), and an occasional particle drawn into it with some of the surrounding water, but these spasmodic sucking actions would never in themselves suggest the highly efficient quick acting pump which the proventriculus becomes when it is pumping out the contents of the gastral cavity of Syncoryne.

Judging by the vigorous growth of the hydroid on the pontoon, it would seem that the attacks of the worm do not injure it much, for the worms were exceedingly numerous on the stems of the hydroid. In small aquaria in the laboratory, no immediate effect was noticeable in the hydranth after the worm had fed, though it is true the hydranths usually dropped off after a day or two. But this dropping off of hydranths after a day or two generally takes place when such hydroids are put in small aquaria, whether the worms are present or not. The case seems to be one of pure parasitism, rather than an association of two species for mutual benefit, for it is difficult to see how the hydroid can get any advantage from the presence of the worm. The worm, on the other hand, obtains a constant supply of food, which the hydroid collects and partially digests. But the worm does not have it quite all its own way, for, on one occasion, a hydranth of the Syncoryne was seen which had half-swallowed a Sacconereis (the female bud full of ripe eggs) that had separated from a Procerastea, and was evidently digesting it.

MALAQUIN'S record of the species from inside the test of Ciona suggests that it may be parasitic not only on hydroids, but on Ascidians as well.

## DESCRIPTION OF PARENT STOCK OR SOUCHE.

As MALAQUIN'S description of *Procerastea Halleziana* is somewhat scattered through his large book on the family of the Syllidæ (1893) and his earlier paper on the reproduction of the Autolytea (1891), it may be useful to summarise it, in the following short account, with such additions as I have been able to make :—

The adult souche, which has just commenced to form the bud-head of a stolon, is a slender worm consisting of fifty to sixty segments, the specimens associated with Syncoryne being of a lemon yellow colour, many tending to become orange posteriorly (Plate 11, fig. 1). A narrow line of orange runs in a median position along the ventral surface of the body. When fully mature, but before the stolon has separated, the length of the worm when crawling is about 25 mm. (fig. 2). The ordinary body segments possess simple undivided parapodia without either a ventral or a dorsal cirrus, and carrying a single bundle of compound setæ (Plate 14, fig. 19). As will be shown later, when describing the polybostrichus, this simple parapodium represents the ventral division or neuropodium of the annelid foot. The parapodium agrees with that found in the genus Autolytus in consisting of a single lobe and in the absence of a ventral cirrus, but differs in the suppression of the elongated dorsal cirrus which is found in Autolytus. It is, however, not quite correct to say, as MALAQUIN and LANGERHANS do, that the dorsal cirrus is absent, for a comparison with the developing stolon makes it clear that it is in reality represented by a large rounded lobe or swelling of somewhat transparent tissue, which is seen especially in larger specimens of the worm, and occupies the posterior dorso-lateral angle of the segment. This swelling is seen in all the figures of adult segments, and is especially well shown in Plates 15 and 16, fig. 20 (7), (8), (9) and (10). Fig. 2 (Plate 11), which shows the development of the dorsal cirrus in the segments of the stolon, makes it clear that this cirrus is merely an elongation of the lobes of transparent tissue seen in the segments of the souche.

As in the allied genus Autolytus, the head tentacles and tentacular cirri of Procerastea are well developed. The tentacles, which are club-shaped and covered with numerous fine hairs, are three in number, an anterior pair inserted ventrally below the margin of the head, and a single median dorsal tentacle, the largest of the three (figs. 1 and 2). Immediately behind the head there arises on each side a pair of tentacular cirri, each pair consisting of a larger dorsal cirrus and a smaller ventral one. These may be interpreted as the dorsal and ventral cirri of the first segment of the body, in which the parapodia and setæ are entirely absent. Behind these cirri there is 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 regenerating heads (Plate 11, fig. 3, and Plates 15 and 16, fig. 20), belongs to the region in front of the first setigerous segment. Whether it represents the dorsal cirrus of a second body segment whose parapodium and setæ are suppressed, or whether it is simply a second dorsal cirrus developed on the first body segment, has not been determined. That it is not the dorsal cirrus of the first setigerous segment seems certain, as the rudiment of that cirrus is seen clearly as a transparent lobe behind the first bundle of setæ. Similar relations will be described later in the heads of the Polybostrichus and Sacconereis.

There are thus altogether nine elongated, club-shaped appendages associated with the head region of Procerastea, three on the head itself, and three on each side immediately behind the head, all of which are covered with fine hairs, the hairs being more marked in young or recently regenerated heads.

In addition to the tentacles, MALAQUIN mentions a pair of palps situated ventrally immediately behind the anterior margin of the head, but these are little developed in the souche head, and are difficult to make out. There are four red eyes all conspicuous in a dorsal view, the anterior pair lying deep in the tissue of the head, the posterior pair being on the dorsal surface.

On the upper surface of the body, immediately behind the head, there is on each side a definite ridge of tissue, which commences near the middle line and runs backwards and outwards, finally passing around the base of the second dorsal tentacular cirrus (Plate 12, fig. 5; Plate 15, fig. 20 (1)). Below the outer faces of these ridges are the nuchal organs, the cilia of which can be seen in rapid motion in the living animal. The mouth, a small triangular slit on the ventral surface of the head, occupies a median position just at the junction of the head with the first segment (Plate 14, fig. 16). The proboscis or pharynx is protruded through the mouth when the worm is feeding, and it can sometimes be made to protrude by treating with very weak alcohol (Plate 14, fig. 17).

The alimentary canal is visible through the body wall, especially in young or in recently regenerated worms. Its parts resemble closely those found in Autolytus. The mouth leads into the pharynx or œsophagus, which consists of a long, thin chitinous tube surrounded by a muscular sheath, and having, when withdrawn within the body, a single S-shaped loop, which lies in the third or fourth setigerous segments. When the pharynx is protruded this loop straightens out.*

* It seems to me likely that LANGERHAN'S figure of *P. nematodes* (LANGERHANS, vol. 15, fig. 5 (1884)), is drawn from a specimen in which the pharynx is protruded. Its appearance suggests also that it has been flattened under a cover glass.

The mouth of the chitinous tube of the pharynx, with its surrounding sheath is shown in Plate 14, fig. 18. It is provided with a "trepan" of 18 to 22 minute teeth. The sheath, which is composed of the muscle bands by means of which the pharynx is withdrawn into the body, is thrown into a series of about six folds or ridges, which lie just in front of the trepan when the latter is inside the body.* The function of the trepan is evidently to pierce the body-wall of the hydroid on which the worm feeds.

The pharynx opens posteriorly into a short, muscular proventriculus with a narrow lumen and about twenty ridges, having apparently the usual structure of this organ in the Syllidæ, which has been described so thoroughly by MALAQUIN (1893, for Procerastea, p. 221). According to that author (p. 249), the diastole of the proventriculus is sudden and always progresses from before backwards, whilst the systole is slow and runs in the same direction. In the rapid pulsation which I observed when Procerastea was feeding, these details of the process were not followed, though they doubtless occurred and explain the way in which a practically continuous current of food passes into the intestine.

The proventriculus, when the pharynx is not protruded, occupies the fourth and fifth setigerous segments. It is followed immediately by the intestine and ventricular cæca, such as are present in many Syllids, are but little developed, if present at all. The intestine is thin-walled and elastic, and when full of food is distended so as almost to fill each segment of the body.

## STOLON FORMATION.

Sexual reproduction in Procerastea takes place by simple schizogamy, with the production by each individual of a single stolon, either male or female. According to MALAQUIN'S account (1891, 1893), the formation of the stolon is preceded by a proliferation of the body segments in the middle of the body, but a study of the phenomena of regeneration described in the present paper makes it clear that this view is due to a misinterpretation, the condition described by MALAQUIN being ordinary regeneration following fragmentation.

With great constancy, the stolon head forms at the anterior end of the fourteenth setigerous segment (Plate 11, figs. 1 and 2), showing first as a small dorsal plate, on which later the tentacles and tentacular cirri originate as buds and the eyes appear. Even before the stolon head appears, the body segments behind the fourteenth show the first signs of a modification of shape, which leads ultimately to the development of the dorsal cirri and the dorsal or notopodal divisions of the feet. In the living worm the first sign of the approaching formation of the cirrus is the enlargement of the small transparent lobe at the posterior dorsolateral angle of the segment, already described (p. 5), which gradually elongates in the female, but remains small and

* Perhaps it is these ridges of the sheath which LANGERHANS means when he says that *P. nematodes* has six indistinct teeth.

foliaceous in the male, and becomes separated by an articulation from the body wall. As the transparent cirrus becomes larger, the tissue immediately below it also continues to grow, producing a pigmented lobe, which is the dorsal division of the parapodium (notopodium) of the stolon (Plate 11, figs. 1 and 2), from which the long swimming setæ arise.

The male and female stolons will be described separately.

*The Polybostrichus.*

The fully formed male stolon or polybostrichus, which has separated from the souche and become an independent free-swimming individual, is shown in Plate 12, fig. 4. The head is provided with two pairs of bright red eyes, with distinct lenses, the anterior pair being very large and ventral in aspect, whilst the posterior pair are smaller and dorsal. As is usual in the polybostrichus of Autolytus, the palps have developed into large organs, consisting of an enlarged basal portion distinctly divided into two lobes, the distal lobe bifurcating to form two elongated, tapering, tentacle-like processes, the inner of which is both longer and larger than the outer. Three head tentacles, corresponding to the three tentacles of the souche, are present, but in a very modified form (Plate 12, fig. 4). The median tentacle is extraordinarily enlarged and is thrown into a series of spiral coils, which extend backwards on the dorsal surface of the anterior segments. The two anterior lateral tentacles, on the other hand, are greatly reduced in size and are represented by two small leaf-like processes, which, springing from the dorsal surface of the head, partly obscure the anterior pair of eyes. Behind the head, the anterior pair of tentacular cirri on each side are present as rather slender structures, the dorsal one being the longer. Further back still, but well in front of the first setigerous segment, is the third tentacular cirrus on each side. These two cirri are very massive and are carried in spiral coils, resembling in these respects the median tentacle of the head.

Behind the tentacular cirri are the first parapodia, each with a bundle of compound setæ (Plate 14, fig. 19), behind and above which the dorsal cirrus is present as a small leaf-like process. Then follow five other similar segments, with bundles of compound setæ and lamellar dorsal cirri, which become larger as we proceed backwards, reaching a maximum at segment 6.

With the seventh setigerous segment the parapodia specially modified for swimming commence. One of these is shown in Plate 14, fig. 15. It consists of a comparatively small ventral division or neuropodium, with a few compound setæ, a large and massive dorsal division or notopodium, from which a bundle of large, flat, flexible swimming setæ arises and a small leaf-shaped dorsal cirrus, these cirri being much smaller than those in segments 1–6.

The polybostrichus from which fig. 4 was drawn had twenty-six of these modified segments, whilst other specimens recorded had twenty (two specimens), twenty-three (two specimens), twenty-four and twenty-five (2 specimens).

Behind these modified segments the body becomes very narrow and the dorsal cirri become gradually smaller and smaller. This posterior or tail portion of the worm has from ten to seventeen setigerous segments and is followed by the pygidium and two leaf-like anal cirri.

*The Sacconereis.*

The female stolon or sacconereis has been described by MALAQUIN. It is represented in Plate 12, fig. 5. The large red eyes are similar to those of the Polybostrichus, but the appendages connected with the head are much simpler than those of the male. The large, bifurcated palps are not present, whilst the three head tentacles of the souche are represented by long, smooth, tapering tentacles. Behind the head there is on each side a pair of rather slender tentacular cirri, followed by a single dorsal tentacular cirrus, which, as in the souche, is well in front of the first setigerous segment. The tentacular cirri are all smooth and tapering.

In the second, third, fourth and fifth setigerous segments, the dorsal cirrus is represented by a broad, rounded, transparent swelling, but the notopodium is not developed. In the sixth setigerous segment the dorsal cirrus is long and tapering, but there is still no development of notopodium. These six segments carry only compound setæ like those of the souche. With the seventh setigerous segment the special modifications for swimming commence. In addition to the neuropodia with bundles of compound setæ, the notopodia are well developed, and carry long, flat swimming bristles, as well as long, slender, tapering dorsal cirri. In the individual figured there were fourteen of these modified swimming segments. The degree of development of the notopodia, of the cirri, and of the swimming bristles, gradually increases in the eighth, ninth, and tenth segments, and then, after remaining at about the same level for two or three segments, gradually falls off, until at the twentieth segment it is comparatively small. Behind the twentieth segment the notopodia and the swimming bristles are absent, but the dorsal cirri still persist, at first as short tapering processes, which afterwards become reduced to small knobs of transparent-looking tissue. In the individual figured there are twenty-eight setigerous segments in the posterior region, followed by the pygidium and anal cirri. The number of anal cirri in this particular worm is three, a variation from the usual two, which very rarely occurs. When the animal is swimming, the posterior segments are coiled up in a spiral beneath the body. The general colour of the sacconereis, when full of eggs, is greenish from the colour of the eggs themselves inside the body, but it takes on a more yellow tint as the eggs ripen. The intestine shows as a median orange line, and a number of chocolate brown flecks are developed on the parapodia and lateral walls of the body. Posteriorly, where there are no eggs, the prevailing colours are orange and yellow, but the lateral chocolate markings continue to the last setigerous segment.

A sacconereis in which the eggs have been extruded has not been seen, so that the characters of the egg-sac remain unknown.

Mature Polybostrichus and Sacconereis, nearly ready to detach themselves from the souche, or which had just been detached, were found from July to December.

## Asexual Reproduction.

The abundant supply of material associated with the Syncoryne obtained from Millbay Dock has enabled me to satisfy myself that Procerastea, in addition to its sexual reproduction, with the formation of free-swimming male and female stolons, also multiplies by means of a process of asexual reproduction, by fragmentation with accompanying regeneration of the missing parts. This process, which has been called by F. von Wagner "architomie" (Korschelt and Heider, 1910, p. 473* and p. 600), is well known in the lower annelids (for literature, see Korschelt, 1919), but I have found no reference in the literature to its having been seen in Polychætes.

Between July and November, when the Syncoryne was growing luxuriantly and the Procerastea was very numerous upon it, the great number of specimens which showed indications of having originated by architomy made it probable that nearly all had in reality originated in this way. By examining large numbers of individuals, the process could be followed in all its stages, and in quite a large proportion of the individuals, after some experience had been gained, it was possible to pick out, even when regeneration was well advanced, the particular segments which had come from the parent worm, and from which regeneration had taken place.

The following types of regenerated individuals were those most frequently met with :—

1. Head ends of from nine to sixteen original segments, with regenerated posterior segments and tail.
2. Tail ends of six to twenty original segments and tail, with regenerated anterior segments and head.
3. Three original segments or four original segments, with regenerated anterior segments and head, and also regenerated posterior segments and tail (Plate 13, figs. 6, 9, 10 and 11).
4. Some other number of original segments, generally a simple multiple of three or four, with regenerated anterior and posterior portions.

### *Experimental Results.*

It will simplify the explanation of the phenomena as they occur under natural conditions, if before discussing in more detail these different groups of regenerated animals, we first of all describe some experimental results which have been obtained.

These experiments originated in consequence of an observation made by

* It is doubtful whether a sharp line of distinction can be drawn between "architomie" and "autotomie."



PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Mrs. SEXTON that if the sea water in which a Procerastea was living on a microscope slide gradually evaporated the worm tended to break up in a constant and regular way. Between particular segments the intestine seemed first to break across and a constriction of the body wall then took place. Often this would be followed by a complete break at some of the places so affected, and at all of them it was easy to make a break by gentle pulling with two fine camel-hair brushes,* whereas other segments could not be separated at all, even by pulling with considerable force until the whole tissue was very much stretched. The kind of condition produced, is illustrated by fig. 13 (Plate 14), which was drawn from an actual specimen. It can be induced without much difficulty when desired by placing the worm on a glass slide, drawing off most of the sea water with a camel's-hair brush and letting it dry a little, brushing it gently from time to time to keep it straight, adding a little sea water before the drying proceeds too far and repeating the process two or three times. Or, as we found out subsequently, it can be induced even more readily by adding alternately distilled water and sea water, brushing in a similar way. The anterior end generally breaks more easily than the segments near the tail, which it is often impossible to cause to separate.

What may be regarded as the normal fragmentation is as follows :—The head and the first seven setigerous segments always remain as one piece without any sign of division; three groups of two segments each follow, which brings us to the thirteenth segment and to the point of separation between souche and stolon. Then follow three groups of three segments each bringing us to the twenty-second segment,† after which there are, according to the size of the worm, three, four, or five groups of four segments each, followed by groups of three segments to the pygidium or tail. This may be conveniently expressed in the following formula :—

$$\text{Head}\quad 7+2+2+2+3+3+3+4+4+4+4\,(+4)+3+3+3+3+\ldots\ldots\text{P.}$$

in which the numerals represent the number of segments in each group and the + signs indicate the points at which breakage occurs.

Specimen 1‡ was a worm which broke up in a typical way, according to the above formula. Set out in detail, with each segment numbered according to its position in the body and segments between which no break occurred united by brackets, the broken worm may be represented as follows :—

* The brushes used were cut down until only two or three hairs were left.

† Fig. 13 presents a special feature at this point, which will be explained later (see p. 161).

‡ Regenerated specimens are numbered consecutively, 1, 2, 3, etc., in the order in which they are first mentioned in this paper.

Head.
1, 2, 3, 4, 5, 6, 7
8, 9
10, 11
12, 13
*14, 15, 16
17, 18, 19
20, 21, 22
23, 24, 25, 26
27, 28, 29, 30
31, 32, 33, 34
35, 36, 37, 38
39, 40, 41, 42
43, 44, 45
46, 47, 48
49, 50, 51
Short regenerated tail.

* The Stolon head forms on this segment.

The following are other instances which have been observed. Variations from the typical arrangement are probably due to regeneration, as will be seen later, when the description of the phenomena of regeneration in Procerastea has been given. In some cases the breaking is not complete.

| Specimen No. | Total No. of segments. | |
|---|---|---|
| 2 | 57 | H7+2+2+2+3+3+3+4+8+1+4+3+3+3+3+3+3 P. |
| 3 | 34+ | H7+2+2+2+3+3+3+8+4 broken. |
| 4 | 64 | H7+2+2+2+3+3+3+4+4+4+12+3+3+12 P. |
| 5 | 42 | H9+2+2+3+3+3+8+3+9 P. |
| 6 | 60 | H9+2+2+3+3+3+4+4+4+4+4+3+3+3+3+6 P. |
| 7 | 61 | H13+3+3+3+4+4+4+27 P. |
| 8 | 51 | H7+2+2+2+3+3+3+4+4+4+3+3+3+3+5 P. |
| 9 | 44+ | H7+2+2+2+3+3+3+4+4+3+5+3+3 broken. |
| 10 | 42 | H7+2+2+2+3+3+5+4+4+4+6 P. |
| 11 | 41 | H7+2+2+2+3+3+6+4+4+8 P. |
| 12 | 39+ | H9+2+2+3+3+3+4+4+9 and regenerating tail. |
| 13 | 63 | H7+2+4+6+ (4+2) +2+8+4+3+3+6+3+9 P. |
| 14 | 51 | H13+3+3+3+4+6+3+3+3+3+7 P. |

Experiments were made to test the power of regeneration of groups of segments taken from different parts of the body. Individuals were broken up in the way described above with fine camel-hair brushes, and each group as it was taken off was placed in sea water in a numbered watch glass, the exact order of the segments as they had been in the living worm being carefully preserved. Subsequently the pieces were transferred to finger-bowls of clean sea water in which they were allowed to regenerate, being examined and sketched at first daily and later at intervals of a few days. When these experiments were done, the way in which Procerastea feeds had not yet been discovered, and although attempts were made to feed the regenerating individuals in several ways it is probable that these were seldom or never successful, and the results recorded may be taken to represent the rate and degree of regeneration when the worms are not taking food, but are living at the expense of the original tissue. The regenerating pieces died at the end of at most three or four weeks. As the final stages of regeneration can to a large extent be followed on material brought in from outside, which has grown under natural conditions, and as a repetition of the experiments under satisfactory conditions of food supply is attended with considerable difficulties, on account of the small size of the pieces, it is thought advisable to publish the results so far obtained.

*Experiment* I. (Specimen No. 15.)

The first experiment to be described was made with a Procerastea consisting of fifty-four segments, in which there was as yet no indication of the formation of the stolon-head on the fourteenth segment. The worm was broken into thirteen pieces, which were kept in separate finger bowls, as follows :—

(1) Head with seven setigerous segments; (2) Segments 8 and 9; (3) 10 and 11; (4) 12 and 13; (5) Here would be stolon head. 14, 15 and 16; (6) 17, 18 and 19; (7) 20, 21, 22 and 23; (8) 24, 25, 26 and 27; (9) 28, 29, 30 and 31; (10) 32, 33, 34 and 35; (11) 36, 37, 38 and 39; (12) 40, 41 and 42; (13) 43 to 54, growing zone and and tail.

Piece 13 showed a tendency to split after segment 45, and again after 48, which would have given two groups of three segments, but it did not actually divide. It will also be noticed that in this individual there are only two groups of three segments after segment 14, instead of the usual three groups, but a growing piece was present between segments 19 and 20, which as will be explained later, indicates that the worm is regenerating and the anterior regeneration is not yet complete (see p. 161).

All the thirteen pieces underwent regeneration, the head section forming a new tail, the tail section a new head, and the intermediate sections both new heads and new tails. The experiment was commenced November 27, 1919, and the regenerated worms lived from one to two months. The rate of regeneration, and therefore the number of new segments added, varied greatly according to the part of the body from which the original segments were derived.

(1) *Head and Setigerous Segments* 1 to 7 (Plate 15, fig. 20. 1, A to D).—Lived till about December 29, but did not grow after December 20. The regenerated piece then consisted of four segments, the first three of which were setigerous, a fairly long zone of growth, with pygidium and anal cirri. It made a tube on a stem of Syncoryne.

(2) *Segments* 8 *and* 9 (fig. 20. 2, A to G).—On December 2, five days from the beginning of the experiment, there was a considerable outgrowth of regenerated tissue at the anterior end, but it did not yet show any sign of segmentation nor of the budding of the appendages of the head region. Posteriorly there was an unsegmented spherical outgrowth, carrying the buds of two anal cirri. Seven days later (December 9) the three head tentacles were conspicuous as distinct rounded buds and the beginnings of the tentacular cirri had appeared, but no eyes were visible. There was a considerable zone of growth behind the buds of the last pair of tentacular cirri, but it did not yet show signs of segmentation. At the posterior end one segment was distinct, followed by zone of growth, pygidium, and anal cirri. On December 12 the most noticeable advance was the presence of the eyes, all four of which were well pigmented. On December 16, *i.e.*, nineteen days from the commencement, a degree of development was reached which was only exceeded very slightly afterwards. The regenerated anterior portion consisted of the head region, with its three tentacles and six tentacular cirri, three setigerous segments, followed by a fourth segment in which the setæ were not yet to be seen, and a short zone of growth. The posterior region showed one distinct segment, but with no setæ visible, a zone of growth, pygidium, and anal cirri. The worm was alive on December 29, but on January 5 only macerated remains were found. When last seen, the anterior regeneration had three segments with setæ, followed by one distinct segment without setæ and a zone of growth; and the pharynx and proventriculus were fully developed. The posterior regeneration had one well-developed segment with setæ and showed also the rudiment of the dorsal cirrus. This was followed by two distinct segments without setæ, the zone of growth, pygidium, and anal cirri. The original segments had diminished to at least half their original volume.

(3) *Segments* 10 *and* 11 (fig. 20. 3, A to F).—Regeneration was a little more rapid than in piece 2, and on December 20, the last time the worm was seen alive, the anterior regeneration consisted of the head region with eyes and appendages, three segments with setæ, followed by one or two faintly indicated and a zone of growth. The posterior regeneration had one segment with setæ, one without setæ, the zone of growth, pygidium and anal cirri.

(4) *Segments* 12 *and* 13 (fig. 20. 4, A to F).—The increase in rapidity of regeneration compared with piece 2 was here decided. On December 20, when last seen alive, the head region, with eyes and appendages, was well developed, setæ were present on three segments, which were followed by three segments clearly differentiated and a short zone or growth. The posterior regeneration had two segments with setæ, followed by two indicated, growing zone, pygidium and anal cirri.

5. *Segments* 14, 15, *and* 16 (fig. 20. 5, A to G).—This piece is of interest, because it is from the front of segment 14 that the stolon head always buds. In this experiment, however, the only special feature is the slow rate at which the anterior regeneration took place in comparison with the pieces both before and behind it, but this was probably due to an injury when the segment was broken off, which caused the front part of it to macerate. It was only on December 16 that the appendages of the head region were well developed, and the eyes were not seen until the 20th. The piece was last seen alive on December 29, when, following the head region with its appendages, there were four well-developed segments bearing setæ, followed by a zone of growth. The posterior region had two segments with setæ, growing zone, pygidium and anal cirri. Pharynx and proventriculus were well developed.

6. *Segments* 17, 18, *and* 19 (fig. 20. 6, A to F).—This piece is instructive, because segment 17 was rather seriously damaged when it was separated from the one in front, and in the course of the healing of the wound it was almost entirely absorbed by the eighteenth segment, though traces of it were retained until the end. In consequence of this healing process the regeneration of the head was greatly delayed, and it was not until December 16 that the head appendages were seen, and on that date there were no eyes. On December 20, the last day it was seen alive, eyes were present, appendages of the head region were developed only moderately, and this region was followed by one segment on which no setæ had developed, and by a short zone of growth. The seventeenth segment was indicated only by the presence of a rudiment of the dorsal cirrus on the left side. The posterior regeneration had one well-developed segment with setæ, one segment without setæ, growing zone, pygidium, and anal cirri.

7. *Segments* 20, 21, 22 *and* 23 (fig. 20. 7, A to H).—This is the first piece containing four segments, and there was a short growing piece in front of segment 20, which was soon absorbed. We are now in the region where normally the modified segments of the stolon are formed. Regeneration is altogether more rapid than it was in the pieces already described, and is carried to a much more advanced stage. On December 20 the appendages of the head region and the eyes were all well advanced, the appendages being covered with cilia. There were behind this four segments with setæ, one without setæ and a growing zone. In the posterior region, four segments with setæ, followed by growing zone, pygidium and cirri. On December 29 the anterior region had seven setigerous segments, followed by two without setæ and a growing zone, whilst on January 5, the last time the worm was seen alive, setæ had developed on eight segments. On both the latter dates the posterior region contained still four segments with setæ, as on December 20, but they had increased considerably in size. By December 12 the worm had already made a membranous tube. It may also be noted that there were three pigment spots on the left side of the head, in addition to the usual eyes.

8. *Segments* 24, 25, 26 *and* 27 (Plate 15, fig. 20. 8, A to G).—Again, there is an

increase in the rate and extent of the anterior regeneration. By December 20 there were seven segments with setæ, two with no setæ, and a zone of growth. The pharynx and proventriculus were fully formed, and pigmentation of the body was well developed. On December 29 ten setigerous segments, and on January 12, the last time it was seen alive, twelve setigerous segments. The posterior regeneration on December 20 had four setigerous segments, growing piece, pygidium, and anal cirri. The number of segments bearing setæ did not increase after this date, though the segments increased in size until the first of the regenerated segments was only slightly smaller than the last of the original ones.

9. *Segments* 28, 29, 30 *and* 31 (Plate 16, fig. 20. 9, A to G).—In this piece the rate and extent of regeneration reach a maximum. On December 20 the head and its appendages were well advanced, eyes were present, pharynx and proventriculus fully formed; there were ten segments in the anterior regenerated portion with setæ and one without, followed by a very long zone of growth. In the posterior region there were five segments with setæ, followed, as usual, by zone of growth, etc. On December 29 the setigerous segments in the anterior regeneration were fourteen, and five other segments were indicated. On January 5 there were fifteen setigerous segments, but, although the worm lived till January 26, this number was not added to, and no further growth took place. The posterior regeneration did not add more segments after December 20, but the segments increased in size until there was no marked break in appearance between the old and the new. In all this region of the body, the considerable development of the dorsal cirri is very marked, and is quite as conspicuous on the regenerated segments as on the original ones.

10. *Segments* 32, 33, 34 *and* 35 (fig. 20. 10, A to G).—Very similar to the last piece described, but regeneration not quite so rapid nor as far advanced; December 20, anterior region with seven setigerous segments and posterior with four; December 29, anterior with eleven and posterior with five. The worm lived until January 26, but only added one more anterior setigerous segment.

11. *Segments* 36, 37, 38 *and* 39 (fig. 20. 11, A to H).—Regeneration still further reduced. December 20, anterior region with six setigerous segments, posterior with two; December 29, anterior with ten, posterior with two; January 5, anterior with eleven, posterior with two. The worm lived till January 19, but did not grow further.

12. *Segments* 40, 41 *and* 42 (fig. 20. 12, A to G).—December 20, anterior region with seven setigerous segments, posterior with two; December 29, anterior with nine, posterior with two; January 5, anterior with ten, posterior with two. Lived till January 19 without growing further.

13. *Segments* 43 *to* 54 *and Tail* (fig. 20. 13, A to H).—Regeneration was rapid from this last portion of the worm. By December 20, the head, eyes, pharynx and proventriculus were well developed, and the regenerated region had six segments with setæ and six or seven without and a zone of growth. It lived to January 19, but did not grow further.

TABLE I.—Regeneration Experiments.

Specimen No. 15 was used in Experiment I, No. 5 in Experiment II, No. 2 in Experiment III, and No. 13 in Experiment IV.

| Number of experiment. | Original segments. | Days from commencement. | Regeneration. Setigerous segments. Anterior. | Regeneration. Setigerous segments. Posterior. |
|---|---|---|---|---|
| I | Head to 7 | 23 | — | 3 |
| II | Head to 9 | 36 | — | 1 |
| IV | Head to 7 | 27 | — | 1 |
| I | 8 and 9 | 23 | 3 | 0 |
| I | 8 and 9 | 39 | 3 | 1 |
| IV | 8 and 9 | 27 | 3 | P |
| I | 10 and 11 | 23 | 3 | 1 |
| II | 10 and 11 | 36 | 3 | 1 |
| III | 10 and 11 | 27 | 4 | 3 |
| III | 10 and 11 | 39 | 6 | 3 |
| IV | 10, 11, 12 and 13 | 27 | 4 | 1 |
| IV | 10, 11, 12 and 13 | 39 | 4 | 1 |
| I | 12 and 13 | 23 | 3 | 2 |
| II | 12 and 13 | 36 | 2 | P |
| III | 12 and 13 | 27 | 7 | 4 |
| III | 12 and 13 | 39 | 7 | 4 |
| I | 14, 15, 16 | 23 | 2 | P |
| I | 14, 15, 16 | 32 | 4 | 2 |
| II | 14, 15, 16 | 36 | 3 | 3 |
| III | 14, 15, 16 | 27 | 2 | 5 |
| III | 14, 15, 16 | 39 | 4 | 6 |
| IV | 14, 15, 16, 17, 18, 19 | 27 | 4 | 3 |
| IV | 14, 15, 16, 17, 18, 19 | 39 | 7 | 3 |
| I | 17, 18 and 19 | 23 | 0 | 1 |
| II | 17, 18 and 19 | 36 | 0 | P |
| III | 17, 18 and 19 | 9 | 0 | P |
| I | 20, 21, 22 and 23 | 23 | 4 | 4 |
| I | 20, 21, 22 and 23 | 32 | 7 | 4 |
| I | 20, 21, 22 and 23 | 39 | 8 | 4 |
| II | 20, 21 and 22 | 36 | 2 | P |
| III | 20, 21 and 22 | 27 | 5 | 1 |
| IV | 20 to 25 | 27 | 8 | 3 |
| IV | 20 to 25 | 39 | 11 | 3 |
| I | 24, 25, 26 and 27 | 23 | 7 | 4 |
| I | 24, 25, 26 and 27 | 32 | 10 | 4 |
| II | 23 to 30 | 36 | 2 | P |
| III | 23, 24, 25 and 26 | 27 | 7 | 2 |
| IV | 26 and 27 | 27 | 5 | P |
| IV | 26 and 27 | 39 | 7 | P |

TABLE I—*continued.*

| Number of experiment. | Original segments. | Days from commencement. | Regeneration. Setigerous segments. | |
|---|---|---|---|---|
| | | | Anterior. | Posterior. |
| I | 28, 29, 30 and 31 | 23 | 10 | 5 |
| I | 28, 29, 30 and 31 | 32 | 14 | 5 |
| I | 28, 29, 30 and 31 | 39 | 15 | 5 |
| III | 27 to 34 | 27 | 5 | 4 |
| III | 27 to 34 | 39 | 9 | 4 |
| IV | 28 to 35 | 27 | 7 | 2 |
| IV | 28 to 35 | 39 | 12 | 2 |
| I | 32, 33, 34, 35 | 23 | 7 | 4 |
| I | 32, 33, 34, 35 | 32 | 11 | 5 |
| I | 32, 33, 34, 35 | 39 | 12 | 5 |
| II | 31, 32, 33 | — | — | — |
| I | 36, 37, 38 and 39 | 23 | 6 | 2 |
| I | 36, 37, 38 and 39 | 32 | 10 | 2 |
| I | 36, 37, 38 and 39 | 39 | 11 | 2 |
| III | 35 to 39 | — | — | — |
| IV | 36, 37, 38 and 39 | 27 | 7 | 1 |
| IV | 36, 37, 38 and 39 | 39 | 9 | 1 |
| I | 40, 41 and 42 | 23 | 7 | 2 |
| I | 40, 41 and 42 | 32 | 9 | 2 |
| I | 40, 41 and 42 | 39 | 10 | 2 |
| III | 40, 41 and 42 | 27 | 0 | 3 |
| III | 40, 41 and 42 | 39 | 0 | 3 |
| IV | 40, 41 and 42 | 27 | 7 | P |
| IV | 40, 41 and 42 | 39 | 11 | P |
| IV | 43, 44 and 45 | 27 | 5 | 1 |
| IV | 43, 44 and 45 | 39 | 9 | 1 |
| IV | 46 to 51 | 27 | 8 | P |
| IV | 46 to 51 | 39 | 15 | P |
| IV | 52, 53 and 54 | 27 | 4 | P |
| IV | 52, 53 and 54 | 39 | 6 | P |
| I | 43 to 54 and tail | 23 | 6 | — |
| I | 43 to 54 and tail | 39 | 11 | — |
| II | 34 to 43 and tail | 36 | 0 | — |
| IV | 55 to 63 and tail | 27 | 3 | — |

P = Pygidium.

The main features of the above experiment (I) are summarised in Table I, and, for comparison, the results of three other similar experiments are given. In this Table the number of regenerated segments in which setæ are actually protruded is given as a measure of the degree of regeneration. This is a more definite figure than that for the total number of regenerated segments which can be detected, whether the setæ have yet formed or not, since it is often difficult to say how many segments are really differentiated in the neighbourhood of the zone of growth. In some respects, however, the latter figure, though less definite, is more significant, and it is used in later sections of this paper, *e.g.*, Table II.

Experiment I was commenced on November 27, 1919; Experiment II on December 3, 1919; Experiments III and IV on January 22, 1920. Experiment III was the least successful, as a number of the pieces died, and others did not regenerate very much. In Experiment II the pieces were not kept in finger-bowls, but in glass capsules containing only a small quantity of sea water.

Experiments in which the regenerated worms are properly and constantly fed will be necessary before many of the problems presented can be solved, but the practical difficulties of carrying out such experiments are considerable. Some points are, however, clear from the results already obtained.

All the worms experimented on were large adults in which the modifications of the segments which result in the formation of a stolon had already commenced, though the stolon head itself had not yet begun to bud. It is a fact of great interest that regeneration is most rapid and extensive in those segments which undergo normally the greatest modification to form large swimming feet and dorsal cirri, commencing at segment 20, and so far as regeneration of the anterior region is concerned with a maximum in the region of segment 30. Experiment IV suggests that there may be a second maximum as the tail region is approached (segments 46–51), and the final segments in Experiment I also made a good growth anteriorly.

To what if any extent the rate or degree of regeneration is dependent upon the number of segments in the original piece or upon the actual bulk of the original piece is not clear from these experiments, though the good growth of segments 14–19 in Experiment IV certainly suggests that the number of segments is important. On the other hand the growth from segments 10 to 13 in Experiment IV is not as great as that from 10 and 11 in Experiment III.

The regeneration of posterior segments attains its maximum in the same region as that in which the regeneration of anterior segments is a maximum, namely about segment 30, though the results are not uniform in the different experiments. In Experiment IV there was clearly a falling off in the regeneration of posterior segments, as the original piece was taken nearer and nearer to the tail of the worm.

## Asexual Reproduction under Natural Conditions.

These experimental results throw much light upon the question of asexual reproduction by fragmentation and regeneration, and are in agreement with what one finds when examining large numbers of Procerastea, which have just been collected from their natural habitat or have been living for two or three weeks in glass dishes in the laboratory. Regenerated portions, whether anterior or posterior ends, are at first easily distinguished from original segments derived from the older worm which has broken up, by their slender size, greater transparency of tissue and almost complete absence of pigment. A regenerated anterior portion is also clearly separated from the original segments by the characteristic appearance of the zone of growth, where new segments are actually being formed. For this reason it is much easier to detect an anterior regeneration in an advanced stage than it is to detect an advanced posterior regeneration, for in the latter the zone of growth is not next to an original segment but at the distal end immediately in front of the pygidium. In both cases, however, as the regenerated portions get older they become broader and more pigmented, until at last they are indistinguishable from the original segments. An anterior end can, however, in most cases be detected until regeneration is complete.

All stages in the regenerative process have been seen repeatedly in fresh material, from those in which they are mere buds of tissue on which there is as yet no sign of tentacles or anal cirri, to those where it is only possible with difficulty to distinguish between the old segments and the new. Particularly instructive are cases in which a number of regenerating pieces are found in the same membranous tube, as the probability is that they are fragments of one original worm.

*Specimen* 16.—Material brought in November 5, 1919, examined November 8. Five pieces in one tube :—

(1) Souche of eleven setigerous segments with short regenerated tail of five or six segments, growing zone, pygidium and two anal cirri.

(2) A piece of three original segments with regenerated anterior portion on which the tentacles and tentacular cirri are just indicated as buds, and with regenerated posterior portion of one or two segments, growing zone, pygidium and anal cirri.

(3) Three pieces of four original segments each, with anterior regenerations with tentacles just budded but tentacular cirri hardly indicated, and short posterior regenerations.

The break in the piece carrying the original head, namely, behind the eleventh setigerous segment, is at one of the usual points. The posterior end of the original worm was not present in the tube and two or three other pieces seem to be missing, as there was no sign of segments 12 and 13, and only one piece with three original segments was found, whereas there were probably three such pieces.

*Specimen* 17.—Found in one membranous tube in a finger bowl containing Syncoryne and Procerastea which had been in the laboratory about a month were the following four regenerating pieces :—

(1) Original head with twenty-two original segments with a posterior regeneration of six setigerous segments, two segments without setæ, growing piece, pygidium and anal cirri.

(2) Four original segments, with anterior regeneration, consisting of head and eight setigerous segments, two segments without setæ, and a growing piece, and with a posterior regeneration of two setigerous segments, one segment without setæ, growing piece, pygidium and anal cirri.

(3) Eight original segments, with anterior regeneration of eight setigerous

segments, two or three without setæ, followed by a growing piece; with posterior regeneration of three setigerous segments, one without setæ, growing piece, pygidium and anal cirri.

(4) Twenty-two posterior original segments, with pygidium and anal cirri, with a regenerated head, four setigerous segments, two or three without setæ, and a growing piece.

*Specimen* 18.—Four regenerating pieces, found in one membranous tube in the same finger-bowl as Specimen 17:—

(1) Original head and sixteen original segments, with a posterior regeneration of thirteen setigerous segments, one segment without setæ, growing piece, pygidium and anal cirri.

This broke up as follows:—

$$\text{Head}\ \underbrace{7+2+2+2+3}_{\text{Original.}}+\underbrace{3+3+4+4}_{\text{Regenerated.}}\ \text{P.}$$

(2) Three original segments, with anterior regeneration, consisting of head, ten setigerous segments and growing piece; with posterior regeneration of seven setigerous segments, growing piece, pygidium and anal cirri.

This broke up as follows:—

$$\text{Head}\ \underbrace{7+2+1}_{\text{Regenerated.}}\ \ \underset{\text{Original.}}{\text{and } 3+}\ \ \underbrace{3+4}_{\text{Regenerated.}}\ \text{P.}$$

(3) Four original segments, with anterior regeneration, consisting of head, twelve setigerous segments, three segments without setæ, and a growing piece; with posterior regeneration of four setigerous segments, growing piece and pygidium.

This broke up as follows:—

$$\underbrace{\text{Head}\ \ 7+2+2+1 \text{ and } 3}_{\text{Regenerated.}}\ \ \underset{\text{Original.}}{\text{and } 4+}\ \ \underbrace{2+2}_{\text{Regenerated.}}\ \text{P.}$$

(4) Ten posterior original segments, with pygidium and anal cirri, with an anterior regeneration, consisting of head and fourteen setigerous segments, two segments without setæ, and a growing piece.

This broke up as follows:—

$$\underbrace{\text{Head}\ \ 7+2+2+5}_{\text{Regenerated.}}\ \text{and}\ \underbrace{2+3+3+2}_{\text{Original.}}\ \text{P.}$$

The above four pieces in all probability do not represent the whole of the original worm, as one section of three segments, and perhaps two or three sections of four segments, remain unaccounted for.

With the specimens just described may be compared *Specimen* 19 (November 14, 1919), which was kept by itself in a finger-bowl of sea water. On November 28 the worm was found broken up as follows, each piece regenerating :—

(1) Original head with sixteen setigerous segments.
(2) One piece of three original segments.
(3) One piece of three original segments.
(4) One piece of eight original segments.
(5) One piece of four original segments.
(6) Original posterior end with about twenty segments, pygidium and anal cirri.

All the evidence tends to show that what happened in this last case is typical of what takes place most frequently when reproduction by fragmentation and regeneration occurs in nature, excepting for the fact that the fourth piece of eight segments would naturally break into two pieces of four segments each.

In the first place, the break after the sixteenth segment is of very frequent occurrence. Amongst worms which had just been brought in from outside, or had been living for a short time, up to three weeks or a month, in finger-bowls in the laboratory, there are definite detailed records of sixty-five cases in which an original anterior portion had regenerated posterior segments.

The numbers of original anterior setigerous segments found in these sixty-five specimens are given in the following Table, with the number of specimens recorded corresponding to each :—

| Number of original anterior segments. | Number of times recorded. | Number of original anterior segments. | Number of times recorded. |
|---|---|---|---|
| *9 | 3 | *19 | 3 |
| *11 | 7 | 20 | 1 |
| *13 | 21 | 21 | 1 |
| 14 | 1 | *22 | 1 |
| 15 | 3 | 24 | 1 |
| *16 | 19 | *26 | 2 |
| 18 | 2 | | |

* A natural breaking point.

It will be seen that the maximum number of specimens, twenty-one, had broken behind the thirteenth segment, and had regenerated posterior segments from there. This was to have been expected, as the Procerastea were producing many stolons, and this is the point at which the stolon separates from the souche. But it is remarkable that there are nearly as many instances, viz., nineteen, in which the break had occurred after the sixteenth segment, at the point where the specimen described above (No. 19) had broken.

The next most numerous breaking point is after the eleventh segment, of which there are seven instances, this being one of the natural breaking points in the scheme explained above on pp. 141 and 142. There are three instances with nine original segments and three with nineteen, both natural breaking points. On the other hand, there are three instances with fifteen original segments, which is not a natural breaking point, two with eighteen, and single instances with other numbers which are unexpected. These irregularities can be explained in two ways, either as being due to injury at the breaking point, which may lead to a whole segment being absorbed or degenerating before regeneration commences, or to the fact that a second fragmentation of the worm has taken place before the regeneration following a previous fragmentation has been quite complete. Probably the three instances of fifteen segments and the two with eighteen are to be explained by the first of these hypotheses.

Turning now to specimens in which there has been clear regeneration of both anterior and posterior ends, the instances of which there are definite records, number 151, and are as follows :—

| | | | | | | |
|---|---|---|---|---|---|---|
| Worms with | 4 | original segments | are recorded | 68 | times. |
| ,, | 3 | ,, | ,, | 63 | ,, |
| ,, | 5 | ,, | ,, | 7 | ,, |
| ,, | 6 | ,, | ,, | 4 | ,, |
| ,, | 8 | ,, | ,, | 5 | ,, |
| ,, | 7 | ,, | ,, | 3 | ,, |
| ,, | 2 | ,, | ,, | 1 | ,, |

Pieces of four and three original segments far exceed the others in numbers. Pieces of five original segments are explained most simply as consisting of the twelfth to sixteenth segments (2+3) remaining together as one piece (spec. 152). The frequency of specimens with eleven original anterior segments (p. 152) lends support to this explanation. Six is clearly two sections of three (see break-up of spec. 157, but *cf.* 155); eight is two sections of four, and seven is probably a section of three and one of four which have remained in one piece (segments 20 to 26 in a worm which has broken normally). A regeneration from two segments has only been recorded once, so that it is probable that breakage behind segments 7, 9, and 11, which is the region where pieces of two segments occur, is relatively not frequent.* This is confirmed by the observations on original anterior ends recorded on p. 152, which show that worms which had broken at the ninth segment, with subsequent regeneration of tail, occurred three times, and those broken at the eleventh segment seven times, whereas those broken at the thirteenth occurred twenty-one times; at the sixteenth, nineteen times.

* It is possible, however, that specimens regenerating from two segments may have been overlooked, as in their early stages they would be very small.

TABLE II.—Anterior and Posterior Regenerations.

| Number of specimen. | Anterior regeneration. Number of setigerous segments. | Anterior regeneration. Total number of distinct segments. | Anterior regeneration. Growing zone.* | Number of original segments. | Posterior regeneration. | Total segments of whole worm. | Percentage of posterior regeneration. |
|---|---|---|---|---|---|---|---|
| 20 | 9 | 9 | O | 2 | 11 | 22 | 52 |
| 21 | 29 | 31 | S | 3 | 12 | 46 | 28 |
| 22 | 22 | 22 | S | 3 | 9 | 34 | 29 |
| 23 | 22 | 22 | L | 3 | 5 | 30 | 18 |
| 24 | 20 | 20 | — | 3 | 23 | 46 | 53 |
| 25 | — | 20 | L | 3 | 6 | 29 | 23 |
| 26 | — | 19 | L | 3 | 16 | 38 | 45 |
| 27 | — | 19 | S | 3 | 5 | 27 | 21 |
| 28 | 19 | 19 | S | 3 | 5 | 27 | 21 |
| 29 | — | 18 | L | 3 | 7 | 28 | 28 |
| 30 | — | 18 | L | 3 | 5 | 26 | 22 |
| 31 | 15 | 17 | O | 3 | 19 | 39 | 53 |
| 32 | 17 | 17 | S | 3 | 17 | 37 | 50 |
| 33 | 17 | 17 | O | 3 | 12 | 32 | 41 |
| 34 | — | 17 | L | 3 | 6 | 26 | 26 |
| 35 | 15 | 16 | L | 3 | 15 | 34 | 48 |
| 36 | 16 | 16 | S | 3 | 15 | 34 | 48 |
| 37 | — | 16 | S | 3 | 4 | 23 | 20 |
| 38 | — | 16 | O | 3 | 14 | 33 | 47 |
| 39 | — | 16 | L | 3 | 6 | 25 | 19 |
| 40 | — | 16 | L | 3 | 4 | 23 | 20 |
| 41 | — | 16 | L | 3 | 4 | 23 | 20 |
| 42 | 16 | 16 | O | 3 | 9 | 28 | 36 |
| 43 | 16 | 16 | O | 3 | 11 | 30 | 41 |
| 44 | — | 16 | L | 3 | 5 | 24 | 24 |
| 45 | 16 | 16 | O | 3 | 20 | 39 | 56 |
| 46 | 15 | 15 | O | 3 | 22 | 40 | 59 |
| 47 | — | 15 | O | 3 | 13 | 31 | 46 |
| 48 | — | 15 | L | 3 | 13 | 31 | 46 |
| 49 | — | 15 | O | 3 | 17 | 35 | 53 |
| 50 | — | 15 | S | 3 | 14 | 32 | 48 |
| 51 | — | 15 | L | 3 | 13 | 31 | 46 |
| 52 | 15 | 15 | — | 3 | 16 | 34 | 52 |
| 53 | — | 15 | S | 3 | 10 | 28 | 40 |
| 54 | 15 | 15 | L | 3 | 4 | 22 | 21 |
| 55 | — | 15 | L | 3 | 6 | 24 | 28 |
| 56 | 15 | 15 | O | 3 | 19 | 37 | 56 |
| 57 | 14 | 14 | S | 3 | 7 | 24 | 33 |
| 58 | 14 | 14 | O | 3 | 13 | 30 | 48 |
| 59 | 14 | 14 | — | 3 | 17 | 34 | 55 |
| 60 | 14 | 14 | O | 3 | 15 | 32 | 52 |
| 61 | — | 14 | L | 3 | 12 | 29 | 46 |
| 62 | — | 14 | L | 3 | 11 | 28 | 44 |
| 63 | 14 | 14 | O | 3 | 14 | 31 | 50 |
| 64 | 14 | 14 | — | 3 | 7 | 24 | 33 |
| 65 | 14 | 14 | — | 3 | 12 | 29 | 46 |
| 66 | — | 13 | — | 3 | 15 | 31 | 54 |
| 67 | — | 13 | — | 3 | 14 | 30 | 52 |

* O means no distinct zone of growth, S a short zone of growth, L long ditto.

TABLE II—*continued*.

| Number of specimen. | Anterior regeneration. | | | Number of original segments. | Posterior regeneration. | Total segments of whole worm. | Percentage of posterior regeneration. |
|---|---|---|---|---|---|---|---|
| | Number of setigerous segments. | Total number of distinct segments. | Growing zone.* | | | | |
| 68 | 13 | 13 | S | 3 | 9 | 25 | 41 |
| 69 | — | 13 | L | 3 | 10 | 26 | 43 |
| 70 | 13 | 13 | O | 3 | 12 | 28 | 48 |
| 71 | — | 12 | S | 3 | 8 | 23 | 40 |
| 72 | — | 12 | L | 3 | 6 | 21 | 33 |
| 73 | — | 12 | — | 3 | 14 | 29 | 54 |
| 74 | 12 | 12 | — | 3 | 10 | 25 | 45 |
| 75 | 11 | 11 | S | 3 | 4 | 18 | 27 |
| 76 | 11 | 11 | S | 3 | 6 | 20 | 35 |
| 77 | 11 | 11 | S | 3 | 8 | 22 | 42 |
| 18 (3) | 10 | 10 | S | 3 | 7 | 20 | 41 |
| 78 | 9 | 10 | L | 3 | 12 | 25 | 55 |
| 79 | — | 10 | L | 3 | 6 | 19 | 37 |
| 80 | 10 | 10 | — | 3 | 12 | 25 | 55 |
| 81 | 9 | 9 | L | 3 | 7 | 19 | 44 |
| 82 | 3 | 9 | L | 3 | 8 | 20 | 47 |
| 83 | — | 24 | — | 4 | 4 | 32 | 14 |
| 84 | — | 24 | — | 4 | 26 | 54 | 52 |
| 85 | 23 | 23 | — | 4 | 3 | 30 | 12 |
| 86 | — | 23 | O | 4 | 10 | 37 | 30 |
| 87 | 22 | 22 | O | 4 | 26 | 52 | 54 |
| 88 | — | 22 | L | 4 | 10 | 36 | 31 |
| 89 | 19 | 21 | — | 4 | 8 | 33 | 28 |
| 90 | — | 21 | L | 4 | 7 | 32 | 25 |
| 91 | 19 | 20 | L | 4 | 11 | 35 | 35 |
| 92 | 18 | 20 | O | 4 | 19 | 43 | 49 |
| 93 | 17 | 20 | S | 4 | 16 | 40 | 44 |
| 94 | — | 20 | S | 4 | 8 | 32 | 29 |
| 95 | — | 20 | — | 4 | 20 | 44 | 50 |
| 96 | — | 20 | L | 4 | 9 | 33 | 31 |
| 97 | — | 20 | L | 4 | 10 | 34 | 33 |
| 98 | — | 20 | S | 4 | 12 | 36 | 37 |
| 99 | 17 | 19 | S | 4 | 14 | 37 | 42 |
| 100 | — | 19 | L | 4 | 7 | 30 | 27 |
| 101 | 18 | 19 | S | 4 | 17 | 40 | 47 |
| 102 | — | 19 | — | 4 | 15 | 38 | 44 |
| 103 | 17 | 19 | S | 4 | 5 | 28 | 21 |
| 104 | — | 19 | S | 4 | 11 | 34 | 37 |
| 105 | 19 | 19 | O | 4 | 18 | 41 | 49 |
| 106 | 19 | 19 | O | 4 | 15 | 38 | 44 |
| 107 | 18 | 19 | O | 4 | 10 | 33 | 34 |
| 108 | — | 19 | S | 4 | 13 | 36 | 41 |
| 109 | 17 | 19 | L | 4 | 20 | 43 | 51 |
| 110 | — | 19 | L | 4 | 8 | 31 | 30 |
| 111 | 18 | 18 | S | 4 | 16 | 38 | 47 |
| 112 | 18 | 18 | — | 4 | 14 | 36 | 44 |
| 113 | 18 | 18 | S | 4 | 12 | 34 | 40 |
| 114 | 17 | 18 | S | 4 | 7 | 29 | 28 |

* O means no distinct zone of growth, S a short zone of growth, L long ditto.

TABLE II—*continued.*

| Number of specimen. | Anterior regeneration. Number of setigerous segments. | Anterior regeneration. Total number of distinct segments. | Anterior regeneration. Growing zone.* | Number of original segments. | Posterior regeneration. | Total segments of whole worm. | Percentage of posterior regeneration. |
|---|---|---|---|---|---|---|---|
| 115 | — | 18 | L | 4 | 10 | 32 | 36 |
| 116 | 13 | 18 | S | 4 | 7 | 29 | 28 |
| 117 | 16 | 18 | S | 4 | 9 | 31 | 33 |
| 118 | 15 | 17 | S | 4 | 5 | 26 | 23 |
| 119 | 17 | 17 | S | 4 | 7 | 28 | 29 |
| 120 | 17 | 17 | S | 4 | 6 | 27 | 30 |
| 121 | 17 | 17 | S | 4 | 11 | 32 | 40 |
| 122 | 16 | 17 | — | 4 | 14 | 35 | 45 |
| 123 | 17 | 17 | O | 4 | 12 | 33 | 41 |
| 124 | — | 17 | L | 4 | 5 | 26 | 33 |
| 125 | — | 17 | L | 4 | 6 | 27 | 26 |
| 126 | — | 17 | L | 4 | 7 | 28 | 28 |
| 127 | — | 17 | S | 4 | 7 | 28 | 28 |
| 128 | — | 17 | L | 4 | 10 | 31 | 37 |
| 129 | — | 16 | L | 4 | 12 | 32 | 43 |
| 130 | — | 16 | L | 4 | 7 | 27 | 30 |
| 131 | — | 16 | L | 4 | 8 | 28 | 33 |
| 132 | — | 16 | L | 4 | 15 | 35 | 48 |
| 133 | — | 16 | L | 4 | 12 | 32 | 43 |
| 134 | — | 16 | L | 4 | 6 | 26 | 27 |
| 18 (2) | 12 | 15 | S | 4 | 4 | 23 | 21 |
| 135 | 15 | 15 | O | 4 | 18 | 37 | 54 |
| 136 | — | 15 | S | 4 | 13 | 32 | 46 |
| 137 | 15 | 15 | S | 4 | 6 | 25 | 28 |
| 138 | — | 14 | L | 4 | 5 | 23 | 26 |
| 139 | 12 | 13 | — | 4 | 4 | 21 | 24 |
| 140 | — | 13 | S | 4 | 3 | 20 | 18 |
| 141 | — | 13 | L | 4 | 7 | 24 | 35 |
| 142 | — | 11 | S | 4 | 9 | 24 | 45 |
| 143 | 10 | 11 | L | 4 | 13 | 28 | 54 |
| 144 | 10 | 11 | L | 4 | 10 | 25 | 48 |
| 145 | 11 | 11 | L | 4 | 4 | 19 | 27 |
| 17 (2) | 10 | 10 | S | 4 | 3 | 17 | 23 |
| 2 (9) | 10 | 10 | S | 4 | 4 | 18 | 28 |
| 146 | — | 10 | L | 4 | 11 | 25 | 52 |
| 147 | — | 9 | O | 4 | 35 | 48 | 80 |
| 148 | — | 16 | O | 5 | 9 | 30 | 36 |
| 149 | — | 15 | L | 5 | 7 | 27 | 32 |
| 150 | — | 11 | O | 5 | 20 | 36 | 64 |
| 151 | $9\frac{1}{2}$ | 10 | O | 5 | 20 | 35 | 67 |
| 152 | $9\frac{1}{2}$ | 10 | O | 5 | 13 | 28 | 56 |
| 153 | — | 10 | O | 5 | 11 | 26 | 52 |
| 154 | $9\frac{1}{2}$ | 10 | O | 5 | 10 | 25 | 50 |
| 155 | 19 | 19 | S | 6 | 12 | 37 | 39 |
| 156 | — | 17 | S | 6 | 8 | 31 | 32 |
| 157 | 16 | 16 | O | 6 | 15 | 37 | 48 |
| 158 | 16 | 16 | O | 6 | 3 | 25 | 16 |

* O means no distinct zone of growth, S a short zone of growth, L long ditto.

TABLE II—*continued.*

| Number of specimen. | Anterior regeneration. | | | Number of original segments. | Posterior regeneration. | Total segments of whole worm. | Percentage of posterior regeneration. |
|---|---|---|---|---|---|---|---|
| | Number of setigerous segments. | Total number of distinct segments. | Growing zone.* | | | | |
| 159 | 20 | 20 | L | 7 | 10 | 37 | 33 |
| 160 | 12 | 13 | — | 7 | 10 | 30 | 43 |
| 161 | — | 13 | S | 7 | 10 | 30 | 43 |
| 162 | — | 19 | — | 8 | 16 | 43 | 46 |
| 163 | 16 | 18 | S | 8 | 6 | 32 | 25 |
| 164 | 15 | 15 | S | 8 | 4 | 27 | 21 |
| 17 (3) | 8 | 11 | S | 8 | 4 | 23 | 27 |
| 165 | 10 | 10 | — | 8 | 9 | 27 | 47 |

* O means no distinct zone of growth, S a short zone of growth, L long ditto.

In Table II are recorded some details of those regenerated worms of which particulars were kept, some of the counts having been made on specimens which had been recently brought in, others on those which had been in finger-bowls in the laboratory from a few days to a month. In some cases both the number of setigerous segments and the total number of distinct segments which could be made out in the regenerated portions are given, in other cases only the total number of distinct segments. The latter figure is not as definite as the former, being often a matter of personal judgment, but it is probably on the whole the more significant. In many cases a statement about the size of the zone of growth behind the distinct segments of the anterior regeneration was made, and these statements have been summarised in the Table under three signs, viz.: O, when there were no visible growing piece between the last distinct regenerated segment and the first original segment; L, when the growing piece was long; and S, when it was distinct but short. It must not, however, be assumed that, because there was no visible growing piece, regeneration was complete, although when a well-formed setigerous segment is in close proximity to the first original segment this is probably the case.

The Table is arranged in groups according to the number of original segments, and in each group the specimens are placed in order of the number of distinct segments in the anterior regeneration. As a measure of the relative development of the anterior and posterior regenerations, a column has been added giving the posterior regeneration expressed as a percentage of the total regeneration. Thus, when there is the same number of distinct segments in the anterior regeneration as there is in the posterior one, the figure in this column is 50 per cent. If there are more segments in the posterior than in the anterior regeneration, the figure is greater than 50, or when the percentage is high the tail is relatively well developed. A more detailed discussion of this Table will be deferred until the experimental results contained in the next section have been considered.

*Regeneration is Complete.*

Although, owing to the difficulty of feeding the worms, it has not been possible, up to the present, to show by direct experiment that an anterior regeneration continues to form new segments until the original segments occupy exactly the same position in the regenerated worm that they did in the original worm, and that when this position is reached no further segments are formed in front of the original ones, nevertheless a study of regenerated specimens, collected from material brought in from the natural habitat or from material which had been living for a time (up to about a month) in small glass aquaria in the laboratory, leaves little doubt that such complete and exact regeneration does actually occur. Thus a piece of an original worm, consisting of the twenty-third, twenty-fourth, twenty-fifth, and twenty-sixth segments will regenerate a new head and twenty-two anterior segments. It will also regenerate a number of posterior segments, but the exact number here is not of such interest or importance, owing to the fact that growth in these worms continues to take place with the formation of new segments in the zone of growth immediately in front of the pygidium.

It is especially by a study of the way in which regenerated specimens fragment that evidence is obtained of the correctness of this view. But before studying the breaking-up of worms with an anterior regeneration it will be useful to show from particular instances that posterior regenerations from original anterior ends break up normally, according to the position which they occupy, so that the whole regenerated worm falls into the usual regular scheme, which was explained on p. 141 and illustrated in fig. 13, Plate 14.

The following instances show quite normal breakage, or have only unimportant irregularities towards the tail :—

Specimen No.

166. Head 7+2+2+2+3 (Original.) + 3+3+4+4+4+3 P. (Regenerated.)

167. Head 7+2+2 (Original.) + 2+3+3+3+4 (Regenerated.) broken here.

168. Head 9+2+2 (Original.) + 3+3+3+4+4+3+1+3+1+8 P. (Regenerated.)

169. Head 7+2+2+2+3+3 (Original.) + 3+2 P. (Regenerated.)

170. Head 11+2+2½ and* 3 (Original.) + 3+4+4+6+5 P. (Regenerated.)

* The word "and" in these formulæ is used to connect segments which differ in some way, but between which there is no break. A break is always indicated by the + sign.

After segment 13 there was an original undivided piece consisting of two segments followed by a half segment with setæ on one side only and then three segments.

Specimen No.

18 (1). $$\underbrace{\text{Head } 7+2+2+2+3}_{\text{Original.}}+\underbrace{3+3+4}_{\text{Regenerated.}}\text{ P.}$$

171. $$\underbrace{\text{Head } 7+2+2}_{\text{Original.}}+\underbrace{2+3+3+14}_{\text{Regenerated.}}\text{ P.}$$

172. $$\underbrace{\text{Head } 7+2+2+2+3}_{\text{Original.}}+\underbrace{3+3+4+4}_{\text{Regenerated.}}\text{ P.}$$

173. $$\underbrace{\text{Head } 7+2}_{\text{Original.}}+\underbrace{2+2+3+3+3+4+4+4+7+3+4}_{\text{Regenerated.}}\text{ P.}$$

174. $$\underbrace{\text{Head } 7+2+2+2+3}_{\text{Original.}}+\underbrace{3+3+4+4+3+4+4+4}_{\text{Regenerated.}}\text{ P.}$$

175. $$\underbrace{\text{Head } 9+2}_{\text{Original.}}+\underbrace{2+3+3+3+4+4+4+4+1+3+2}_{\text{Regenerated.}}\text{ P.}$$

In the following there are important irregularities :—

Specimen No.

176. $$\underbrace{\text{Head } 7+2+2+2+3+}_{\text{Original.}}\overbrace{4\text{ and }3\text{ P.}}^{\text{One piece.}}\quad\text{Regenerated.}$$

The 4 and 3 P subsequently broke into 3+1 and 3 P.

Here the original piece consisted of twenty segments. Possibly two segments were injured and absorbed (*cf.* Experiment I, Piece 6, p. 145). The regeneration has not proceeded far enough to be significant.

Specimen No.

177. $$\underbrace{\text{Head. } 7+1\tfrac{1}{2}+2+3}_{\text{Original.}}+\underbrace{3+3}+\underbrace{4+4+6}_{\text{Regenerated.}}\text{ P.}$$

After segment 8 there is a half segment, with setæ on the left side only. In addition to this a section of two segments seems to be suppressed. Perhaps this is a case of incomplete double regeneration (*cf.* p. 169).

Specimen No.

178. $$\underbrace{\text{Head } 7+2+2+2+3+4}_{\text{Original.}}+\underbrace{4+4+4}_{\text{Regenerated.}}\text{ P.}$$

This is difficult to explain but it resembles Specimen 176. A note made at the time of the experiment suggests that the first four may possibly be the original segments, but there was nothing in their appearance to indicate this. There was a clear break between segments 16 and 17, which would not be expected if 16 and the segments anterior to it were regenerated segments (see p. 161).

Specimen No. 179.

One piece. (over "2 and 1")

$$\underbrace{\text{Head}\quad 7+2+2+2+3+2}_{\text{Original.}}\ \text{and}\ \underbrace{1+1+9}_{\text{Regenerated.}}\ \text{P.}$$

The seventeenth and eighteenth were large and obviously old segments, whilst the nineteenth which was joined to them was small and seemed to be a regenerated one. An alternative suggestion is that the nineteenth segment is an old one, which has been partially absorbed after injury.

We may now pass on to consider instances in which the anterior ends are regenerated. These are of two kinds, those which originated from segments from the middle of the body of the parent worm, and have therefore both anterior and posterior regenerations, and those which originated from terminal segments of the parent and have therefore only anterior regeneration. The two kinds may, however, be considered together.

Specimen No. 157.

6 (over "3 and 3")

$$\underbrace{\text{Head}\quad 7+2+2+2+3}_{\text{Regenerated.}}\ \text{and}\ \underbrace{3+3}_{\text{Original.}}+\underbrace{4+4+4+3}_{\text{Regenerated.}}\ \text{P.}$$

The whole specimen consisted of thirty-seven setigerous segments, of which sixteen were in the anterior regeneration, six were original segments and fifteen were in the posterior regeneration. When broken up it divided as shown in the above formula. The anterior regeneration divided quite normally, but its last section of three segments did not separate from the first section of three original segments, the two united sections forming a piece of six segments. This was followed by the remaining three original segments in one section, and then came the posterior regeneration commencing with three sections of four segments each. Finally, there were three segments, the pygidium and two anal cirri all in one piece.

There can be little doubt that the conclusion is justified that the anterior regeneration is just complete, and that the original segments have come to occupy in the regenerated worm the position which they had occupied in the parent worm, that is to say that the original piece consisted of the six segments, 17 to 22, that they regenerated a head and sixteen anterior segments, so that the six segments have again become the seventeenth to twenty-second. The posterior regeneration has attained three of the sections of four segments to be expected, but has not yet finished growing and as new segments are added immediately in front of the pygidium there is every reason to expect that when further growth has taken place the next section will be one of four segments.

One point mentioned above needs to be emphasized. No indication of a break occurred at the point where the anterior regeneration joined the original segments, so that here we had a section of six segments consisting of three regenerated segments (segments 14 to 16) and three original segments (segments 17 to 19). This is indicated in the formula by the use of the word "and" instead of the + sign. The absence of a breaking point at the zone of growth, where an anterior regeneration joins an original segment, is a constant feature in all the worms which have been experimented with, and it is very difficult to bring about a separation at such a point. On the other hand, between an original segment and a posterior regeneration, a break invariably takes place. It will be remembered that there is no zone of growth between these segments, new segments in a posterior regeneration being added immediately in front of the pygidium.

In Specimen 157, which has just been described, the regenerated portions, both anterior and posterior, were exceptionally clear, and distinct from the six original segments. This worm and Specimen 87 which will next be described are the most striking cases of complete anterior regeneration, which were studied and recognised as such.

Specimen No.

87. Head 7+2+2+2+3+3+3 and 4 + 4+4+4+6+3+3+3+2 P.

(brace over "3 and 4": 7)

(Head 7+2+2+2+3+3+3: Regenerated.) (and 4: Original.) (4+4+4+6+3+3+3+2 P.: Regenerated.)

Fig. 13 (Plate 14) is an outline drawing of this specimen showing how it broke up. The different sections were not actually separated, and the specimen was subsequently put back in sea water where it recovered.

As will be seen from the formula, regeneration had taken place from four original segments, which could be clearly discriminated by the coarser texture of the skin and their stronger pigmentation. They were segments 23, 24, 25 and 26. Segment 22, the last segment of the anterior regeneration, was short, being less than half the length of the segment immediately in front of it (see fig. 13). As usual there was no breaking point between the last segment of the anterior regeneration and the first of the original segments. It is very probable that the anterior regeneration is complete, though it is just possible that another section of four segments remains to be regenerated, since there are often five sections of four after the three threes. The fact, however, that there is no marked growing zone between segments 22 and 23 favours the view that regeneration is complete, as does also the fact that the worm recovered and remained alive for two months, at the end of which time there were no additional segments; segment 22, the last of the anterior segments, being considerably reduced and only detected with difficulty. The four original segments could still be distinguished.

Specimen No.

15. Head 7+2+2+2+3+3+4+4+4+4+4+3+3+3+6 P.

(Head 7+2+2+2+3+3: Regenerated.) (4+4+4+4+4+3+3+3+6 P.: Original.)

There was a distinct growing zone after segment 19. One section of three segments remained to be regenerated. This is the worm used in the experiment described on p. 143.

Specimen No.
180. $\underbrace{\text{Head } 7+2+2+2+3+3+3}_{\text{Regenerated.}}$ and $\underbrace{4+4+4+3+3+3 \text{ P.}}_{\text{Original.}}$ ($\overbrace{3 \text{ and } 4}^{7}$)

Perhaps a section of four or two such sections remain to be regenerated. The posterior twenty-one segments showed no distinct sign of regeneration, except that the pygidium itself looked as if it had recently regenerated, and they were probably the original posterior end of a worm. But it must be pointed out that, in the direct experiments on regeneration, the segments in the posterior regenerations had often become almost indistinguishable from the original segments, whilst the anterior ones were still far from complete and very markedly different. In the present case there is the possibility that the original segments numbered four or eight, and that those behind are regenerated. This, however, makes little if any difference to the argument about the completeness of the anterior regeneration.

Specimen No.
181. $\underbrace{\text{Head } 7+2+2+2+3+3+3+3\tfrac{1}{2}}_{\text{Regenerated.}}$ and $\underbrace{4+4+3+3+3+3 \text{ P.}}_{\text{Original.}}$ ($\overbrace{3\tfrac{1}{2} \text{ and } 4}^{7\frac{1}{2}}$)

As usual, there was no break between the last section of the regeneration and the first section of the originals. The former (segments 23, 24, 25 and 26) were clearly regenerated. Segment 26 was small, and had only setæ on the left side. The glands of the old segments were well developed and dark, and the colour of the tissues was a much brighter yellow than in the regenerated segments. The specimen was particularly clear and certain. Comparison with Specimen 180 is interesting, and a discussion of the completeness or otherwise of its regeneration would follow similar lines.

Specimen No.
85. $\underbrace{\text{Head } 7+2+2+2+3+3+3+1}_{\text{Regenerated.}}$ and $\underbrace{4}_{\text{Original.}}$ + $\underbrace{1+2 \text{ P.}}_{\text{Regenerated.}}$ ($\overbrace{1 \text{ and } 4}^{5}$)

There are four original segments, and the anterior regeneration is not yet complete. The specimen is noteworthy on account of the relatively very small posterior regeneration, in which the last two segments had not yet developed setæ. Posterior regeneration generally lags behind anterior, but the difference in this case is so great that it seems to call for some special explanation. Perhaps the original segments were far back in the parent worm—the last of the fours.

Specimen No.
152. $\underbrace{\text{Head } 7+2\tfrac{1}{2}}_{\text{Regenerated.}}$ and $\underbrace{2+3}_{\text{Original.}}$ + $\underbrace{3+3+4+3 \text{ P.}}_{\text{Regenerated.}}$ ($\overbrace{2\tfrac{1}{2} \text{ and } 2}^{4\frac{1}{2}}$)

Anterior regeneration not yet complete. The small half segment, with setæ on the right side only, represents the growing zone. The completion of this half segment, and the growth of an additional segment behind it, would make everything normal.

$4\frac{1}{2}$
Specimen No. 182. Head $7+2+2+2+1\frac{1}{2}$ and $3+3+4+4+4+4+4+3+4$ P.
Regenerated. Original.

The half segment has setæ on the right side only. This segment requires to be finished, and one other segment formed, to make the worm complete and normal.

4
Specimen No. 58. Head $7+2+2+2+1$ and $3$ + $4+4+5$ P.
Regenerated. Original. Regenerated.

Requires $2+3$ to complete.

5
Specimen No. 112. Head $7+4+5\frac{1}{2}+1$ + $4$ + $14$ P.
Regenerated. Original. Regenerated.

The section of $5\frac{1}{2}$ in the anterior regeneration had six parapodia on the left-hand side, the extra half segment being between segments 12 and 13. This, together with the imperfect way in which the worm broke up, makes the interpretation doubtful.

6
Specimen No. 183. Head $7+2+2+2+3+3+3$ and $3+1+3+3+1+2+4$ P.
Regenerated. Original.

Anterior regeneration probably not yet complete, as some sections of four are wanting.

9
Specimen No. 163. Head $7+2+2+2+5$ and $4$ + $4+4+2$ P.
Regenerated. Original. Regenerated.

Regeneration from eight original segments not yet complete. The five posterior segments of the anterior regeneration consist of three segments with setæ and a growing zone in which two segments were differentiated, but in which the setæ had not yet developed.

6
Specimen No. 164. Head $7+2+2+2+2$ and $4$ + $4+4$ P.
Regenerated. Original. Regenerated.

Specimen No. 75.

5
Head 7+2+2+2 and 3 + 4 P.
Regenerated. Original. Regenerated.

The last two segments of the anterior regeneration, which remained as usual united to the three original segments, had not yet developed setæ. Regeneration had not yet proceeded far enough to give any indication as to which section of threes the original segments belonged.

Specimen No. 2. (9).

$5\frac{1}{2}$
Head 7+2+$1\frac{1}{2}$ and 4 + 4+4 P.
Regenerated. Original. Regenerated.

Regeneration has not proceeded far.

Specimen No. 18. (2).

8
Head 7+2+2+4 and 4 + 2+2 P.
Regenerated. Original. Regenerated.

The last four of the anterior regeneration consist of one segment with setæ and three without setæ.

Specimen No. 18. (3).

4
Head 7+2+1 and 3 + 3+4 P.
Regenerated. Original. Regenerated.

Specimen No. 184.

5
Head 7+2+2+2+3+2 and 3+4+4+3+3+3+2 P.
Regenerated. Original.

The interpretation is doubtful owing to the fact that there are only two sections of four in the original portion of the worm. Perhaps the initial section of three in this original portion was a four, in which one segment was injured and absorbed (*cf.* Experiment 1, Piece 6, p. 145).

Specimen No. 18. (4)

7
Head 7+2+2+5 and 2+3+3+2 P.
Regenerated. Original.

Interpretation doubtful. Of the last five regenerated segments three are setigerous and two have not yet got their setæ.

Specimen No. 155.

$5\frac{1}{2}$
Head 7+2+2+2+3+$2\frac{1}{2}$ and 3+3+4+4+4 P.
Regenerated. Original. Regenerated.

The last section of the anterior regeneration had three bundles of setæ on one side and two on the other. It was united by a growing piece to the first section of three original segments. On the face of it, the manner of breaking up suggests that the anterior regeneration had overshot the mark, as it has produced one section of three too many. An alternative to this view is to suppose that the second of the original sections of three was at first a section of four, the last segment of which was damaged and absorbed. This would bring the worm into the normal scheme.

*Specimen* 185.

This is one of the most interesting cases of regeneration which has occurred. It is shown in fig. 7, Plate 13. The original segments are the posterior portion of a female stolon full of eggs. The first seven segments of this portion are modified segments with long dorsal cirri and well developed swimming bristles. These are followed by about twenty-three segments of the usual kind without swimming bristles and with gradually diminishing dorsal cirri, all of them apparently original segments. Regeneration has taken place anteriorly, and a perfect souche or parent head has been produced together with exactly thirteen setigerous segments, the usual number found in the souche. Immediately behind the thirteenth setigerous segment there has been formed what is evidently the commencement of a new stolon head, with a fairly long median tentacle and two lateral buds, the latter evidently representing the commencement of lateral tentacles. Behind this there are indications of two further pairs of lateral buds before the original tissue is reached.

It is a fact of great interest that a portion of a stolon should in this way regenerate the whole of a new souche and a new stolon head.

Returning now to the records of regenerated specimens contained in Table II, it will be seen that they lend considerable support to the view which has been put forward already, that when regeneration takes place from any particular section of segments it proceeds until the section comes to occupy in the new worm the same position which it occupied in the old one.

The records need to be treated with some caution, and are not well adapted for statistical study, since there was certainly some selection in picking out the particular specimens which were examined, in favour, on the one hand, of those which showed obvious signs of regeneration and in which therefore regeneration was still in a moderately early stage, and, on the other hand, of those large specimens in which regeneration was nearly complete, which were specially searched for. The points to be considered here are not affected by such selection, however, unless a particular statement is made to indicate the fact.

*Regeneration from three and four Original Segments.*

The records in Table II are arranged in groups according to the number of original segments from which regeneration has taken place. The two most important groups are those with three and four original segments. Of those with three original segments there are sixty-three specimens of which records of both anterior and posterior regenerations are available; of those with four original segments there are sixty-eight specimens, so that the two groups contain approximately equal numbers.

It will be remembered that in a worm which breaks normally, three sections of three segments occur between segments 14 and 22, whilst sections of three occur again towards the tail end, following four or five sections of four. It is clear, therefore, that if the anterior regeneration is exact, always stopping at the right segment, all the specimens from three originals with more than nineteen segments in the anterior regeneration, or those with nineteen segments and a growing piece, must have come from one of the sections of three which occur near the tail end, behind the sections of four. There are eight worms recorded which come under this head (Nos. 21–28).

If we compare the specimens regenerated from three original segments with those regenerated from four, it is clear that the anterior regenerations on the whole contain more segments when the number of original segments is four, which agrees with the fact that the sections of four lie behind the principal sections of three. Thus, whilst from the sections of three there are ten specimens with eighteen or more segments in the anterior regeneration (eight of which, as was shown, are probably derived from the posterior sections of three), from the sections of four there are thirty-five specimens with eighteen or more segments in the anterior regeneration. Also from the sections of three there are four specimens with seventeen segments in the anterior regeneration, from the sections of four there are eleven specimens.

On the other hand, the relative number of segments in the posterior regeneration is larger in the specimens which have regenerated from three original segments than it is in those which have regenerated from four. There are seventeen specimens derived from three original segments in which the number of segments in the posterior regeneration is 50 per cent. or more of the total regeneration, whereas there are only nine such specimens derived from four original segments, of which the largest, with 80 per cent. posterior regeneration, as will be seen later, should be omitted in this connection. If we take those in which the posterior regeneration is 40 per cent. and over, the numbers are forty specimens derived from three originals, twenty-eight derived from four originals.

On the whole, therefore, the specimens regenerated from three segments have shorter anterior regenerations and longer posterior regenerations, as measured by the number of segments in each, than those regenerated from four segments, which agrees with the view that regeneration proceeds until the original segments are restored to the position which they occupied in the parent worm.

If the figures for the percentage of tail regeneration are considered in connection with the total number of segments in the specimens, it will be seen that, on the whole, the larger specimens with most segments have the highest percentages of segments in the posterior regenerations, which would naturally follow from the fact that the posterior regeneration continues to grow after the anterior one is complete. Thus, amongst specimens from four original segments, there are seven specimens in which the total number of segments exceeds forty, and, for all of these, the relative number of segments in the posterior regeneration exceeds 48 per cent. In those derived from three originals, there are only two specimens with more than forty segments, in one of which the posterior regeneration is 53 per cent., in the other 28 per cent.

At the same time, specimens with a high percentage of posterior regenerated segments are quite as frequent amongst the smaller specimens as they are amongst the large ones, as the following figures show:—

Posterior Regeneration 50 per cent. and over.

From Three Original Segments.

| Total segments in specimens | Number of instances. | |
|---|---|---|
| 17 | 1 at 57 per cent. | |
| 25 | 2 at 55 ,, | |
| 29 | 1 at 54 ,, | |
| 30 | 1 at 52 ,, | |
| 31 | 1 at 50 ,, | 1 at 54 per cent. |
| 32 | 1 at 52 ,, | |
| 34 | 1 at 52 ,, | 1 at 55 ,, |
| 35 | 1 at 53 ,, | |
| 37 | 1 at 50 ,, | 1 at 56 ,, |
| 39 | 1 at 53 ,, | 1 at 56 ,, |
| 40 | 1 at 59 ,, | |
| 46 | 1 at 53 ,, | |

From four Original Segments.

| Total segments in specimens | Number of instances. |
|---|---|
| 25 | 1 at 52 per cent. |
| 28 | 1 at 54 ,, |
| 37 | 1 at 54 ,, |
| 43 | 1 at 51 ,, |
| 44 | 1 at 50 ,, |
| 48 | 1 at 80 ,, |
| 52 | 1 at 54 ,, |
| 54 | 1 at 52 ,, |

Amongst the specimens regenerated from four original segments, there is one which is of special interest and importance, viz.:—

*Specimen* 147.

This worm stands apart from all the others derived from four original segments, owing to the relatively large number of segments in the posterior regeneration, the percentage rising to 80, whereas no other specimen in the group exceeds 54 per cent. The percentage is far higher also than that found in any specimen regenerated from three original segments, in which group 59 per cent. is the highest recorded. The details of the specimen, which was found amongst some worms which had been preserved in alcohol, and therefore could not be broken up, are as follows: It consisted of forty-eight segments in all, of which four were clearly original segments. The head and the first nine setigerous segments were regenerated, there was no evident growing piece, and the ninth segment was well formed, so that there was every reason to suppose that regeneration was complete. The posterior regeneration consisted of about thirty-five regenerated segments, with pygidium and two anal cirri, this number of posterior regenerated segments being the largest that has been found in any specimen examined.

There can, I think, be no doubt that the four original segments in this specimen were segments 10, 11, 12 and 13 of the parent, the last two sections of two segments, the two sections having remained together as one piece. The anterior regeneration has been completed, the four original segments have become segments 10, 11, 12 and 13 in the regenerated worm, and the posterior regeneration has continued to grow.

*Regeneration from two Original Segments.*

Only one instance has been met with amongst the natural material of regeneration from two original segments, Specimen 20 (Table II, p. 154), which had nine distinct segments in the anterior regeneration. The ninth segment was well formed, and no growing piece could be seen behind it, so that it is quite probable that regeneration was complete, and that the original segments were ten and eleven, that is, the middle section of the three sections of two, which normally follow after the head and seven section. The worm was first examined after preservation in spirit, so that it was not broken up. The posterior regeneration consisted of eleven segments, giving a percentage of 52 of the total regeneration.

*Regeneration from five Original Segments.*

Seven specimens (see Table II). One of these, Specimen 152, was seen alive and broken up (see p. 162). The five original segments broke into 2+3, so that it may be concluded that they were segments 12, 13, and 14, 15, 16, the last section of two and the first section of three, which had remained together. Specimens 150, 153, 154 and 151 are no doubt similar, and, as no large growing piece was present in front of the original segments, the anterior regeneration was nearly complete. In these specimens the posterior regeneration was from 50 to 67 per cent. of the total regeneration, high figures which are consistent with a forward position of the original segments.

The two remaining specimens (148 and 149) from five original segments require some other explanation, as the anterior regenerations have fifteen and sixteen distinct segments. They are perhaps from pieces of six original segments, with one segment absorbed after injury. The posterior regenerations are 32 and 36 per cent., so that segments 17 to 22 of the original worm seem to be indicated.

*Regeneration from six Original Segments.*

Four specimens (Table II, p. 156). Of these specimens, 157 was broken up, and has been described already on p. 160. The six original segments were clearly made up of two sections of three, segments 17 to 22. Specimen 158 was preserved before it was examined. There was no growing piece after segment 16, so that the condition is quite similar to that of Specimen 157 just described. Specimens 155 and 156, with nineteen and seventeen segments in the anterior regeneration, do not fall into line unless we assume either that the six originals are from the posterior threes, or from some imperfect arrangement of the sections of four.

*Regeneration from seven Original Segments.*

Three specimens (Table II, p. 157). These are all consistent with the supposition that the seven original segments are made up of 3+4, the last of the sections of three and the first of the fours. If they came from further back (last of fours and first of threes), one would expect the posterior regeneration to be shorter.

*Regeneration from eight Original Segments.*

Five specimens (Table II, p. 157). Of these, 163 and 164 were shown by breaking up to be from 4+4 original segments (p. 163), and 17 (3) is probably the same. 162 and 165 were preserved before examination, but there is nothing to suggest that they are not of the same character as 163 and 164. It should be noted that the posterior regenerations are relatively longer.

## Double and Irregular Regeneration.

In the course of the work three or four cases of double regeneration have occurred, which are worth description.

*Specimen* 186.

This was a specimen with good anterior and posterior regenerations from four original segments, which was being kept by itself in a finger-bowl. On November 14, 1919, the head with five segments was found broken off, the end of the piece broken off being somewhat macerated, making it possible that one or two segments had been lost. Both the detached anterior end (A) and the main portion of the worm (B) were kept in the finger bowl, and both commenced to regenerate.

A. On November 22 this piece had seven setigerous segments, growing piece and pygidium, on November 28 nine setigerous segments. When drawn on December 10 (Plate 11, fig. 3 A) it still had nine setigerous segments, all of which were normally pigmented. This piece was not found subsequently and it was concluded that it had macerated. It is of interest because it shows that regeneration can take place from the fifth setigerous segment.

B. On the main portion of the body, on November 19, a new head was seen to be regenerating, and by November 28 this was fully formed. This was then followed by nine setigerous segments and a growing piece belonging to the first regeneration. The worm was drawn on December 10 (Plate 11, fig. 3 B). The new head, with tentacles, tentacular cirri and four eyes, was well developed and in the most recent regeneration (second regeneration) there were four setigerous segments, followed by a fifth segment without setæ and a growing zone. The first regeneration now had ten setigerous segments and growing zone. This was followed by the four original segments, still quite distinct, behind which again was the posterior regeneration with nine setigerous segments, growing zone, pygidium and two anal cirri.

On January 19, 1920, the worm was again drawn (Plate 12, fig. 3 C). The second anterior regeneration was now complete and no sign of a growing piece could be detected. This regeneration indeed had become so complete that the point at which it joined the first regeneration was not detected, so that it is not possible to say the exact number of setigerous segments which it contained. A comparison of figs. 3 A and 3 B makes it certain that there were at least six segments, and the probability is that there were seven. When fig. 3 C was drawn there were altogether seventeen setigerous segments in the anterior regeneration, with a distinct growing piece showing that regeneration was not yet complete. On this date the posterior regeneration had so far advanced that it was difficult to distinguish it from the four orignal segments, and would probably have been impossible had not the history of the specimen been known.

On January 22 this specimen was put in a watch glass with some polyps of healthy Syncoryne and watched carefully. Although at this time its head was the second head that had regenerated it climbed the hydroid stem and after a quarter of an hour, it settled in a position where its mouth was applied to the mouth of the hydroid. It remained for an hour in the same general position, with its head moving about amongst the tentacles at the end of the hydranth, and its mouth applied from time to time to the mouth of the hydranth. At one time it remained with its mouth in this position for two or three minutes and a peculiar movement of the anterior part of the body was observed, which (with our later knowledge) was without doubt due to the pumping of the proventriculus. The worm had found its natural food.

*Specimen* 12 (6).

On November 26, 1919, a large Procerastea was broken up and the different sections allowed to regenerate. A section of seven segments (segments 20–26) produced an anterior regeneration which resembled in every way the anterior regenerations of the sections in front up to Dececember 18, when those regenerations had four or five setigerous segments. On that day, however, the section under discussion (segments 20 to 26) was found with the head broken off and only two setigerous regenerated segments left in front of the seven original segments. By January 20, 1920, another new head and three setigerous segments had regenerated to replace what was broken off, and as there was no growing piece after the third setigerous segment this new regeneration was presumably complete. The first regeneration now had three setigerous segments, so that altogether there were six setigerous segments anterior to the original segments. The posterior regeneration in this specimen did not get further than pygidium and two anal cirri.

*Specimen* 187.

This specimen with six original segments and double anterior regeneration broke up as follows :—

$$\underbrace{\text{Head}\ \ 7}_{\substack{\text{2nd}\\ \text{Regeneration.}}} + \underbrace{2+2}_{\substack{\text{1st}\\ \text{Regeneration.}}} + \underset{\text{Original.}}{6} + \underbrace{4 \text{ and } 4 \text{ P.}}_{\text{Regenerated.}}$$

There were distinct growing zones between the second regeneration and the first regeneration, and between the first regeneration and the original segments, so that probably neither was complete. In the posterior regeneration the first four segments had setæ ; the second four had none.

*Specimen* 188.

A worm, which broke as shown below, may be a case of double regeneration, but it is difficult to interpret.

$$\underbrace{\text{Head}\ \ 7+2+2+2+3+2}_{\text{Regenerated.}} \text{ and } \underbrace{4 \text{ and } 1 \text{ and } 2+3+3+3+8\tfrac{1}{2} \text{ P.}}_{\text{Original.}}$$

(The braced group "2 and 4 and 1 and 2" is marked 9 above.)

The section of nine segments (from the seventeenth to the twenty-fifth) was made up of two regenerated segments, followed by four normal original segments, one segment of half the normal size, and then two normal segments. The segment of half the normal size may perhaps be the last trace of a previous regeneration.

*Specimen* 189.

This specimen was found amongst material collected at the docks, and is represented in Plate 3, fig. 8. The explanation of the condition in which it was found appears to be that two sections, each of three original segments, were imperfectly separated from one another, but each section commenced to form both an anterior and a posterior regeneration. In the specimen, as found, there was first a well developed anterior regeneration, with head and about thirteen recognisable segments, of which seven were setigerous, followed by three original segments, from which this regeneration had proceeded. At the posterior end of these three segments there is an irregular mass of tissue on the left side of which there are two bundles of setæ, followed by four tentacular outgrowths and another bundle of setæ. On the right side there is one bundle of setæ, then a small rounded bud of tissue, behind which is another bundle of setæ. Then come seven or eight obviously regenerated segments with a growing zone behind them, which has its origin in another section of three original segments. At the posterior end of these three is an ordinary posterior regeneration, consisting of two segments (one setigerous), with growing zone, pygidium and two anal cirri. The feature which calls for explanation is the irregular mass of tissue behind the first section of three original segments. This has probably been formed by the growing together in an irregular way of the posterior regeneration of the first three original segments with a regenerated head and first setigerous segment, produced from the anterior end of the second three original segments. The tentacles of the regenerated head have all been pushed to the left-hand side, whilst the small bud of tissue on the right may represent an anal cirrus of the posterior regeneration.

*Specimen* 190.

*Lateral Regeneration.*—A well-grown worm of about fifty-two segments, which was kept alive for over two months. It broke as follows:—

$$\text{Head}\quad 7+2+2+2+4\tfrac{1}{2}+4+4+4+4+4+3+3+3+6\ \text{P}.$$

Fig. 14, A, Plate 14, is a drawing of segments 14 to 20, which shows two peculiarities. In the first place, following segment 14, there is a portion with two bundles of setæ on the right side and one bundle on the left. Judging by the distribution of the gland cells in the skin of the dorsal surface, the explanation of this appears to be that the left half of the fifteenth segment is suppressed, whilst the right half of this segment is intimately united with segment 16.

The second peculiarity is a lateral outgrowth on the right side from the front end of segment 19 (see figure). This consists of a single long tentacle, springing from a nearly spherical lobe, followed by four rudimentary segments having four bundles of setæ on the right (or posterior) side and one bundle on the left (or anterior). The whole growth looks like an abnormal and imperfect anterior regeneration, which may have originated from an injury.

It will be noticed that these two peculiarities have led to the worm breaking up in an abnormal way. The first thirteen segments are quite regular (head, 7+2+2+2), but instead of the usual three sections of three segments each, we then have four and a half, followed by five sections of four. In a Procerastea of fifty-two segments we should expect five sections of four, in which case we are left with four and a half segments to represent the three sections of three. On the other hand, the three sections of three may be represented by $(4\frac{1}{2}+4)$, and there would then be four sections of four before coming to the terminal sections of three.

For a discussion of the literature on lateral regeneration, see KORSCHELT (1919), pp. 670–679.

## SUMMARY.

*Procerastea Halleziana* was found in numbers associated with the hydroid Syncoryne. It was living in membranous tubes, which it had secreted, along the stems of the hydroid. The worm was observed to feed by piercing the body wall of the hydranths with its extruded pharynx and pumping out the contents of the gastral cavity of the hydroid. The proventriculus of the worm functions as a quick-acting pump, making from 150 to 200 pulsations a minute.

Sexual reproduction in Procerastea is quite similar to that in the genus Autolytus, each worm forming a single long stolon, which develops either into a male Polybostrichus or a female Sacconereis. The stolon head is always formed on the fourteenth setigerous segment. After the fully formed Polybostrichus or Sacconereis has become detached, the souche proceeds to regenerate posterior segments.

In addition to sexual reproduction, the worms were found to be undergoing rapid multiplication by a process of asexual reproduction, consisting of fragmentation, followed by the regeneration of anterior and posterior ends.

Fragmentation can be induced by artificial means, especially by the action of fresh water, and takes place in a definite way (Plate 14, fig. 13). The first break takes place between the seventh and eighth setigerous segments, so that the head and seven segments form one piece. This is followed by three sections of two segments each. Then follow three sections of three segments each, behind which come four or five sections of four segments each. Then sections of three segments reappear and are continued to the pygidium, though the fragmentation towards the posterior end is often incomplete.

The mode of breaking up is expressed in the following formula :—

$$\text{Head } 7+2+2+2+3+3+3+4+4+4+4\,(+4)+3+3+\ldots\text{P.}$$

Experiments were made by breaking worms up in this way, placing the different sections in separate vessels of clean sea water and allowing them to regenerate. It was found that regeneration took place at different rates according to the region of the body from which the pieces came, being most rapid in those from the middle region, that is to say those segments which become modified for swimming purposes in the Polybostrichus and Sacconereis.

Although these experiments in regeneration could not be carried far enough to

demonstrate the point directly, a study of the way in which regenerating individuals, found amongst specimens collected in the open or from small aquaria in the laboratory, broke up under the action of distilled water, made it clear the regeneration of anterior segments continued until the original segments occupied the same position in the regenerated individual as they had occupied in the parent worm and then stopped. Posterior regeneration was more active when the original segments came from the anterior end of the parent worm. A posterior section of a female stolon which had broken about the middle of the stolon body regenerated a complete souche head and thirteen segments, and had commenced the regeneration of the stolon head and anterior segments when it was found.

The asexual method of reproduction here described is very similar to that which occurs in Ctenodrilus, which has recently been re-investigated by KORSCHELT (1919), whose paper contains a good summary of the literature of the subject. The case of Lumbriculus is of a similar kind, but as far as known this is the first time "architomy" has been described in the Polychæta. Indeed the process of regeneration of the anterior portion of the body as described by IWANOW (1906, p. 35, and 1908) seems to be very different in some other Polychætes (*e.g.*, Spirographis) from what it is in Procerastea.

## LITERATURE.

1884. LANGERHANS. "Wurmfauna von Madeira, IV.," 'Zeitschr. wiss. Zool.,' vol. 40.

1886. DE SAINT JOSEPH. "Annélides Polychètes des côtes de Dinard," 'Ann. Sci. Nat. Zool.,' 7e série, T.I.

1891. MALAQUIN, A. "Sur la Reproduction des Autolyteæ," 'Revue Biologique du Nord de la France,' III.

1893. *Idem.* "Recherches sur les Syllidiens," 'Mém. Soc. Sc. Arts, Lille.'

1906. IWANOW, P. "Die Regeneration der Segmente bei den Polychäten," 'Zeitschr. wiss. Zool.,' vol. 85.

1908. *Idem.* "Die Regeneration der Körperenden bei *Spirographis spallanzanii*," 'Zeitschr. wiss. Zool.,' vol. 91.

1910. KORSCHELT UND HEIDER. 'Lehrbuch der vergleichenden Entwicklungsgeschichte.' Allgemeiner Theil, IV, 2.

1915. ALLEN, E. J. "Polychæta of Plymouth and the South Devon Coast," 'Journ. Mar. Biol. Assoc.,' X, 1915, p. 592.

1919. KORSCHELT, E. "Ueber die naturliche und kunstliche Teilung des *Ctenodrilus monostylos*, ZEPPELIN," 'Arch. f. Entwick. mechanik,' vol. 45.

## EXPLANATION OF PLATES.

(All figures of *Procerastea Halleziana*, from drawings by Mrs. E. W. Sexton.)

### Plate 11.

Fig. 1.—*Procerastea Halleziana*. Stolon head commencing on segment 14. × 20.

Fig. 2.—Female stolon, well advanced. × 20.

Fig. 3.—A. The first regenerated head of fig. 3, B, which broke off and has regenerated posterior segments and pygidium. Drawn December 10, 1919. × 45.

B. Double regeneration from four original segments (Specimen 186, p. 169.) The first regenerated head, and probably seven anterior segments, have broken off, and a second head with anterior segments is regenerating. Drawn December 10, 1919. × 45.

### Plate 12.

Fig. 3.—C. Specimen B, drawn January 19, 1920. The second head and anterior regeneration can no longer be differentiated from the first anterior regeneration. The posterior regeneration cannot be differentiated from the four original segments. × 45.

Fig. 4.—Polybostrichus, or male stolon, drawn as when swimming. × 20.

Fig. 5.—Sacconereis, or female stolon, just detached from parent, drawn as when crawling. When swimming the segments behind the modified ones are coiled ventrally. × 20.

### Plate 13.

Fig. 6.—Regeneration from three original segments. Specimen 45, from raft in Cawsand Bay, September 29, 1914. × 42.

Fig. 7.—Portion of a Sacconereis, which has regenerated a complete souche, and is commencing to regenerate a stolon head. (Specimen 185, p. 165.) × 20.

Fig. 8.—Regeneration from two sections, each of three segments. (Specimen 189, p. 171.) × 42.

Fig. 9.—Early stage of regeneration from three original segments. × 20.

Fig. 10.—Later stage from three segments. (Specimen 82.) × 20.

Fig. 11.—Regeneration from four original segments. (Specimen 116.) × 20.

PLATE 14.

Fig. 12.—Procerastea feeding on Syncoryne. × 42.

Fig. 13.—Procerastea regenerated from four original segments, and showing the normal way of breaking up. (Specimen 87, p. 161.) × 20.

Fig. 14.—A. Lateral regeneration, dorsal view. (Specimen 190, p. 172.) × 58.
B. The same—ventral view. × 58.

Fig. 15.—The seventh modified parapodium, left side, of the Polybostrichus. View of anterior surface. × 75.

Fig. 16.—Regenerated head seen from the ventral side, showing mouth, pharynx, and proventriculus. × 45.

Fig. 17.—The same, with pharynx extruded. × 45.

Fig. 18.—Enlarged view of the end of the pharynx, showing the "trepan." × 435.

Fig. 19.—Compound bristle of Procerastea from parapodium 11. × 435.

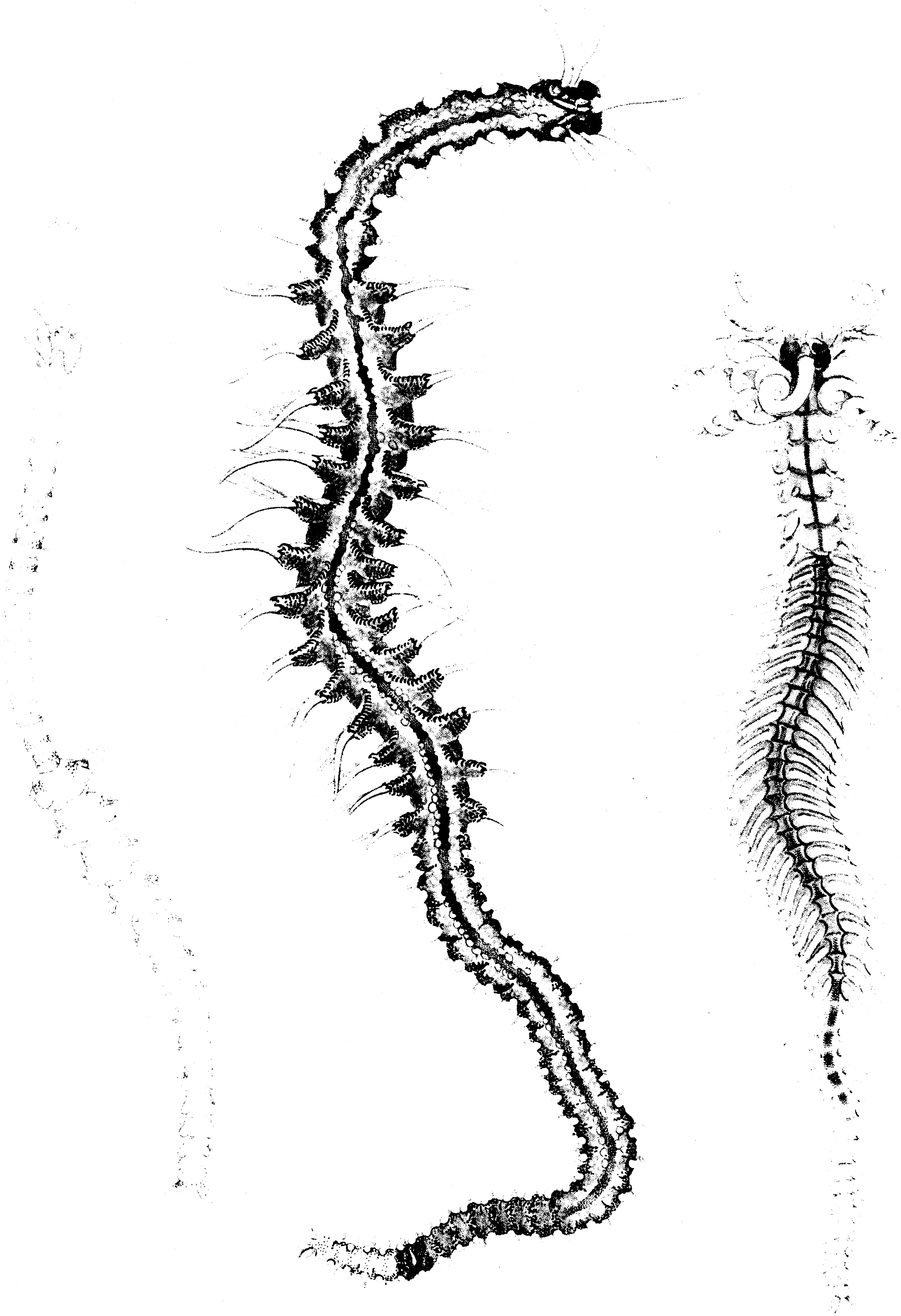
PLATE 15.

Fig. 20.—Regeneration from the different sections of one specimen of Procerastea (Specimen 15), broken up November 27, 1919. All figures × 30.

1. Head and segments 1–7. A, December 2; C, December 9; E, December 16; F, December 20.
2. Segments 8 and 9. A, December 2; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29.
3. Segments 10 and 11. A, December 2—same as 2, A; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20.
4. Segments 12 and 13. A, December 2—same as 2, A; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20.
5. Segments 14, 15, 16. A, December 2; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29.
6. Segments 17, 18, 19. A, December 2; B, December 5; C, Decem- 9; D, December 12; E, December 16; F, December 20.
7. Segments 20, 21, 22, 23. A, December 2; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29; H, January 5.
8. Segments 24, 25, 26, 27. A, December 2; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29.

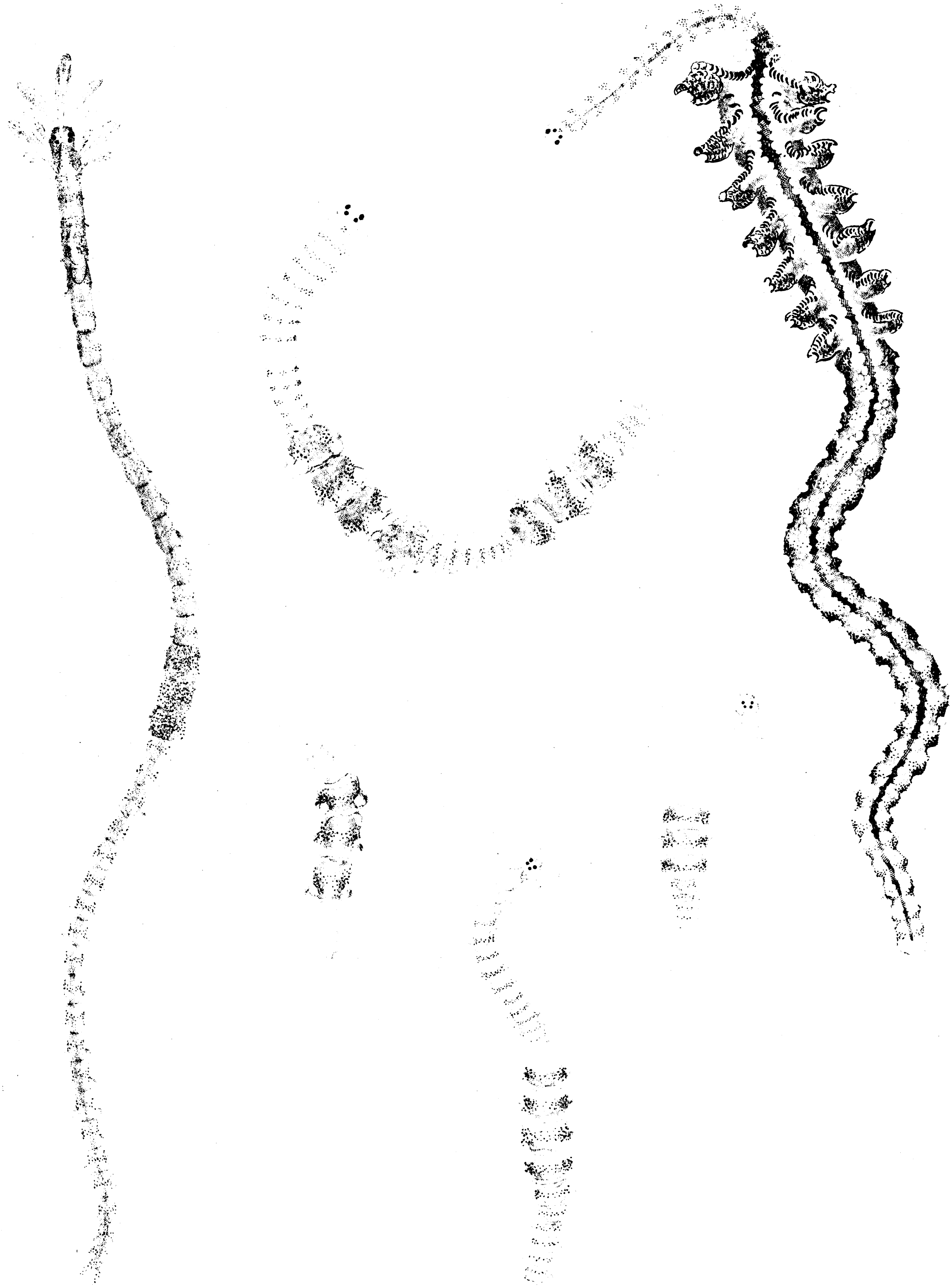


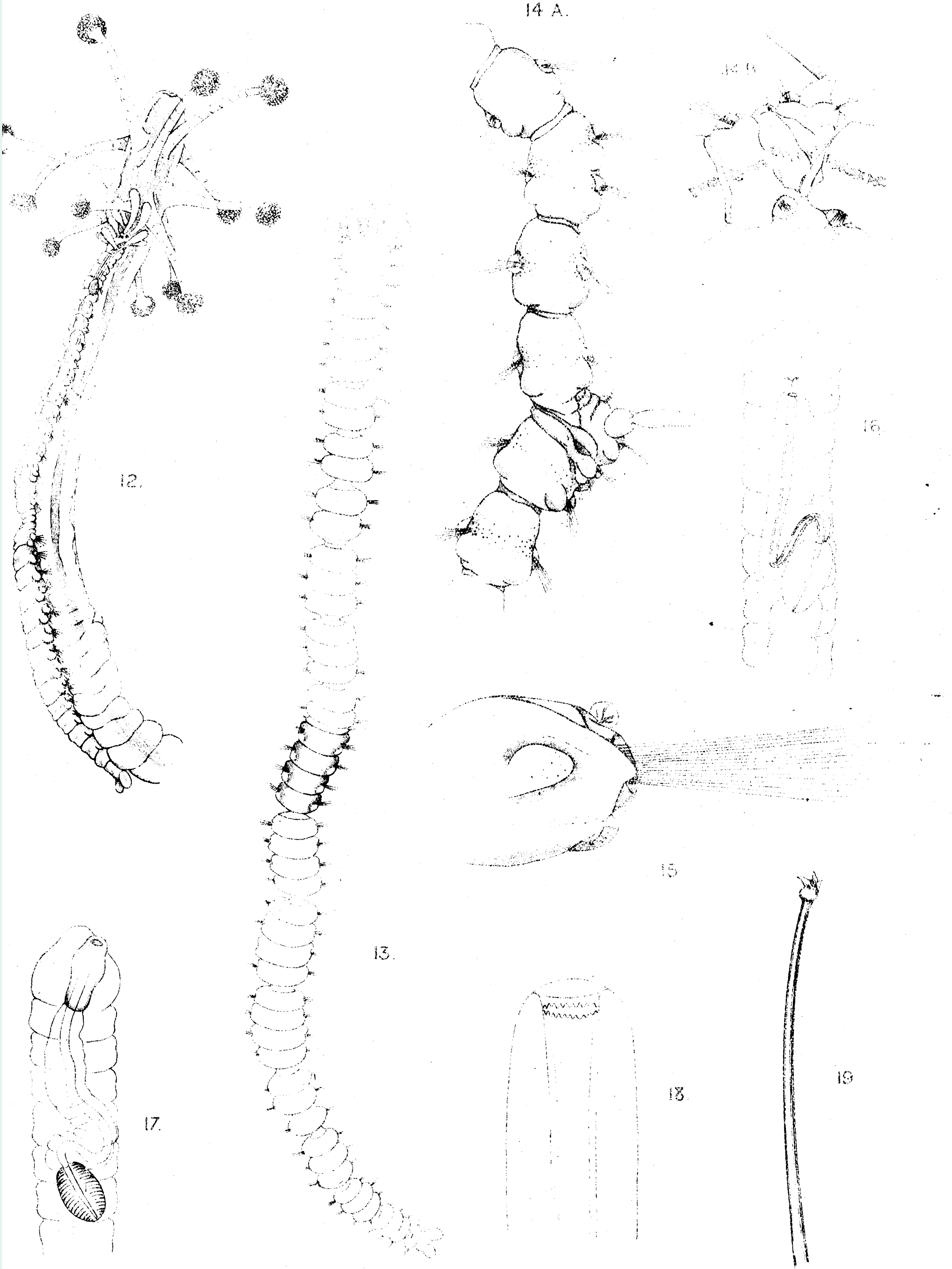
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES





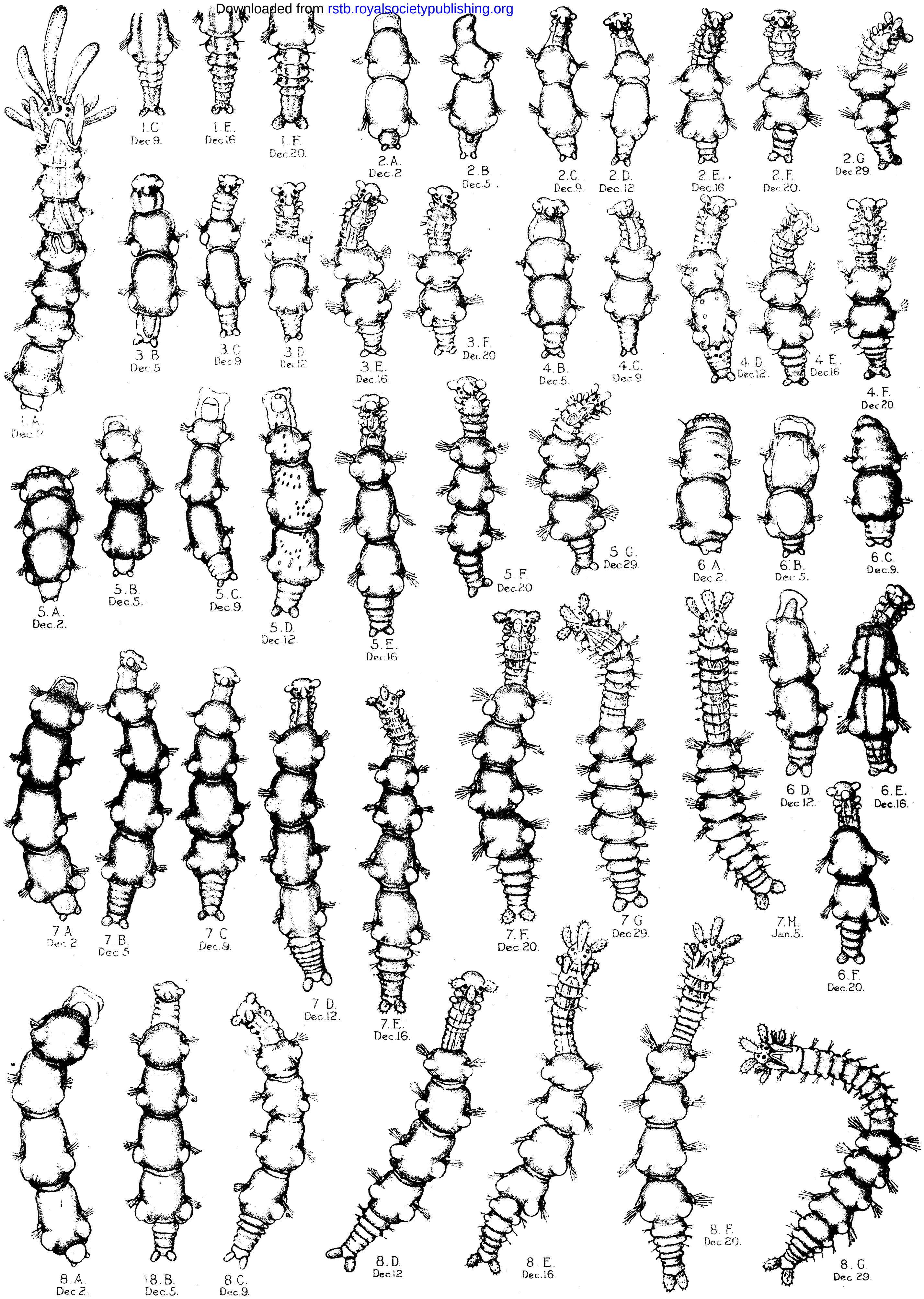
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES






W. Saxton, del.

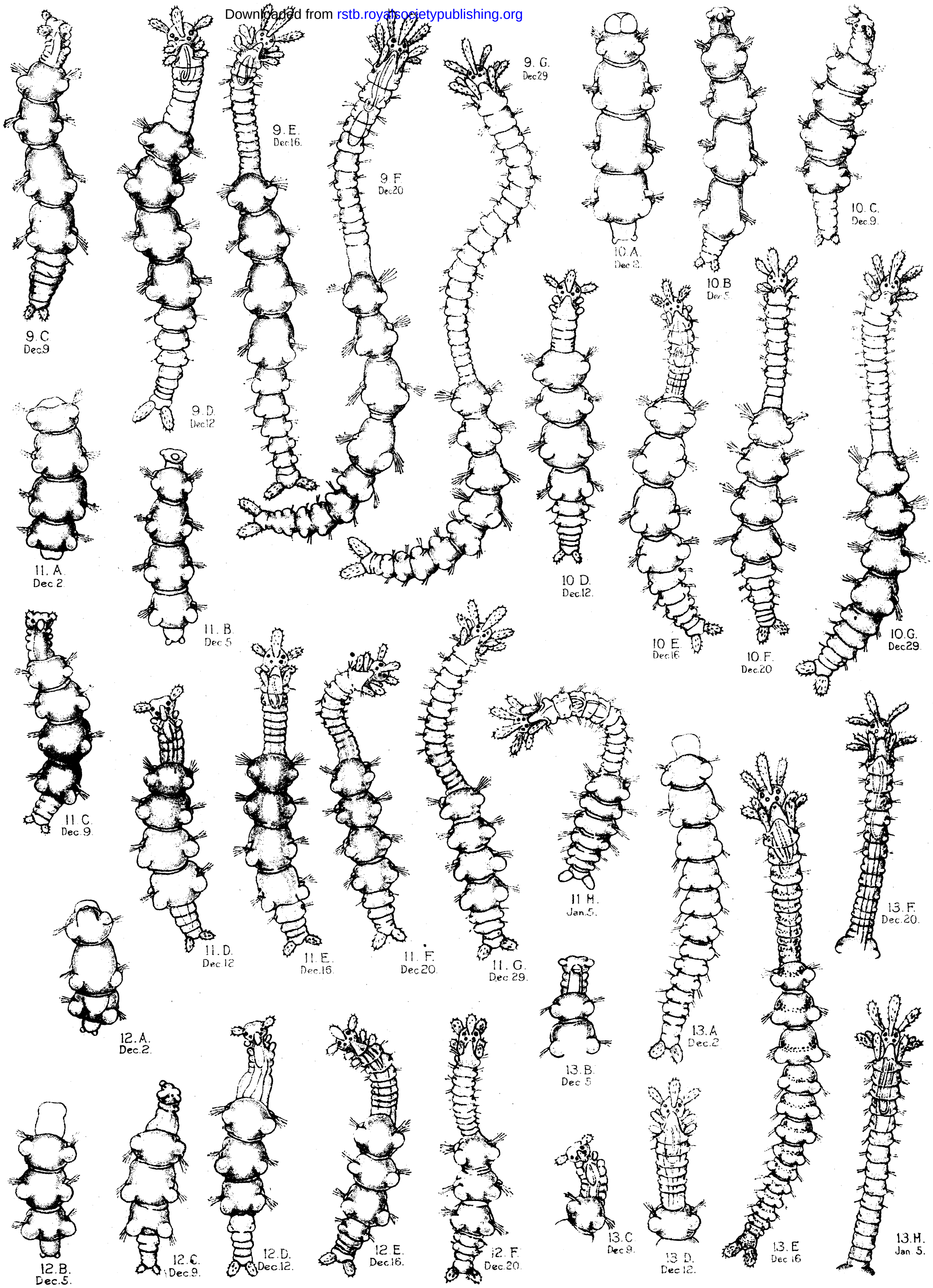
WATERLOW & SONS LIMITED, LONDON, DUNSTABLE & WATFORD




WATERLOW & SONS LIMITED, LONDON, DUNSTABLE & WATFORD.

E. W. Sexton, del.

*Figure 20.*




WATERLOW & SONS LIMITED, LONDON, DUNSTABLE & WATFORD.

W. Sexton, del.

Figure 20 (Continued)

PLATE 16.

Fig. 20 (*continued*) × 30.

9. Segments 28, 29, 30, 31. A, December 2—same as 7, A; B, December 5—same as 7, B; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29.
10. Segments 32, 33, 34, 35. A, December 2; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29.
11. Segments 36, 37, 38, 39. A, December 2; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29; H, January 5.
12. Segments 40, 41, 42. A, December 2; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29.
13. Segments 43 to 54. A, December 2; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29—same as 13, H; H, January 5.



PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES




PLATE 11.

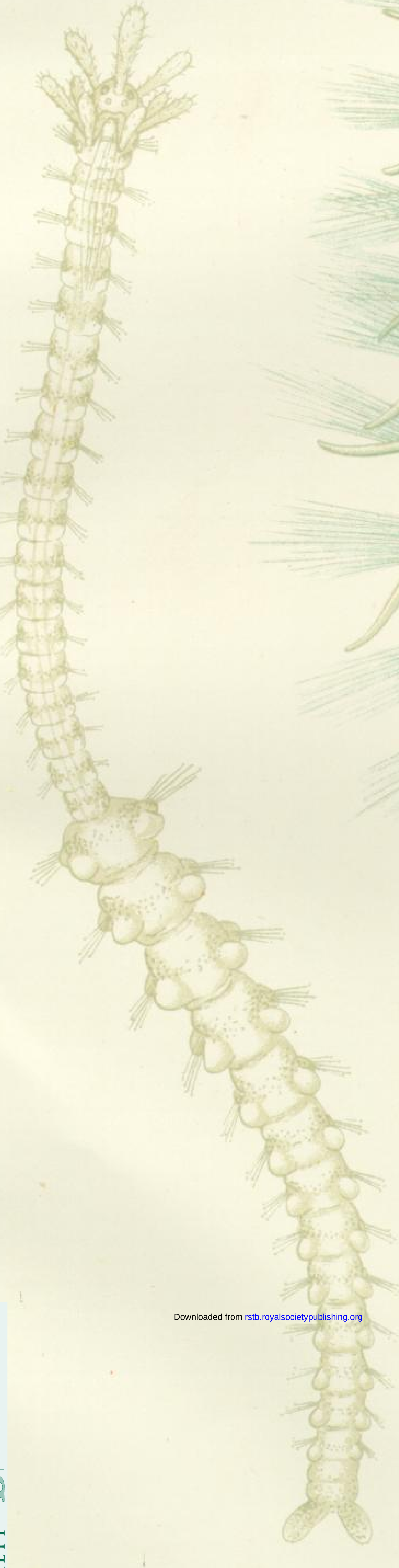
Fig. 1.—*Procerastea Halleziana.* Stolon head commencing on segment 14. × 20.

Fig. 2.—Female stolon, well advanced. × 20.

Fig. 3.—A. The first regenerated head of fig. 3, B, which broke off and has regenerated posterior segments and pygidium. Drawn December 10, 1919. × 45.

B. Double regeneration from four original segments (Specimen 186, p. 169.) The first regenerated head, and probably seven anterior segments, have broken off, and a second head with anterior segments is regenerating. Drawn December 10, 1919. × 45.

3 C.



5.

4.

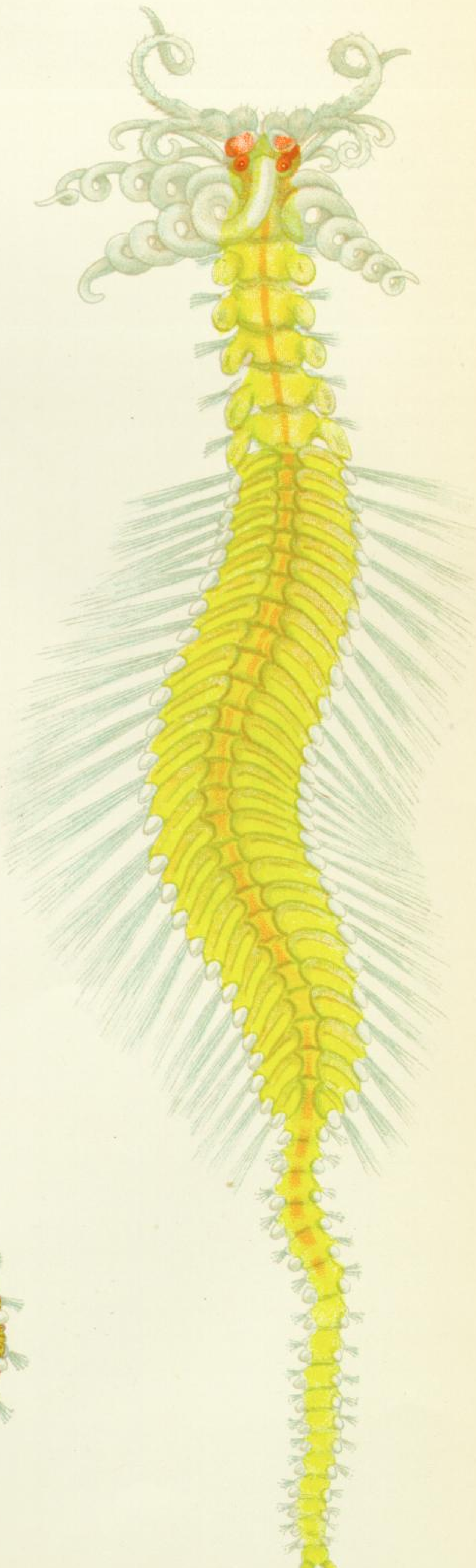




PLATE 12.

Fig. 3.—C. Specimen B, drawn January 19, 1920. The second head and anterior regeneration can no longer be differentiated from the first anterior regeneration. The posterior regeneration cannot be differentiated from the four original segments. × 45.

Fig. 4.—Polybostrichus, or male stolon, drawn as when swimming. × 20.

Fig. 5.—Sacconereis, or female stolon, just detached from parent, drawn as when crawling. When swimming the segments behind the modified ones are coiled ventrally. × 20.



PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

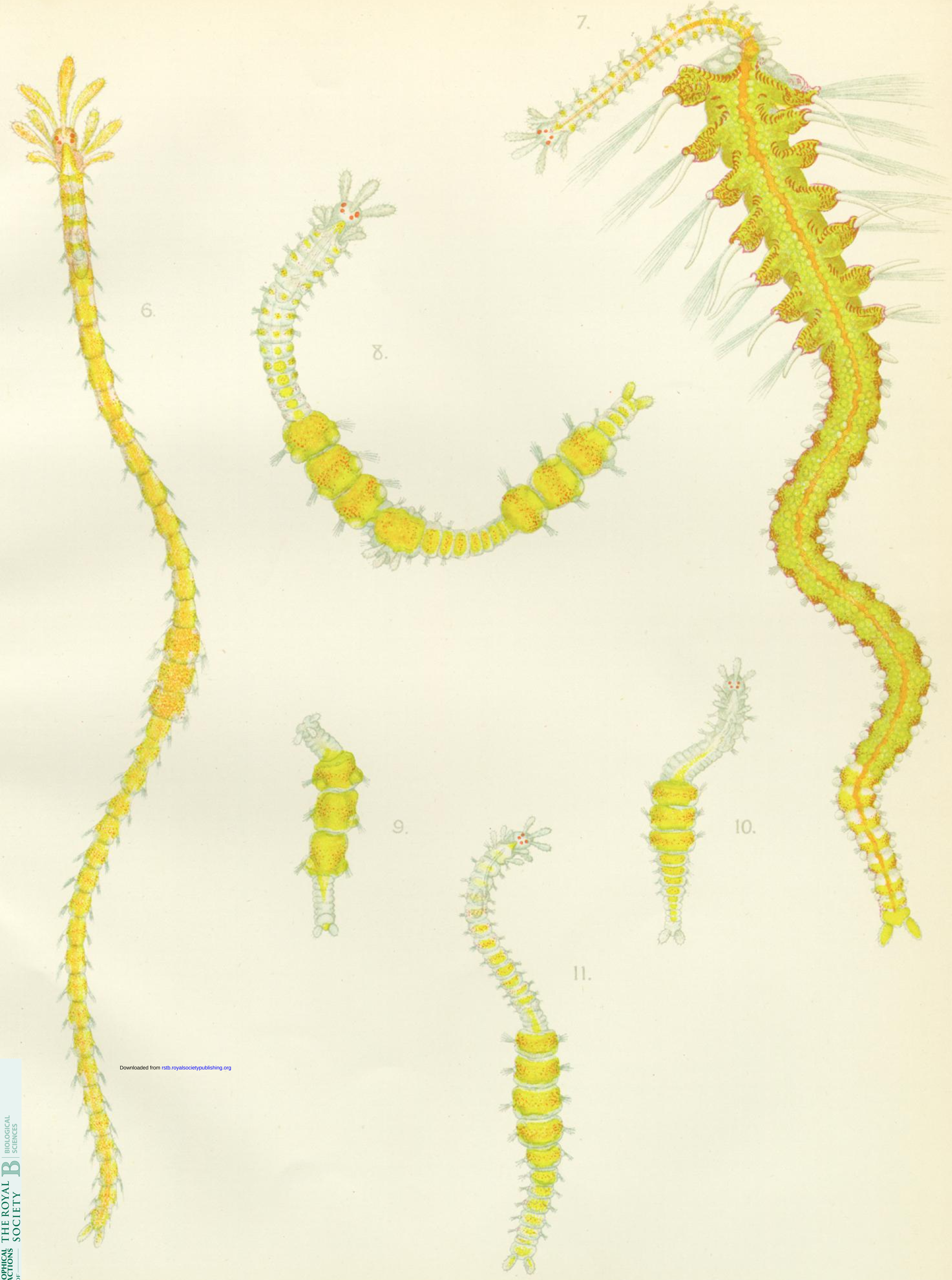



PLATE 13.

Fig. 6.—Regeneration from three original segments. Specimen 45, from raft in Cawsand Bay, September 29, 1914. × 42.

Fig. 7.—Portion of a Sacconereis, which has regenerated a complete souche, and is commencing to regenerate a stolon head. (Specimen 185, p. 165.) × 20.

Fig. 8.—Regeneration from two sections, each of three segments. (Specimen 189, p. 171.) × 42.

Fig. 9.—Early stage of regeneration from three original segments. × 20.

Fig. 10.—Later stage from three segments. (Specimen 82.) × 20.

Fig. 11.—Regeneration from four original segments. (Specimen 116.) × 20.


PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

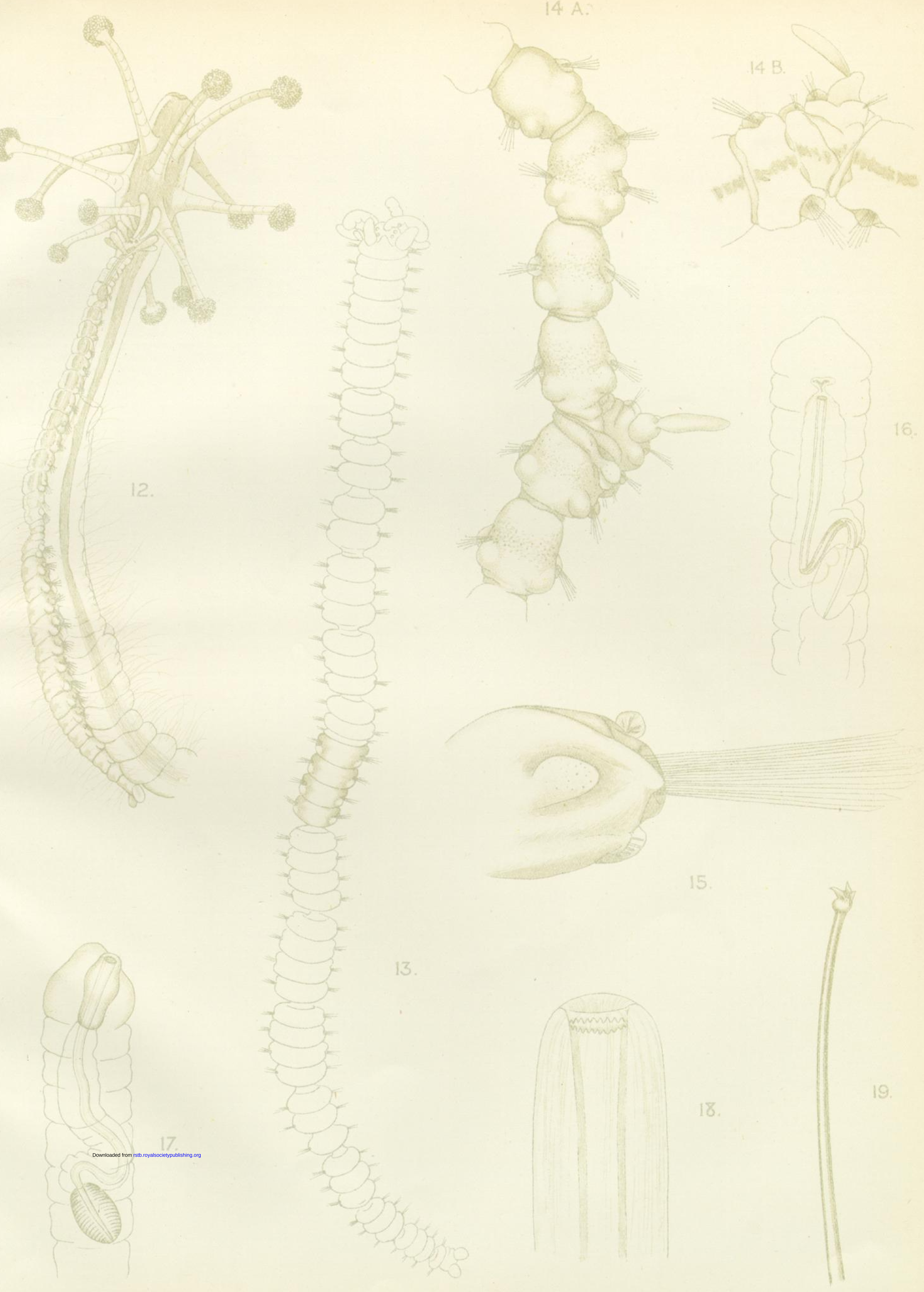





PLATE 14.

Fig. 12.—Procerastea feeding on Syncoryne. × 42.

Fig. 13.—Procerastea regenerated from four original segments, and showing the normal way of breaking up. (Specimen 87, p. 161.) × 20.

Fig. 14.—A. Lateral regeneration, dorsal view. (Specimen 190, p. 172.) × 58.
B. The same—ventral view. × 58.

Fig. 15.—The seventh modified parapodium, left side, of the Polybostrichus. View of anterior surface. × 75.

Fig. 16.—Regenerated head seen from the ventral side, showing mouth, pharynx, and proventriculus. × 45.

Fig. 17.—The same, with pharynx extruded. × 45.

Fig. 18.—Enlarged view of the end of the pharynx, showing the "trepan." × 435.

Fig. 19.—Compound bristle of Procerastea from parapodium 11. × 435.


*Figure 20.*

## Plate 15.

Fig. 20.—Regeneration from the different sections of one specimen of Procerastea (Specimen 15), broken up November 27, 1919. All figures × 30.

1. Head and segments 1–7. A, December 2; C, December 9; E, December 16; F, December 20.
2. Segments 8 and 9. A, December 2; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29.
3. Segments 10 and 11. A, December 2—same as 2, A; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20.
4. Segments 12 and 13. A, December 2—same as 2, A; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20.
5. Segments 14, 15, 16. A, December 2; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29.
6. Segments 17, 18, 19. A, December 2; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20.
7. Segments 20, 21, 22, 23. A, December 2; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29; H, January 5.
8. Segments 24, 25, 26, 27. A, December 2; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29.




*Figure 20 (Continued)*

PLATE 16.

Fig. 20 (*continued*) × 30.

9. Segments 28, 29, 30, 31. A, December 2—same as 7, A; B, December 5—same as 7, B; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29.
10. Segments 32, 33, 34, 35. A, December 2; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29.
11. Segments 36, 37, 38, 39. A, December 2; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29; H, January 5.
12. Segments 40, 41, 42. A, December 2; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29.
13. Segments 43 to 54. A, December 2; B, December 5; C, December 9; D, December 12; E, December 16; F, December 20; G, December 29—same as 13, H; H, January 5.