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EMBRYOLOGY OF AUTOLYTUS CORNUTUS.

BY

A. AGASSIZ.

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By A. AGASSIZ.

O. F. Müller, in his Zoölogia Danica, figures a small worm (*Nereis prolifera*), in the act of reproducing itself by division. For many years this mode of reproduction among the higher Annelids remained unconfirmed, and many authors, Ehrenberg especially, began to throw doubts upon the observation of Müller. He even went so far as to establish a division among worms, founded entirely upon the mode of reproduction by division such as had been observed among *Naidina* (called by him *Somatotoma*), in opposition to the others in which this mode of reproduction does not obtain, and to which *Nereis prolifera* is referred. It was not until Quatrefages and Milne Edwards had both traced a similar phenomenon in two other genera (*Syllis and Myrianida*), that Müller's observation was placed beyond the question of a doubt; and after the same mode of development had been noticed by Sars in *Filograna*, and his observations had been repeated a few years later by Schmidt in a second species of that same genus, it was evident that this mode of reproduction was not confined to the *Naidina*, and that we might expect to find it in other families of Annelids as well as in

the two in which it had been observed. The peculiar phenomena preceding the separation of the sexual individuals, the fact that the eggs and spermatozoa seemed to be developed only in the part which was to form a new individual, soon suggested the idea that we might have here a phenomenon, similar to that of alternate generation, taking place among the Annelids.

Müller* had observed that the individuals about to separate were alone filled with eggs, and that these eggs were less advanced in those sexual individuals which were farther from the posterior extremity. He also says, that he found as many as three proliferous individuals placed like links in a chain, one behind the other, the smallest (the youngest) being placed nearest the anterior extremity. Quatrefages† found on the coast of Bretagne a species of Syllis which reproduced itself by division, producing, however, only a single individual, either a male or a female, and he observed that the anterior part never showed the slightest trace of either male or female organs. This led him to suppose that the individuals which became detached were alone capable of sexual reproduction. It is not until several years afterwards, when he returns to the same subject‡, and publishes more in detail his observations, that he comes to the conclusion that these phenomena of reproduction by division may be satisfactorily explained as cases of alternate generation. According to his observations, striking differences between the young males or females and the parent stock [le parent, l'individu primitif, la souche] are developed after their separation.

* Müller (O. F.) Zoölogia Danica II., Pl. 52, fig. 5–9, p. 15. Havniæ, 1788. Copied Ency. Method. (Vers. Vol. I., Pl. 56, fig. 12–15.)

† H. Milne Edwards, Rapports sur une série de Mémoires de M. A. de Quatrefages, relatifs à l'organisation des animaux sans vertébres. Comptes Rendus, 15 Janv. 1844. Ann. des Scien. Nat. 1844, I., p. 22.

‡ A. de Quatrefages, Mémoire sur la génération alternante des Syllis. Ann. des Sc. Nat. 1854, II., p. 142, Pl. IV., fig. 3–15.

He says nothing of the development of the eggs of these individuals [l'individu adventif, la nourrice,* la fille] into the parent stock, and simply states the fact of the alternate generation, without having actually observed it. Milne Edwards † observed a case more similar to that which Müller had seen. He found in *Myrianida* five or six young already quite well developed, the more advanced being nearer the tail: he did not observe the mode of development; but by carefully comparing the less with the more advanced, he shows how closely this mode of development of the different parts corresponds to the development of the same parts of an embryo from an egg. He also observed that the proliferous individuals were provided with sexual organs, and that they seemed alone capable of reproducing the species from eggs. Sars ‡ observed the same phenomenon in the *Serpulacea*, in *Filograna implexa*, and shows on what slight grounds Ehrenberg § had based his class of *Somatotoma*. These observations of Sars were soon after repeated in a second species of the same genus, *Filograna Schleideni*, by Schmidt; and his observa-

* Quatrefages has applied the word *nurse* (nourrice), as generally used, to denote the individual from which the sexual individuals are developed, in a manner very different from that of Steenstrup. He seems to have misunderstood the application of the "Amme" of the Germans, and has applied his term "nourrice" to a different stage. He has given to the individuals which the Germans call "Amme," the name of "parent," and has given the name of "nourrice" to the males and females developed from this "parent." This is certainly not the meaning of Steenstrup, and of the German writers on alternate generation. For according to this nomenclature of "Quatrefages," we should call "*parent*" the Strobila, Cercaria, and call "nourrice" (Amme) Aurelia, Distoma, instead of calling the former (Strobila and Cercaria) the nurses, as is done by Steenstrup. The name of "parent," also, for the "Amme," is objectionable, as it is contrary to the usual meaning of the word; and the application of the word "nourrice" to *males* and *females* is certainly not in accordance with our understanding of the meaning of that word. What I have called the "*parent stock*" corresponds to the "Amme" of Steenstrup. I have given to the offspring the name of sexual individuals, or of "males" and "females" simply.

† Milne Edwards (H.) Ann. d. Sc. Nat., 1844, III., p. 170.

‡ Sars (M.) Fauna litoralis Norvegiæ, p. 86. Christiana, 1846.

§ Ehrenberg (C. G.) Die Akalephen des rothen Meeres, p. 82. Berlin, 1836.

tions plainly show that a part of the parent stock passes into the sexual individuals when the division takes place. Only one individual is formed at a time in this species. Frey and Leuckart * repeated the observations of Müller in "*Nereis prolifera*" to a certain extent: they found several of the young in a slightly advanced state of development; but as their observations were intended to show that the development of *Nereis prolifera* was a case of budding and not one of division, that there was nothing in the development to justify the assertion of an alternate generation made by Quatrefages, and as their conclusions were based upon these slightly developed males and females, it is not astonishing that we find them assert that there is not the slightest difference between the young and the parent stock, and that they never found spermatozoa developed in the former. It was not until Krohn † was fortunate enough to observe the whole development of *Nereis* (*Autolytus*) *prolifera*, that it became evident that the remarkable phenomena which he observed connected with the differences developed in the male and female young could only be explained on the supposition of an alternate generation. He dwells particularly on the striking difference between the males and females, and is led to believe that Müller ‡ must have observed the male of his *Nereis prolifera*, and described it as a different species, (*Nereis corniculata*,) on account of the great differences of the anterior part. He says, the only link now wanting, is to trace the development of an embryo coming from the egg of one of the female individuals into a parent stock similar to that from which the sexual individual was

* Frey (Dr. H.) und Leuckart (Dr. R.) Beiträge zur Kenntniss Wirbelloser Thiere, mit besonderer Berücksichtigung der Fauna des Norddeutschen Meeres. Braunschweig, 1847.

† Krohn (Dr. A.) Ueber die Erscheinungen bei der Fortpflanzung von Syllis prolifera und Autolytus prolifer. Wiegman. Archiv 1852, I., p. 66, Pl. III., fig. 1.

‡ Zool. Dan., Pl. 52, fig. 1–4, p. 15.

produced, and which should in its turn produce males or females only by division, and not by sexual reproduction.

It is this link which I have been able to supply, having had the good fortune to observe in a species of *Autolytus* of our coast the development of male and female individuals, differing to a degree almost unknown in the class of Annelids,* from parent stocks different from both of these proliferous individuals. I have also succeeded in tracing from the eggs the growth of the young embryo into a parent stock, identical in every respect with the parent stocks from which the males and females were produced by division. There can no longer be any doubt that we have in the higher Annelids an alternate generation. It seems to me highly probable that further investigations will show this to be the case for other genera, such as *Psammathe*, *Heteronereis*, *Exogone*, *Cystonereis*, and all those Annelids in which we find a specialization of a certain number of rings, as is the case in the sexual individuals of Autolytus. Whether alternate generation will explain the phenomena of unsexual reproduction of *Nais*, cannot be settled without further investigations; as the contradictory statements of the different authors leave it very doubtful whether there is anything like a parent stock existing in Naidina.†

Species allied to *Nereis prolifera*, owing to this remarkable difference between the males, females, and parent stock, have been placed in no less than four different gen-

* Oersted (Mag.) had observed in Exogone naidina great differences between the two sexes, but they were not as striking as in Autolytus. As this genus is closely allied to Autolytus we may look for phenomena similar to those observed in that genus.

Oersted (Mag.), Ueber die Entwickelung der Jungen bei einer Annelide, etc. Wieg. Archiv, 1845, I., p. 20. See also Kölliker on the development of Cystonereis, Nouv. Mém. de la Soc. Helvet. des Sc. Nat. VIII., 1847.

† Schultze (Dr. Max Sigm.), Ueber die Fortpflanzung durch Theilung bei Nais proboscidea. Wieg. Archiv, 1849, I., p. 293. Leuckart (Dr. R.), Ueber die ungeschlechtliche Vermehrung bei Nais proboscidea. Wieg. Archiv, 1851, I., p. 184.

era. Örsted * is the first who has given a good description of the male of an Autolytus, under the name of *Polybostrichus longosetosus*. Unfortunately, this name cannot stand, as it had been applied before by Brandt, in 1838, to a genus of Acalephs, and must give way to Autolytus which was given by Grube † to the parent stock. From the figure of O. F. Müller he established a new genus for the male under the name of *Diplocerœa corniculata*.‡ Johnston § had given a very good description of the parent stock in the 15th vol. of the "Annals and Magazine." Finally, the female was first seen separated from the parent stock by Johannes Müller; ‖ and he made still another genus, *Sacconereis*, for a small worm which he observed in Trieste, belonging to the same cycle. There is also an account of two remarkable worms found by Max Müller ¶ in Helgoland, and which I am inclined to think are the free young (♂ and ♀) of the *Nereis prolifera* of Müller. This is the more probable, as the observations of Frey and Leuckart were made at the same place, and is confirmed also by the descriptions given by Krohn, apparently agreeing closely with the drawings given by Müller (M.), as well as by what I have observed in our own species (*Autolytus cornutus*), where we have males and females differing only slightly from the *Sacconereis* of M. Müller; — we find still less difference when we compare the figures of the parent stock given below (Pl. X., fig. 1,) with that given by Johnston, of (*Syllis prolifera*) the parent stock of the European species.

* Örsted (A. S.), Grönlands Annulata Dorsibranchiata, p. 30, Pl. V., fig. 62. Kjöbenhavn, 1843.

† Grube. Die Familien der Anneliden, Wieg. Archiv, 1850, I., p. 310.

‡ Grube. Die Familien der Anneliden, Wieg. Archiv, 1850, I., p. 312.

§ Johnston (Geo.), Syllis prolifera, Ann. and Mag., XV., p. 146, pl. IX., fig. 4.

‖ Müller (Joh.), Ueber den Allgemeinen Plan in der Entwickelung der Echinodermen, p. 7. Berlin, 1853.

¶ Müller (Max), Müll. Archiv, 1855, p. 18.

The synonymy of this genus will therefore be as follows:

AUTOLYTUS.

Autolytus (*Grube*), Wieg. Archiv. 1850, I., p. 310 (parent stock).

Polybostrichus (*Örsted*, A. S.), Grönlands Ann. Dorsib. 1843, q. a., (♂) (preoccupied).

Diploceræa (*Grube*), q. a., (♂).

Sacconereis (*J. Müller*), q. a., 1853, (♀).

" (*M. Müller*), q. a., 1855, (♀ and ♂).

Syllis (*Johnston, Geo.*), q. a., 1845 (parent stock).

From what precedes it is seen, that there are known at present three species of Autolytus besides that found on our coast, and for which I have proposed the name of *Autolytus cornutus*. They are *Polybostrichus longosetosus*, from the coast of Greenland; *Sacconereis Schultzii*, from Trieste, and *Sacconereis Helgolandica*. There are good figures of two of these species; so that I have satisfied myself that the species found on our coast cannot be identical either with the species of Greenland or with that of the German Ocean. As Max Müller had ample opportunity of satisfying himself of the identity or difference of the species from Helgoland and that of Trieste, there can be no doubt of their specific difference.

Autolytus cornutus resembles more in its general appearance the *S. Helgolandica* than the Greenland species. It has a smaller number of rings than *P. longosetosus;* the tentacles of the head are shorter. (The figure of Örsted being that of a male, the comparison made here applies only to the male). The cirri of the anterior and posterior rings are more equal in length, while in *longosetosus* the cirri of the rings with long setæ are exceedingly short when compared with those of the anterior rings. It differs from *S. Helgolandica* in having a larger number of rings;

the rings without the long setæ are more numerous in both the sexes than in *Helgolandica*. In the latter the female has two, and the male three rings, having only stiff bristles, while in the *cornutus* the female has six, and the male five rings, in which the long setæ are wanting. The number of rings of *Autolytus cornutus* in the full-grown males and females is different: usually from twenty-seven to thirty in the former, and from thirty-five to forty or even fifty in the latter. *Sacconereis Helgolandica* has fewer rings, and *P. longosetosus* a greater number than the species found on our coast.

The most striking characteristic of the genus Autolytus is the remarkable difference between the sexes. Had I not observed the development of these males and females, so widely different, coming from parent stocks * (from which they are produced by transverse division, as I shall show hereafter), developed from eggs laid by the same individual, I could scarcely have credited their generic identity. (See Pl. IX., fig. 1, and Pl. XI. fig. 8). It is therefore perfectly natural that Johannes Müller should not recognize in a female Autolytus the genus *Polybostrichus*, which was characterized by Örsted from a male. At the time when Max Müller discovered his *Sacconereis Helgolandica*, he used to find also in great numbers a small worm (invariably a male), which he says had the general appearance of *Sacconereis*, but differed in such a remarkable manner, that it seemed to him impossible that there should be such an exceptional case of difference between the males and females, entirely unprecedented in the class of Worms. It was only after tracing the complete development by "transverse division" of males and females, differing in such a remarkable manner, from parent stocks in which I could not perceive the slightest difference, that I satisfied myself that these individuals, which seemed to have so

* See below for description of parent stock, p. 397.

little in common, were only the two sexes of one species. I have before me the drawings of a male and female of *Polybostrichus longosetosus*, Örst., made under the direction of my father in 1849, from specimens observed in the Bay of Boston, and referred by him to two different genera.*

The female *Autolytus cornutus* (Pl. IX., fig. 1,) is a small worm about one half an inch in length, of a flesh color, the alimentary canal appearing as a green tube extending from one end to the other; the posterior and the anterior rings are of a greenish tinge. The cirri are also flesh-color, and the eyes a dark chestnut-brown. The head has three long tentacles, the longest (*a*) placed directly in front on the middle of the head, and one tentacle, (*a' a''*), nearly as long as the central one, placed on the dorsal side directly in advance of the eyes, which are placed on each side of the head. The eye consists of two lenses of unequal size. This compound eye (*b*) is placed in an oblique position, so that the larger eye is nearer the ventral side and in advance of the smaller eye, which is placed nearer the back, but farther from the anterior part. Directly behind the eyes, on the ventral side, we find a tentacular cirrus (*c*) about one third the length of the tentacle (*a''*); this cirrus is slender and placed on an exceedingly narrow ring, which can hardly be distinguished from the head. The next ring has a long dorsal cirrus (*c'*), fully as long as the central tentacle (*a*), though somewhat more slender. The six rings following have a dorsal cirrus (*c''*) of the length of the tentacular cirrus (*c*). The rings of the body increase gradually in width towards the middle, and then taper off towards the tail. The dorsal cirri of these six rings are all of the same length; but beyond those rings the dorsal cirri gradually increase in length, reach their maximum about the middle of the body, and then diminish again in the same ratio towards the tail,

* See also Grube, q. a., who does the same. The specimens observed by my father were unfortunately lost.

where they are hardly perceptible. The rings following the six rings, with dorsal cirri of the same length, differ in many respects from them. In the former there are two bunches of bristles, the dorsal made up of long, thin, needle-like bristles (Pl. IX., fig. 5), supported by a tubercle (fig. 4, *h'*), which are not retractile, and a ventral cluster (fig. 4, *h*) made up of shorter, stout bristles (Pl. IX., fig. 6). They are composed of two joints, the smaller exterior joint having the shape of a claw. The ventral bristles are retractile, and easily movable. These long, needle-shaped bristles are wanting in the anterior rings, which are not provided with a dorsal tubercle (see Pl. IX., fig. 3), and have only a ventral tubercle supporting the short, stout, retractile bristles like those of the posterior rings.

The eggs, in their earlier stages of development, are found thickly packed between the walls of the alimentary canal and the outer wall, on each side of the body for its whole length. The eggs, however, do not attain their maturity in the cavity of the body. As they develop, and fill more and more the space between the wall and the alimentary canal, some of them even finding their way into the dorsal cirri, there is developed on the lower side of the body a large bag, into which they pass. This pouch extends from the 12th to the 25th or 26th ring when fully swollen with eggs; it has an elliptical shape (Pl. IX., fig. 2), with a slightly wavy outline, the length of the smaller axis of this ellipse being about three times the breadth of the body. In this bag, which communicates freely with the cavity in which they are formed, the eggs come to maturity; and soon after the young embryos have been hatched from the eggs, the envelope of the pouch bursts, and the young are left to swim freely about.

The anal cirri are more flattened than the dorsal, and are as long as those of the anterior rings. They are almost always wanting, dropping off a few days after the separation of the female from the parent stock.

The general appearance of the male is entirely different from the female, (see Pl. XI., fig. 8): the body, instead of tapering gradually from the middle towards both extremities, attains its greatest width much nearer the head, about the 12th ring. The number of rings which are not provided with long setæ, and have short dorsal cirri, are five, instead of six as in the females. The spermatazoa (Pl. XI., fig. 8, *o*,) are found on the sides of these six rings only, and extend also into the cirri, but never into the posterior rings, as is the case with the eggs of the female which fill the cavity on both sides of the alimentary canal for the whole length of the body. The dorsal cirri of the male are shorter than those of the female, both in the anterior and posterior rings. The greatest and most striking difference we find in the head and in the first ring. (See Pl. IX., fig. 7 and Pl. XI., fig. 8.) The two large tentacles which are placed slightly in advance of the eyes, instead of being, as in the female, simple tentacles having the same breadth and rounded at the extremities, are very broad at the base where they are united by a prolongation of the anterior part of the head. At a small distance from the head they bulge out, giving the two tentacles the appearance of having been united and separated afterwards by a punch, the two swellings almost meeting and leaving only a round space between the two tentacles, which divide into two branches (see *a'* and *a''*, Pl. XI., fig. 8) at the extremity; the inner side of this tentacle is thickly covered with minute cilia. The median tentacle, *a*, is much larger than that of the female, and takes its origin farther back, directly above the opening of the mouth (*m*), between the two large dorsal cirri (*c'*). Directly behind the eyes we find a small cirrus (*c*), as in the female; but when the animal is seen from below, as in Pl. XI. fig. 8, we notice an additional, still smaller cirrus (*c'''*) which is entirely wanting in the female, as well as the small tentacular cirri (*a'''*) (Pl.

IX., fig. 7), which are found at the base of the tentacles (a' and a'') on the upper side of the head. The large dorsal cirri of the first ring are usually carried slightly curved back at the extremity (Pl. XI. fig. 8, c'). The needle-shaped bristles are somewhat longer than those of the females; otherwise neither these nor the hooked bristles differ in any way in the two sexes. The alimentary canal, in both the males and females, is narrower while it passes through the anterior rings (f), which have only stout bristles, widening suddenly as it reaches the rings where the setæ begin (f').

Besides these two sexes differing to such an extraordinary extent, there is still a third kind of individuals (Pl. X., fig. 1), which is neither male nor female, never has either eggs or spermatozoa developed, and differs more from the males than they differ from the females, and yet belongs to this same species. In fact, these individuals are the parent stocks, as I have called them above, from which males and females (Pl. IX., fig. 9) are developed by transverse division. We cannot call this mode of reproduction a case of budding: it is the development of a head and all its appendages, either male or female, and the gradual addition of a very small number of rings, between this head and the tail-ring, which was at first a part of the parent stock, and remains the tail-ring of the male or female after it has separated from the parent stock; a large portion of the original parent stock becoming separated, to form part of individuals which alone have the power of developing eggs and spermatozoa, this power being entirely wanting in the parent stock. We have here, therefore, an actual case of alternate generation, just as much as in the case of the "*Strobila;*" an individual entirely different from the males or females, from which are developed, by a peculiar mode of transverse division, those very males and females which have spermaries and ovaries. These eggs, as I shall show below,

instead of developing into males and females, are transformed into these parent stocks; which produce in their turn individuals having sexual organs, by transverse division, and never any thing else. During a whole summer I have had daily a large number of these worms alive; and have traced individuals raised, from the eggs until they reached the condition of the parent stock, upon which I was observing the growth of the males and females.

The parent stock (Pl. X., fig. 1) has the same color as the males and females. The tentacles of the head are like those of the female, the middle tentacle being longer, however; while the first ring instead of being consolidated with the head, as in the males and females, is distinct from it, and on each side of it we find two cirri, one long one (*C*), and a short one (*C'''*) in advance and below it. The second ring has a long dorsal cirrus (*C'*) on each side, corresponding to the cirrus *c'* of the males and females. The third ring has a shorter dorsal cirrus (*C''*) of the length of the cirrus *C'''*. The succeeding rings all have cirri, diminishing in length as they recede from the head, until near the tail, which has two large cirri, where they are hardly perceptible. In place of the large, highly-developed eyes of the males and females, we find two large and two small eyes, which are mere accumulations of pigment cells. The larger eye is placed below in advance of the smaller, and is nearer the edge of the body, the small eyes being quite close together (Pl. X., fig. 1, *O*). The rings are provided only with one kind of bristles, the short stout ones, exactly like those of the males and females (Pl. IX., fig. 6). The lower tubercle (*h*) (Pl. IX., fig. 3,) is more developed, and the bristles are placed nearer the dorsal cirrus, than is seen in that figure.

This lower tubercle is proportionally well developed in the anterior rings, diminishing in size as the dorsal cirrus becomes smaller. The dorsal cirri are much flatter and more

pointed than is the case with the sexual individuals. We find, also, a great difference in the alimentary canal of the parent stock; the anterior portion is specialized to a degree which does not exist in the males and females; where the alimentary canal is simply the cutting off of a portion of the tube forming the common digestive cavity of the parent stock and the sexual individual while they were still attached. We have in the parent stock a narrow tube (œsophagus), winding from the mouth to a kind of true stomach, (Pl. XI., fig. 9); thence the alimentary canal passes as a wide, almost straight, tube through the whole length of the body.

The parent stock has from forty to forty-five rings before the swelling which eventually forms the head of the sexual individual can be distinguished. This swelling, without exception, is found on the upper side of the thirteenth or fourteenth ring, or one of the adjacent rings, (Pl. IX., fig. 9); and I have never seen a single case among the great number which I have observed, where this swelling of the head appeared in any other place. As a general rule, it was on the thirteenth ring that the head was developed. As the central swelling increases, there are formed on the two sides of this ring (see Pl. IX., fig. 11,) two additional swellings, (a', a''), which soon become as large as the middle one. They increase in size very rapidly, and soon outstrip the middle swelling, (Pl. IX., fig. 12). These three swellings are the tentacles of the head. The large eye next makes its appearance, (Pl. IX., 13, b), and also the dorsal cirrus (c'). After this has reached the length of the tentacles of the head, the second eye can be distinguished, (Pl. IX., fig. 17). At this point the three tentacles of the head and the dorsal cirrus have about the same length. If we trace further the development in different individuals, we find that there is a marked difference in the growth of the tentacles in parent stocks which are

identical; and this difference in the growth of the tentacles is a sexual difference, the tentacles of the males being developed in one way, and those of the females in an entirely different manner. When the head of the young has reached the state represented in Pl. IX., fig. 15, if it is a male we soon notice on the inner side of the lateral tentacles (a', a'') a slight swelling, (Pl. IX., fig. 19); the tentacle soon divides at this point by sending out a short branch, which grows larger and larger, (Pl. IX., fig. 20); the tentacles remain attached together at the base. In the development of the same tentacles in the female, we have simply a lengthening of the tentacles, and a tendency in the three tentacles to become well separated. So that a female would gradually pass from the state represented in Pl. IX., fig. 17, to that of Pl. IX., fig. 18. The head becomes more and more distinct; the small, tentacular cirri (c''') (Pl. IX., fig. 20) of the males become visible as a slight protuberance on the lower surface, when the tentacular cirrus (c) is about one half as long as the tentacle. At the same time in the males the long dorsal cirrus (c') and the middle tentacle (a) assume the curled attitude in which they are usually carried by them, while in the females these tentacles simply increase in length, the tentacle (a) always being carried in advance of the head, and not turned back as in the males. The five rings following the head in the males (six in the case of the females), undergo scarcely any change, with the exception of a slight elongation of the dorsal cirri, (compare Pl. IX., figs. 1 and 9 and Pl. XI, fig. 8); but in the succeeding rings very striking differences are observed: the dorsal cirri increase still more in length, a slight protuberance is formed immediately below the dorsal cirrus, from which a bundle of fine, needle-like bristles, like those of Pl. IX., fig. 6, are developed. Thus the anterior rings have two bunches of bristles, as in the adult males and females, and the upper bunch attains its full

size before the young separates from the parent stock. The eggs and spermatozoa are likewise developed, and we find females whose bodies are entirely filled with eggs on each side of the alimentary canal, while they are still attached to the parent stock; while in the parent stock, in the twelve anterior rings, not the least trace either of eggs or spermatozoa could be detected. In the males the anterior rings alone are filled with spermatozoa.

The parent stock, with the sexual individual attached, moves freely about, leaving its case (Pl. XI., fig. 10) and returning to it. The males and females, after they have separated from the parent stock, do not build cases, but creep along the stems of Campanularians, and are often found swimming about in the bay. The parent stock, with the proliferous individual attached, is very sluggish in its movements, especially towards the time of separation of the male or female; when the latter has become so much more powerful than the parent stock that it guides all the motions by twisting its body from one side to the other, while the parent stock seems to be only an inert mass pushed about by its powerful and active young. The males and females lose the upper bunch of needle-like bristles, owing to the violence of their motion; and it is only just after they have separated that they have all their appendages, as they also lose with great facility the anal cirri. Soon after the females have become detached from the parent stock, the bag, into which the eggs are received before they are discharged from the cavity, is formed. This soon becomes very much distended with young embryos, bursts, and then the females disappear. It is probable that they are killed by this, as I have never succeeded in finding a single female after it had discharged its embryos. The agamous individuals continue to live after the separation of the males and females. New rings are formed, (Pl. XI., fig. 7); and the same process appar-

ently begins again, (Pl. XI., fig. 6,) as I have frequently found parent stocks from which sexual individuals had evidently already been separated, in the state represented in this figure. I am unable to say how many times this is repeated, and what is the length of life of the parent stock. They are found in large numbers on the stems of all the Campanularians of our bay, where they build their thin, transparent cases. Especially numerous upon those Campanularians which are attached to Laminaria. This same species I have also observed south of Cape Cod, in Buzzard's Bay.

I did not observe the young embryos while they were still inclosed in the bag of the female; my principal object being to satisfy myself about the alternate generation, and to see how far the mode of development by division from the parent stock agreed with the more advanced stages of the embryo after it had left the egg. The young, when it escapes from the bag in which the eggs come to maturity, is triangular, tapering very rapidly towards the posterior extremity (Pl. X., fig. 2); it has two large eyes quite distinctly marked. The alimentary canal (F) follows the outline of the young embryo; it has slightly undulating walls corresponding to two very faint constrictions, one directly behind the eyes, and the other at the same distance from the posterior end. There is no appearance of a mouth. In the next stage (Pl. X., fig. 3) the indentation behind the eyes becomes more deep, thus separating slightly the head from the rest of the body, the anterior part at the same time bulging out, (Pl. X., fig. 3, A), the alimentary canal, as well as the young embryo, assuming a more elongated shape; and another constriction, placed about the middle, is noticed, dividing the alimentary canal into three regions. In the next stage (Pl. X., fig. 4,) the embryo is divided still more plainly by the constrictions, the three regions of the alimentary canal are more marked,

the head with the eyes is more distinct, the triangular shape has completely disappeared, and the mouth can be seen as a small slit on the lower surface. In figure 5, three rings or folds of the skin extend across the embryo; the anterior portion of the alimentary canal has become still more narrow. Figure 6, which is figure 5 seen in profile, shows the position of the alimentary canal near the upper side, and the first appearance (*A*) of a slight swelling between the two large eyes, the rudiment of the middle tentacle. In the following stage (fig. 7) the lateral tentacles (A′, A″) appear as diminutive swellings in advance of the eyes. These soon outstrip in growth the middle tentacle (fig. 8), which in its turn makes up what it had lost, and the embryo takes the shape of fig. 9, Pl. X.; it has three short tentacles equally developed in the anterior part of the head; the anterior part of the alimentary canal is very narrow, widening suddenly when it opens into the main digestive tube. There are six rings, the anterior ring being provided with a bunch of stiff bristles, and the anal ring having on each side very small anal cirri (*E*). The number of rings formed, till an embryo reaches a certain state of development, does not seem to be constant: in figure 10, Pl. X., we have a larger number of rings, though the tentacles of the head are not as advanced as they are in figure 9. The tentacles of the head increase in length (fig. 12), two or three additional rings are formed, and bristles are found in each ring except the first and last. When it has reached this state (fig. 12) the embryo does not increase in length until the appendages of the different rings are so well developed that it can be unmistakably recognized as a parent stock of Autolytus with a small number of rings (see Pl. X., figs. 13 and 14). Slight swellings having made their appearance on the sides of the first ring, then the second, and so on, and being gradually changed into the dorsal cirri, as seen in

fig. 14, *C*, *C'*, Pl. X., the anal cirri increase in length; and by the time the last ring has a dorsal cirrus developed, the middle tentacle (*A*) (Pl. XI., fig. 1) has again outgrown the lateral tentacles, the tentacular cirrus (*C''*) has been developed, and the worm has all the appearance of a parent stock with short cirri, (*C*, *C'*, *C''*, *C'*). From this stage the development goes on very rapidly, the number of rings increases very fast, the tentacles and cirri grow to their full length soon after, and in a couple of weeks the embryo has passed through the stages represented in figures 2, 3, Pl. XI., and has reached its full size, (Pl. X., fig. 1,) when it is ready to begin the reproduction by division, as I have described it above.

If we compare the embryonic development of the parent stock from the egg to the development of the different parts of the male and female from the parent stock, we cannot fail to be struck with their perfect coincidence. The middle tentacle (A, *a*) is developed first in both, then the lateral tentacles of the head (A', A'', *a'*, *a''*). The large eye is first visible, and then the smaller one; it is only when they are quite advanced that the long dorsal cirri make their appearance in the embryo and in the sexual individual; the long setæ of the latter developing at a time which corresponds to the formation of the stout bristles in the embryo; thus showing a perfect correspondence in the successive development of the different parts in these two modes of reproduction, and giving us a true perception of the value of embryological characters for classification. We cannot fail to see that the stages through which the embryo Autolytus passes will give us valuable hints for the classification of Annelids. All the earlier stages, before the rings can be seen, have a very striking resemblance to the *Planarians*, and similar worms. They are flat, the eyes are simple accumulations of pigment cells, there are no divisions into rings perceptible, and the principal feature is the great development of the alimen-

tary canal. In the next stage they become more elongated, the rings are strongly marked, there are rudimentary bristles, or gills in the case of the embryo of *Leucodore* and *Hæmatorhea;* and in this more advanced stage they recall to us the *Nematodes*, or round worms. In the still more advanced stages, the tentacles of the head, the division of the alimentary tube into distinct regions, the presence of well-developed cirri and setæ, represent the true Annelids; thus plainly placing, upon embryological data, the *Planarians* and the flat worms (*Platodes*), in which the great preponderance of the alimentary tube is the main feature, lowest; then the round worms (*Nematodes*), in which we have rudimentary gills, etc., next in rank; and ending with the true Annelids, in which we have the greatest specialization of the appendages of different rings. The number of worms whose embryology is well known is so small, that it is impossible to collect sufficient data for tracing out this correspondence as minutely as could be desired. It is apparent from these observations upon the alternate generation of the higher Annelids, that henceforth an accurate knowledge of their complete development will be necessary before we can arrive at any satisfactory conclusions with respect to their classification; and that, since we now know that Annelids thus far referred to genera hitherto placed in different families are only different generations of one and the same species, we should be particularly cautious in characterizing genera, however much they may apparently differ from one another before their mode of development has been traced.

SPECIES OF AUTOLYTUS KNOWN AT PRESENT.

Autolytus *Grube.*

For synonyms see page 390.

Autolytus prolifer *Grube* q. a.; Nereis prolifera *O. F. Müller;* Nereis corniculata *O. F. M.;* Diploceraea corniculata *Grube;* Syllis prolifera *Johnst.;* Sacconereis

Helgolandica *M. Müller.* Polybostrichus Müllerii *Keferst.** England, (*Johnst.*); German Ocean, Helgoland (*M. Müller*).

Autolytus longosetosus *A. Ag.*; Polybostrichus longosetosus *Örst.* Greenland (*Örst.*); New England, Bay of Boston (*L.* and *A. Agassiz*).

Autolytus Schultzii *A. Ag.*; Sacconereis Schultzii *J. Müller.* Trieste (*J. Müller*).

Autolytus cornutus *A. Ag.* Coast of New England, *A. Agassiz.*

I have quoted *Autolytus longosetosus* as probably occurring on the coast of New England, as I found the "parent stock" and my father males and females of a second species of Autolytus which is much larger than the *A. cornutus*, and which may, on further investigation, prove to be the *Autolytus longosetosus* of Greenland. It reaches a length of more than an inch, has very broad and flat feet, and much longer stiff bristles than the parent stock of *Autolytus cornutus.*

[Since this paper was written I have found anew the males and females of the parent stock mentioned above. The male agrees with the figure given by Örsted of *Polybostrichus longosetosus.* The female can easily be distinguished by the small size of the anterior pair of tentacles, and the great number of the anterior rings, no less than ten, which are not provided with long setæ. This species is quite common about the wharves in the harbor of Boston during the month of April, which is their breeding season.]

EXPLANATION OF THE PLATES.

PLATE IX.

(*Autolytus cornutus — male and female.*)

Fig. 1. — An adult female, full of eggs, seen from above; the eggs are placed in all the rings on each side of the

* Zeit. f. Wiss. Zool. 1862, p. 118.

alimentary canal (*f*); *a*, the middle tentacle of the head; *a'* and *a''*, the left and right tentacle in advance of the eyes *b*; *c*, the small tentacular cirrus placed behind the eyes on the lower side; *c'*, the large dorsal cirrus of the second ring developed into a tentacular cirrus; *c''*, the dorsal cirrus of the rings in which there are only one kind of bristles; *d*, the dorsal cirrus of the rings in which the two kinds of bristles are found; *m*, the mouth; *o*, the eggs; *f*, the anterior part of the alimentary canal.

Fig. 2. — The sac of a female in which the young parent stocks of *Autolytus cornutus* are developed previous to hatching; *O* shows this membrane and the young parent stocks in one side of it.

Fig. 3. — One of the feet of the rings provided with one kind of bristles; *c*, the dorsal cirrus; *h*, the tubercle from which project the hooked bristles.

Fig. 4. — One of the feet of the posterior rings provided with two kinds of bristles; lettering as in fig. 3; *h'*, the tubercle from which project the thin, needle-shaped setæ.

Fig. 5. — A bristle from the upper bunch of setæ.

Fig. 6. — Bristle, with sickle-shaped hook, taken from the lower bunch of bristles.

Fig. 7. — The head of a male seen from above. Lettering as in fig. 8, Pl. XI., *a'''* being a small tentacular cirrus placed at the base of the forked tentacles.

Fig. 8. — Shows the shape of the dorsal cirri.

Fig. 9. — Parent stock, with a male of *Autolytus cornutus* attached, just ready to separate. The lettering of the male, ready to be separated, is the same as before. Corresponding parts of the parent stock, and males or females are marked by the same capital letter, A, A'' being the middle tentacle and the right tentacle of the head; C, C', C'', C''' corresponding to *c c' c'' c'''* in the figures of males and females; F and F', the anterior and posterior part of the alimentary canal.

Fig. 10. — Still more magnified view of the head of a parent stock; lettering as in fig. 9; M, the mouth; B, the eyes.

Fig. 11. — The ring of the parent stock, in which the tentacles of the head of the individual bearing the sexual organs can be noticed as slight swellings, *a*, *a'* *a''*.

Fig. 12. — The same ring, showing the lateral tentacles of the head (*a'* and *a''*) somewhat more developed than in the preceding figure.

Fig. 13. — Somewhat more advanced; the large eyes have made their appearance, and the long tentacular cirrus (*c'*) is seen behind the eye.

Fig. 14. — The same as fig. 13 seen in profile, somewhat more advanced, as the small eye can be detected as a minute spot above the large eye.

Fig. 15. — The head at the time when the three tentacles are equally developed; the small eye has not yet made its appearance, although the tentacles are more advanced than in fig. 14. This is a male, while the preceding figures were probably females.

Fig. 16. — Head of an individual which can with certainty be recognized as a female; the tentacular cirri are very small, *c*, *c'*.

Fig. 17. — The head of a male previous to the time when the tentacles begin to fork; the tentacle *a* is generally turned towards the tail in the males, and carried straight forward in the females.

Fig. 18. — Head of a female just before it is ready to separate from the parent stock.

Fig. 19. — Head of a male somewhat more advanced than that of fig. 15; there are two eyes, and the tentacles are forking.

Fig. 20. — Head of a male ready to separate; the middle tentacle *a*, as well as the long cirri *c''*, are carried tightly curled up.

Plate X.

Development of the Parent Stock.

Fig. 1. — A full-grown parent stock previous to the formation of male and female individuals, seen from above.

As the embryos which develop from the eggs are the parent stocks from which the males and females are separated, the letters are all capitals, and correspond to those of fig. 9, Pl. IX.

Fig. 2. — A young parent stock of Autolytus just having made its escape from the sac.

Fig. 3. — The digestive cavity has become more insulated, the anterior part shows a tendency to differentiation. The body has lost somewhat its triangular outline.

Fig. 4. — The alimentary canal is divided into three distinct regions, and the body has assumed a more elongated form than in the preceding figures. Sinuosities indicating the rings are clearly seen.

Fig. 5. — The rings have become very distinctly marked; the head is more distinct from the rest of the body.

Fig. 6. — Fig. 5 seen in profile.

Fig. 7. — Head of a young parent stock of Autolytus somewhat more advanced than in preceding figures.

Fig. 8. — The lateral tentacles A′, A″ extend beyond the body.

Fig. 9. — The tentacles of the head are all equally advanced; bristles appear at three of the rings; the caudal stiles are slight swellings on each side of the anal ring, E.

Fig. 10. — Although not quite as advanced as fig. 9, has one more ring.

Fig. 11. — Fig. 10 seen in profile; the last ring seems to be divided into two, giving the figure the appearance of an additional ring.

Fig. 12. — Young parent stock of Autolytus, in which

bristles are developed at all the rings, and the tentacles of the head somewhat more advanced than in fig. 9.

Fig. 13. — First appearance of the tentacular cirrus C. which is developed after the dorsal cirri C″ have been formed on two or three rings, as seen in the next figure.

Fig. 14. — The young parent stock of Autolytus has all the appearance of a full-grown parent stock, having a smaller number of rings, shorter tentacles, and smaller cirri.

Fig. 15. — A more enlarged view of the head of a parent stock slightly older than that of fig. 14.

Plate XI.

Fig. 1. — The smaller tentacular cirri c‴, the stiles of the caudal ring and the appendages of all the rings have been greatly developed since the stage represented in Pl. X. fig. 14.

Fig. 2. — The number of rings is greatly increased, and the cirri C and C′ especially have lengthened.

Fig. 3. — Still more advanced individual.

Fig. 4. — A view of the head of a full-grown parent stock, seen from below, to show the mouth, M.

Fig. 5. — The thirteen rings remaining of the parent stock after the separation of the male or female individual, and the new rings formed since.

Fig. 6. — Parent stock in which new rings have been formed after the Autolytus has separated, and where the eyes of a second individual are perceptible.

Fig. 7. — The posterior extremity, in which the caudal stiles are formed preparatory to the formation of new rings, as in fig. 6.

Fig. 8. — A male, seen from the lower side. The letters correspond to the same parts as those of the figure of the female (Pl. IX., fig. 1), *a′*, *a″* being the forked tentacles which are peculiar to the males; *c‴*, a second cirrus placed beneath the small tentacular cirrus *c*, which is wanting in the female; *o*, are the spermaries, which are found only in the five rings preceding those where the long setæ begin;

f', the posterior part of the alimentary canal, which is wider than the portion leading from the mouth to the 7th ring; *g*, the lower side of the feet, showing deep grooves formed by the deeply indented rings, having the two kinds of bristles.

Fig. 9. — Showing the division of the alimentary canal (in the parent stock) into a small tube (œsophagus) (*l*), leading from the mouth to a true stomach *n*, which empties into a large intestine (F') leading to the anus.

Fig. 10. — Case in which the parent stock of Autolytus lives; *y*, the case attached to a portion of the stem of a *Campanularia*.