

Minor (W.C.) J. Woodward

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with regards of the
author.

Presented by
J. J. Woodward

UPON

MERISMATIC MULTIPLICATION

IN SOME

ANNELIDA.

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IN

ANNALS

[From the records of the ...]

Upon Natural and Artificial Section in some Cœtopod Annelids.

BY W. C. MINOR.

THE circumstances of spontaneous fission have been observed in so few species of annelids at present, as to make every additional observation of value, even though only confirmatory of what is already known upon that subject. This consideration, and the fact that all views of its nature in the *Oligochaeta* seem to be based upon the observations of one species—*Stylaria proboscidea*,—have tempted me to publish the following brief investigations, however they may want of any very special novelty to give them value.

It is now nearly one hundred years since the distinguished Danish naturalist, Otto Fr. Müller, studied the phenomena of spontaneous fission in the fresh water Naids,¹ and his able little work, *Von Würmen des süssen und salzigen Wassers*, Kopenhagen, 1771, largely devoted to that subject, shows that he failed only where the imperfect means at his command led him astray. The multiplication by artificial section had been observed before that, both in the Naids and other animals, and had awakened a good deal of general interest; but the multiplication by spontaneous fission seems to have been very nearly if not wholly disregarded at that time. Nor has its occurrence in the fresh water worms received, since then, the investigation that it seems to demand. For with the exception of a discussion by Schultze and Leuckart upon some of the particulars, and, the significance of this phenomenon in relation to budding, some ten years ago, and a sweeping denial of its occurrence, or at least of its vital and systematic nature, by Dr. Williams, about the same time, no one, so far as I am aware, has published any extended observations upon the fissiparity of the fresh water Naids since the time of Müller.² And yet the statements of Dr. Williams, in regard to both artificial and spontaneous fission, are such as to suggest at once the importance of a reëxamination of the whole subject; while the great interest given to this question by the remarkable speculations of Steenstrup, together with the interesting varieties of the phenomenon as observed in the marine worms by

¹ Trembley had discovered it long before this, as he observes in his *Mémoires p. s. à l'Hist. d'un genre de Polyypes d'eau douce*, 1744;—and Roesel, in his *Insekten belustigungen*, describes the united parent and bud; but the former did no more than observe the fact, and the latter wholly misunderstood what he saw.

² Gruithuisen remarks in his *Anatomie der gezügelten Naide*, (*Nov. Act. Nat. Cur.* T. xi, p. 243.) only that it is uncommon to find a Naid without buds of the second generation, and refers to Müller for the details of their formation. Since writing this, I have seen in Leuckart's valuable yearly report in the *Archiv. f. Naturgeschichte* for 1861, a notice of Claus's observations on fission in *Chaetogaster*, which, so far as there given, I can confirm.

Quatrefages, Edwards, Frey and Leuckart and others, seem to demand a more complete knowledge than we as yet possess of its occurrence in the fresh water group.

I may here remark that the European species chiefly studied hitherto, *Stylaria proboscidea*, has not come under my observation, nor am I aware that it has been found in America. Four species of Naids common in this vicinity, *Stylaria* (*Pristina*) *longiseta*, *Nais rivulosa*, and *Dero limosa*, found in fresh water, and a marine *Enchytræus*, *E. triventralopectinatus*, have been the principal subjects of my investigation. In regard to the first of these, it may be questioned whether our species is identical with that described by Ehrenberg, (*Symbolæ Physicæ*,) as *Pristina longiseta*, for his description is too brief to be of specific value. As, however, the characters given by D'Udekem, in his *Nouvelle Classification des Annélides Sétigères Abranches*, (*Mémoires de l'Acad. Royale de Belgique*, 1859, T. xxxi,) apply equally to the American species, I am compelled to regard it as the same.³ The second species, *Nais rivulosa*, already described by Leidy, (*Journal Acad. Nat. Sci. Phila.*, 1850, vol. ii, pt. 1°, p. 43,) very closely resembles the European *Nais elinguis*, with which D'Udekem regards it as identical. The third species, *Dero limosa*, has also been described by Leidy, (*Proc. Acad. Phila.*, 1857, vol. v, p. 226) and though overlooked by D'Udekem, appears to be distinct from the European form of the same genus. The fourth, *Enchytræus triventralopectinatus*, I have not been able to identify with any species described in works at my command, and have therefore named from the three anterior pairs of ventral combs after which the dorsal combs begin. This character appears to distinguish it from *E. socialis*, if I may judge from the figure given by Leidy (*Jour. Acad. Phila.*). It has no eyes. The pharynx extends nearly to the fourth ventral or the first dorsal combs, from which a narrow esophagus continues to a little back of the sixth ventral combs. Here a gradual enlargement of the alimentary canal occurs, ending abruptly just back of the eighth, in a narrow twisted tube; and this last gradually enlarges, at the ninth ventral combs, into a moderate sized alimentary canal, in

³ D'Udekem remarks: "Je n'ai pas adopté le genre *Stylaria* admis par Lamarck et Ehrenberg, parce que cette espèce ne diffère des autres *Nais* que par l'allongement très grand de la lèvre supérieure. Ce caractère n'étant accompagné d'aucune modification importante dans la forme des autres organes, je ne puis le considérer comme assez tranché pour servir à former un genre nouveau." There is however a marked difference in the form and position of the cordiform anterior enlargement of the alimentary canal, which even the statements and figures of Müller and Grunthuisen indicate, between the Naids with a long upper lip or proboscis and those with a short one, and the manner of fission differs in these two groups as will be shown. Lamarck's genus *Stylaria* is therefore a good one. Ehrenberg's division of this genus however, based upon the absence of eyes, is unfounded, for I have seen *Nais rivulosa* lose them without any other apparent change, and Agassiz has stated that this occurs as a part of the normal development in many Naids.

which I observed nothing specially marked. The entire length of this Naid was about $\frac{3}{8}$ inch.

The occurrence of spontaneous fission in *Stylaria* (Nais) *proboscidea* is described as follows by Müller. "If a virgin Naid, as I may call it, with 16 or more pairs of hair combs or 20 or more pairs of hook combs [there are four pairs of hook combs anterior to the first hair or dorsal combs as in *Nais* and *Dero*] be carefully observed it will be seen that its anal ring slowly elongates and after some days appears to be transversely marked within into rudiments of future rings.⁴ In each of these divisions beneath the skin, germs of hooks and hairs appear, and the pulsations of the artery are evident, while the food forces a way through them. The hooks and hairs gradually come through the skin in succession from before backward, while the rings enlarging, the Naid increases considerably in length. While in this way new segments and their contents are forming within the anal ring, on the other side [anteriorly] of it, a strongly marked transverse line, different from those just mentioned, appears, and extends across the whole width of the animal. The angles formed at the sides of the body project, and on the top a slight projection is evident which gradually becomes a distinct proboscis, while, finally, eyes appear back of this fission. Thus the Naid becomes a mother." . . . "Frequently one may see in the anterior half of the elongated anal ring of the mother Naid a second ring formation similar to the one just described." . . . "This is not all. Hardly has the second bud acquired the length of one mature ring than a third bud appears before it, and I have even seen a fourth." . . . "Further, not only may a parent and its four offspring thus appear, but the buds themselves may give rise to new buds; their terminal joints forming new buds as they themselves were formed. Hence we may find a parent with its children and grand-children attached to its body." (op. cit. pp. 34, 36.)

Müller afterwards gives his observations upon a single Naid from the 20th of May to the 9th of June. During this time, it gave off the buds observed posterior to the 17th pair of combs, after which a formation of rings began, without any trace of separation, until the body was elongated to over 40 pairs of combs. About this time a fission occurred between the 21st and 22nd pairs of combs. Fission occurring in this way after an elongation of the body I shall speak of as the "renewal of fission." Further observation of individual Naid's led him to

⁴ Schultze considers Müller in error as to the position at which fission takes place, because he describes it as occurring in a segment and not between two. The difference of statement however is simply verbal, as Müller speaks of "die Zwischen-Räume der Borsten oder die Gelenke," p. 26, and in many other places shows very plainly that such is his meaning.

conclude that each bud is formed one joint anterior to its predecessor, that there is thus a gradual reduction of the parent segments till a certain point; that then a reformation of rings takes place, and an elongation of the body of the Naid to recommence this circle of fission.

Schultze, in his article, *Über die Fortpflanzung durch Theilung bei Nais proboscidea* (*Archiv f. Naturgeschichte*, 1849, T. xv, p. 293,) confirms the statements of Müller as to the passage over of one of the parental segments to each bud;² though he is not fortunate enough to observe the recommencement of fission in the elongated Naid. He observes also (p. 301) that, contrary to what Steenstrup had supposed from the analogy of marine worms, there is no relation to metagenesis in the phenomena of budding in this Naid, for he had never seen generative organs in the separated buds. He had however never been able to keep these buds long alive. He also had seen (p. 304,) sexual organs in the parent while budding, though he had never seen well developed sperm and ripe eggs present during this process.

The phenomena of fission in *Stylaria longiseta*, so far as I have observed them, confirm the statements of Müller and Schultze in substance; for there is nearly always a passage over of one parental ring to each bud, and since fission takes place, as I have seen, while the parent has eggs and sperm, and I have never seen the fullest development of the latter in the buds, I cannot believe that there is any such metagenetic relation in this process as has been observed in *Syllis* and allied genera.

In *Nais rivulosa*, however, the facts are somewhat different. For in several continued observations of individual Naid, extending in one case over twelve weeks, I have known, but once or twice of a passage of the parental rings into the bud; while, after an elongation of the parent body, I have very uniformly seen fission recommence in the point at which buds were given off before, or at some point posterior to it, and once anterior, and finally, although I have seen fission taking place between each of the rings from the 15th to the 22d, I have not been able to discover that it does so in any order. But here, as in *Stylaria longiseta*, I have found no metagenesis in the fission.

The facts obtained in regard to fission in *Dero limosa* are unfortunately meagre; the comparative slowness of the meristematic function making the only two series of observations carried out proportionately unfruitful. In none however of the succeeding buds, from Aug. 15th to Oct. 10th, was there any carrying off of parental segments by the separating parts, nor was there anything like metagenesis observed.

² Leuckart at first doubted the correctness of this view. (*Über die ungeschlechtliche Vermehrung bei Nais proboscidea*, *Wieg. Arch.* 1857,) but has since been convinced of its justice.

My observations upon *Enchytræus triventralopectinatus* are similarly scanty, but are just sufficient to confirm and extend the facts observed in the two other short-lipped Naids. In all the cases observed, the separation was of a part wholly new formed, without inclusion of the older segments of the parental body.

It is evident from the above facts, that in *Stylaria longiseta*, as Müller and Schultze have shown is the case in *S. proboscidea*, the point of fission moves regularly forward, ring by ring, and more commonly in the former Naid from the 16th to the 12th pairs of hook combs; though the extremes between which I have known it to occur are the 17th and 10th. To judge from Müller's account it occurs further back in the latter Naid. Further, that in *Nais rivulosa*, and, as far as I know, in *Dero limosa*, and in *Enchytræus triventralopectinatus*, all of which have short upper lips, the buds are given off at one point, though that point may vary in different Naids of the same species, or in one and the same Naid at different times. In the latter case the variation occurs as part of a peculiar form of fission of which I shall speak again. Both "parting" (theilung), and "budding" (knospenbildung), occur then in the Naids, and it may be added that the former appears to be peculiar to the genus *Stylaria* or to the proboscis-bearing forms.

I may here remark that the distinction made by Schultze and others between "theilung" and "knospenbildung," though convenient, does not seem to me a fundamental one. The mere inclusion of a portion of parental tissue in the bud does not of itself make an essential distinction between this and a wholly new-formed, but otherwise similar, bud; nor have I been able to see any histological or functional differences. The very fact that individuals, having the same genetic relations to the parent stock, are in one Naid, *N. rivulosa*, always or commonly produced by the so-called "budding," and in another genus, *Stylaria*, by the so-called "parting," leads to this view. Nor, as I think, though observations are largely wanting in that direction, have the two yet been shown to be functionally different in true meta-genetic processes. They are two varieties of one process; and it would be interesting in many ways to know exactly how the various species of Naids, already known, follow distinctly the one or the other plan, or tend to merge them yet more completely as one.⁶

A little detail will show how closely identical the two forms of bud-formation are. In "parting"—"theilung"—as has already, to a great extent, been described by Schultze, we find that from

⁶ I have known "budding" to intercalate once in a series of fissions in *Stylaria longiseta* (May 31), and I have also known "parting" to interrupt a series of bud-dings in *Nais rivulosa* (Sept. 25), which leads me to expect that in some Naids both processes may be regularly present.

the parental ring, as a fixed point, there is a continuous ring-formation and elongation backward; and that anteriorly to it there is a limited elongation of the general body, also by ring-formation from before backwards. There is, then, unlimited growth backward from the fixed point, and a limited or defined growth backward toward the fixed point from the place of fission. The parental included ring, the most anterior of the series, is here the fixed point. In "budding"—"knospensbildung"—the most anterior ring of the series also, though a wholly new-formed one, becomes the fixed point, from which, by continuous ring-formation, the Naid elongates backward, and toward which a limited series of ring-formations proceed from the point of fission.⁷ The resemblance between the two is perfect; and as the fixed point is not related to specializations of the alimentary tube, as I at first supposed, and is in *Stylaria proboscidea*, where it occurs by "parting," four hook-combs back of the mouth, as it is in *Nais* and *Dero*, where it occurs by budding, while in *S. longiseta* it is six hook-combs back, the genetic relations of the two processes, in these genera at least, are completely one. But, as I have already said, though the distinction appears unessential in the genera I have examined, the terms are convenient and as merely descriptive terms are used here.

The "commencement of fission" was observed in a large proportion of the buds given off from the individuals of *Stylaria* and *Nais* which were under observation, and the result is given in the following table.

<i>Stylaria</i> —between 12-13 combs in none.	<i>Nais</i> —between 17-18 combs in 3
13-14 " 2	18-19 " 3
14-15 " 12	19-20 " 4
15-16 " 9	20-21 " 3
16-17 " 1	21-22 " 3

It is evident that fission does not begin at a fixed point, nor have I been able to discover any relation between the place of its occurrence and the time of the year, temperature, &c.

Now, while fission may take place by gradual reduction of the Naid *Stylaria*, between the 10th and 11th hook-combs, the commencement of fission has not been known forward of the 13th. In *Nais rivulosa*, also, fission has been observed as far forward as the 15-16th, while its commencement has not been noted anterior to the 17th hook-combs. This is all the difference between the commencement of fission and continued fission, notwith-

⁷ There is an interesting analogy between this process in the Naids and the embryonic growth of *Terebella*, as described by Milne Edwards. He has remarked, *Obs. sur le développement des Annélides*, *Ann. des Sci. Nat.*, 1845, 3^{me} Série, T. iii, that the first defined part is not the cephalic, nor the anal, but the esophageal, and that growth takes place both anterior and posterior to this by succession from before backward. Other speculations and analogies suggest themselves here, but are in our present knowledge wholly premature.

standing the fact that whether the former is introductory to a series of "partings" or of "buddings," its bud resembles that produced by what I shall call the "renewal of fission."

That the "renewal of fission," in a Naid elongated after reduction by fission, is a somewhat peculiar form of fission would hardly have been known from observations on *Stylaria* alone.* The following summary will illustrate this. In *Stylaria longiseta* one example (April 16) was reduced to 10 rings, grew out but little, and divided between the 12-13th. When again reduced to 10 rings it grew out much longer but renewed fission at the same point as before. It was then reduced to 11 rings, and growing out, again divided between the 12-13th. One of its buds (May 14) began fission between the 15-16th, was reduced to 12 rings, then grew out and recommenced fission between the 14-15th, and was being reduced again when lost. In another case, the Naid was reduced to 12, grew out and renewed fission at the 14-15th, was again reduced to 12, and growing out again renewed fission at the same point. It was a third time reduced to 12, and growing out again, a third time, renewed fission between the 14-15th hook-combs. It was then reduced to 11, when very unfortunately lost. In *Nais rivulosa*, an example, that had been giving off buds just back of the 19th ring, increased to something like 33, and then again renewed fission between the 19-20th. Another example that had given off buds at the 15th, grew out to over 35, and then renewed fission at the 15-16th. After two or three buds had been given off, it again elongated, and then renewed fission between the 20-21st hook-combs.

Now, while in *Stylaria* the "renewal of fission" appears to differ from the commencement of fission, with which I believe it is essentially homologous, only by not occurring as far back, which may be owing to the want of fuller observation, and while in this genus it might be supposed to be merely a means of continuing the process of "parting," which must otherwise soon cease: we find that it occurs in *Nais rivulosa* without any change of the point of budding, without any apparent necessity, without performing the very function that we might judge from *Stylaria* was its peculiarity. And what is more, it also occurs in *Nais rivulosa* for the performance of this very function. This fact suggests something more than a physiological meaning in the "renewal of fission." While the phenomena connected with it seem to show that the distinction between this, the "renewal of fission," and other forms of fission is more than a difference of function, I am far from claiming that there is any fundamental

* Yet Müller seems to notice these two forms of fission, and says that "though at first view different they are fundamentally the same." Op. cit. s. 28.

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difference, like that between metagenetic and monogenetic fissions. I may add that I have not been able to discover that the point of its occurrence bears any relation to the number of buds already given off.⁹

The sum of the preceding observations tends to show, that the "renewal of fission" has some special characters that suggest a wider enquiry as to its true nature; that the two forms of fission already known as "parting" and "budding" both occur in the Naids, and occur so as to prove their morphologic and physiologic identity; that "parting" appears to characterize the Naids with a prolonged upper-lip—the genus *Stylaria*, while "budding" appears to characterize those with a short one—*Nais*, *Dero*, *Enchytræus*, and *Chaetogaster*, according to Claus; that the bud produced by both these processes is identical with the parent; that as the buds are here, so far as I know, identical with their parents in function and structure, there is no metagenetic fission; and that therefore fission in these Naids, whether by "parting" or by "budding," is correlative to genesis in the great function of maintenance of the species, and not a mere step in the history of the individual.¹⁰

It may be worth while to refer briefly here to the power of reproduction from injuries commonly attributed to these little beings, especially as Dr. Williams, in his *Report on the British Annelida*, (*Rep. Brit. Ass. Adv. Sci.*, 1851, p. 247), after quoting a summary of Bonnet's well known experiments, says: "On the authority of hundreds of observations, laboriously repeated at every season, the author of this report can declare with deliberate firmness, that there is not one word of truth in the above statement." It may be presumed from this, that Dr. Williams felt the necessity of thorough and very careful investigations, before contradicting the statements so often repeated upon this subject; and I cannot doubt that his experiments have uniformly failed.

⁹ There are some other differences to be considered in a future paper upon the histologic nature of fission.

¹⁰ "From the analogy of the two species, *Arenicola* and *Nais*, on which the author's observations have been chiefly conducted, the conclusion may be deduced that the 'fission of the body' in every other species of Annelida in which it occurs has for object in like manner to protect and incubate the ova." . . . "It becomes the last act of the parental worm, since the portions into which the body is sub-divided by fission never take food." . . . "It is a catastrophe, in which every autumn involves the whole community."—Williams, *Rep. Brit. Annel.*, pp. 249-250.

I should be far from wishing to extend the conclusions I have made to all other Annelids by mere analogy, but my observations are, at least, wholly incompatible with a general application of Dr. Williams's statements to the Naids.

The exact circle of life and its duration, I have not determined, nor do I feel certain that any of the general statements—see Leidy, *Flora and Fauna within living animals*, on *Stylaria fossularis*, and Williams at large—are absolutely correct. For I have known the process of fission to go on in winter, when the Naids were kept in a warm place; while I have also seen, what appeared to be a loss of this power, as shown in badly formed and incomplete buds, occurring in the warmer parts of the year.

But from the almost uniform success of my own, I should wonder that they have done so, had not others reported complete or partial failures in similar experiments.—See Dugès, *Ann. des Sci.* 1828, 1^{re} Série, T. xv. It must be remembered, however, that such evidence is wholly negative, and cannot weigh with the positive statements of observers like Müller, Réaumur and Dugès.

In regard to my own observations, I may state, in brief, that in *Stylaria*, *Nais*, and *Dero*, I have hardly ever failed to have the head reproduced, and that the anal end has not only been reproduced in these genera, but I have seen it reproduced in *Enchytraeus*, in *Lumbricus*, in *Fabricia*, and even in a *Nereis* common on our coast.¹¹ That in the vast majority of these cases I have seen food taken again; and, in all, I have seen the incurrent anal stream, which ceases while either end is closed, recommence. From these and other observations, I am inclined to believe that this power is far more general in the class than is yet supposed.

That this power plays a part in the natural economy of life, the healing fragments of Nais that I have found in our pools is a proof. When saved from the attacks of *Chaetogaster*, even the shortest, headless, and almost immovable, fragments may go on to as full a recovery as when preserved by the observer. In one instance, I found, Aug. 21st, what was apparently five segments of some Naid's trunk, the two ends of which had closed and elongated. This had been preserved for some time, for the sur-esophageal brain was well formed anteriorly, and the germs of hook combs were well defined posteriorly. It went through a rapid growth, developed eyes about the 22nd, opened the newly formed mouth about the 23rd, was supplied with food, and growing long divided between the 15-16th hook-combs and then gave off 5 buds in succession at that point till Oct. 8th, when it was lost.

The thin film with which the Nais line the jars in which they are kept may be seen to serve, there at least, as a protection against the attacks of the prowling carnivorous *Chaetogasters*, and once beneath this, a fragment, like the one just referred to, may be preserved till the eyes and mouth are formed—a period usually of a fortnight. And though we should hardly have expected a mere piece of five segments to be preserved as this was, even though endowed with the power of recovery, yet we cannot regard so extended and remarkable a function as this appears to be, as useless or inoperative in the natural course of Naid-life.

¹¹ Careless observations made a number of years ago led me to think that the Nereids are destitute of the power of recovery from injuries, and Williams states that they always sloughed away ring after ring, in his experiments. Réaumur remarks: "Les expériences que j'ai fait faire sur des millepieds de mer, d'une toute autre longueur, sur de ces millepieds longs de sept à huit pouces, n'ont pas eu le même succès: mais les essais n'ont peut-être pas été encore assez répétés ni assez suivis."—*Mem. pour s. à l'hist. des Insects*, T. vi, p. 59. Thinking the latter statement very probable I retried the experiments during the past year, with more care, and in every case with success.

