Syllidian Miscellany.

By

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With 6 Figures in the Text.

I. *Autolytus roseus* Claparède with Special Reference to its Head Appendages.

This Autolytus has been known only in the form of Sacconereis, i.e. as the female stolon of an unknown Syllid. It was discovered in 1864 by a French zoologist, E. Claparède, at Port-Vendres (Pyrénées Orientales). According to the original figures and description it is an ordinary female individual in its general appearance, carrying a large egg-sac on the ventral side. The latter is " étranglé en 8 " and turkish blue, the colour being due to the contained eggs. The body consists of about 60 segments, the dorsal surface of which is transversely banded by pigment of rose colour. Modification of the segments for swimming commences at the 9th setigerous segment and stops at the 21st. The following 40 segments (about) are not modified like the 8 in the first region just behind the head. The most striking character, by which the present stolon is distinguished from any other Sacconereis, is the presence of a pair of extra appendages in front of the head in addition to the median and lateral tentacles. Claparède states that the presence of these appendages, " qui n'ont été signalés chez aucune autre Sacconereide," is by no means very astonishing, since there are two such ones in Polybostricus. Claparède clearly predicted their homology to the frontal lobes of the bifid antenna-like appendages in the male head. A. Malaquin (1893) actually explained the bifid condition of the frontal appendages of the male as due to their origin in the fusion of the lateral tentacles and the palpi.

Since its first discovery, there has been no second record of the peculiar Sacconereis in question. Fortunately, during my stay at Plymouth, a female stolon, which is closely allied or even identical to *Autolytus roseus*, was captured at a place two miles east of the Eddystone Lighthouse with a ring-trawl, September 17th, 1928. I am greatly indebted to Mr. F. S. Russell of the Plymouth Laboratory for bringing it to my notice.

Since it was found among other planktonic organisms preserved in

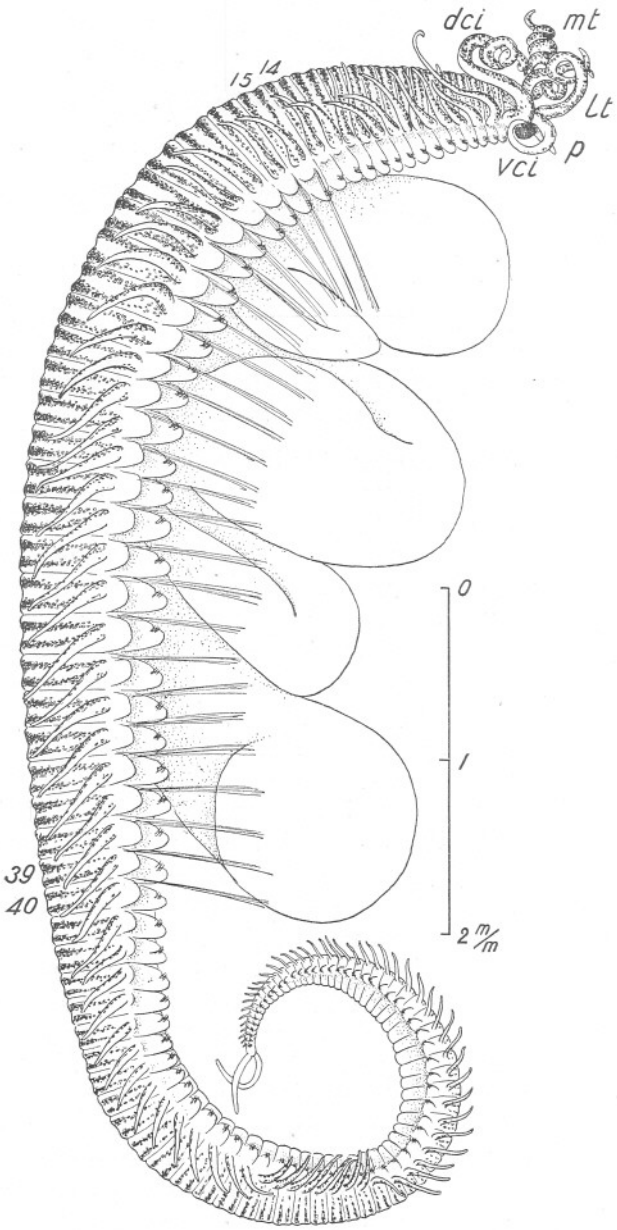

FIG. 1.—*Autolytus roseus ?* from Plymouth district.

5% formalin, its colour in the living condition is not exactly known, although a red hue is still abundantly retained; the colour is due to numerous microscopic patches of red pigment disposed in two transverse bands on the dorsal surface of each segment and its dorsal cirri. On the head the appendages are strongly contracted, coiled in spirals and massed up almost together. Their condition naturally makes the small appendages in question very difficult to examine. At any rate, I shall first sketch out the general appearance of the specimen here (Fig. 1).

As the figure shows, the Sacconereis closely resembles *Autolytus roseus* of Claparède, except in the number of unmodified segments in the first region. Here we count 14 segments as opposed to 8 in that case, and this difference deserves a little consideration before proceeding to the main problem of the present enquiry.

With regard to the sexual metamorphosis of the segments for swimming, the stolons of the Autolytinæ among Syllids may be divided into two categories, the first including those stolons of short length and possessing a smaller number of segments. In these forms the body is generally made up of the anteriorly unmodified and the posteriorly modified segments. The stolons of the second category consist of three regions having modified segments between the anterior and posterior unmodified ones. To the first category belong the stolons of *Myrianida* (Milne-Edwards) and *Autolytus* (Grube), and to the second those of *Procerœa* (Ehlers), *Procerastea* (Langerhans) and *Virchowia* (Langerhans). In the stolons of the first category the anterior unmodified region consists of only two (female) or three (male) segments, but in those of the second category there are, as a rule, 6 segments in this region, whether in the male or the female. The sexual individuals of *Procerœa* (*Autolytus*) *longeferiens* (Saint-Joseph) described under the title of *Autolytus alexandri* by Malmgren are, however, excepted from the general rule, since the first region of this Sacconereis contains 14 unmodified segments (see Okada, 1929, Fig. 30). In *Autolytus roseus*, as mentioned above, 8 segments are assigned to the first region. Therefore, if the original count be not mistaken, we have another exception to the general constitution of the Autolytan stolons of the second category. Now in connection with this number of unmodified segments in the first region the question arises whether it is truly specific to this stolon or whether it is rather due to a chance variation in the only specimen observed. Since the material at my disposal is also single, the problem cannot be settled by the method of simple comparison. Therefore turning to the other side, I examined a large number of stolons of different species, so far as I have been able to capture them by towing, and finally found some stolons of Procerastea having 3 segments in the first unmodified region instead of the usual 6. Hence, a hypomeric variation is possible at least in the case of Procerastea. On the other hand, no single instance

of hypermeric variation was detected during the whole of my examination. Generalising from this result I may conclude that 8 unmodified segments in the first region of *Autolytus roseus* would be due to a hypomeric change of the original 14 segments.

I continued my examination of other Sacconereis belonging to the second category, hoping to find some other forms possessing a pair of problematical appendages in front of the head, and at length found them in

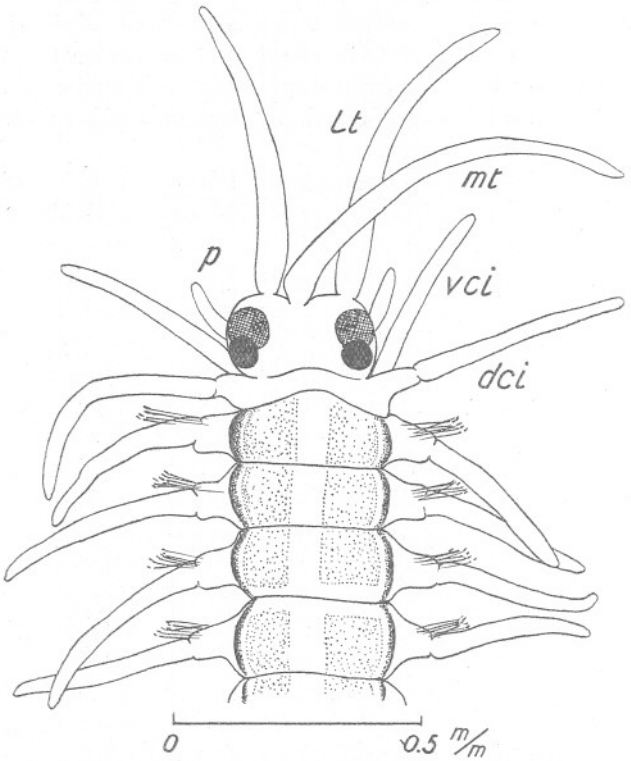

FIG. 2.—Anterior part of female individual of *Procerœa picta*.

female individuals of *Procerœa picta* Ehlers and of *Procerœa aurantiaca* Claparède. A pair of small appendages does exist in the head besides the median and lateral tentacles of the prostomium and the tentacular cirri of the peristomium. The general constitution of the head of the first species is sketched out in Figure 2.

The appendages in question are, however, not exactly in front but slightly posterior to the anterior end of the head, and placed on each side beneath the position of the dorsal eyes. They are, of course, not the lateral tentacles, since the latter, which are highly developed, are found anterior to

them at each frontal edge of the head. Also they do not represent the ventral cirri of the peristomial segment, since there is a pair of cirri, dorsally long and ventrally short, on each side of the posterior boundary of the head. I do not hesitate therefore in comparing this pair of short appendages with the problematical frontal ones of *Autolytus roseus* and to say that they are homologous with the palpi of the asexual animal.* Hence the constitution of the head of *Autolytus roseus* described by Claparède is probably not due to a teratological formation, while the absence of the appendages in the head of other stolons closely allied to it shown in the figures of previous authors is probably incorrect.

II. Appearance of *Autolytus cornutus* A. Agassiz in Europe.

My second visit to the Plymouth Laboratory was in June, 1929. This time I obtained a tiny Syllid abundantly on Laminaria covered by Obelia always in close association with *Autolytus edwarsi* Saint-Joseph. It differs, however, from the latter not only in size but distinctly also in colour, which is rather pale green, and in the fact that the dorsal surface of the segments is fringed with more or less dark pigment. It produces a single stolon, either male or female, and does not carry a chain of stolons, the posterior segments separating from the anterior with a new formation of the head always on the anterior boundary of the 14th setigerous segment (Fig. 3).

The female individual consists of three distinct regions, the first containing 6 unmodified segments, the second 12 modified, and the third again 8–13 unmodified ones.

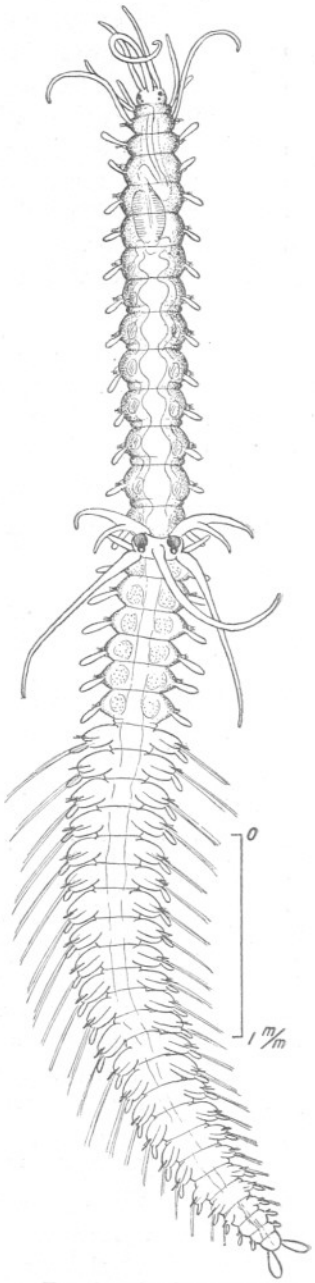

Fig. 3.—*Autolytus cornutus* from Plymouth district.

* In the Autolytinæ the palpi are generally reduced in size and fused into a lip-like structure in front of the mouth opening.

This constitution would make the stolon belong to the type of Proceræa or the second category of my classification. The male individual, however, has only two regions. The anterior unmodified region is made up of 6 segments as in the other sex, while in the following region of the body all the segments except the anal one are metamorphosed for swimming. According to my classification, stolons having more than 6 segments in the first region must belong to the second category, although the Polybostricus of the present species represents the type of the first category.

In connection with the number of segments in the first unmodified

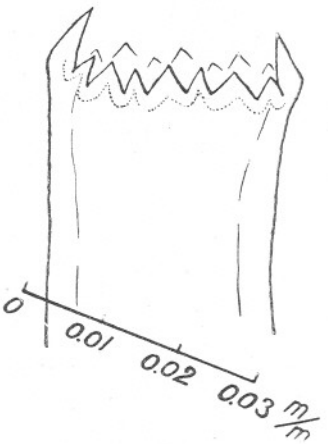

Fig. 4.—Trépan of *Autolytus cornutus*.

region, A. Agassiz (1862, p. 394) has mentioned that " the number of rings which are not provided with long setæ, and have short dorsal cirri, are five, instead of six as in the female." But judging from the subsequent statement that " the spermatozoa (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," Agassiz seems to have mistakenly counted the most anterior segment as being in the head, since the spermatozoa are only produced in the original segments, i.e. from the 14th to the 20th setigerous segment of the asexual stage, and never in the new head.

Agassiz did not give the dentation of the pharynx, so it may be rather risky to identify the present species with the American only by its external resemblance. Nevertheless, the following two reasons would make this identification not improbable : first, the species was not found before during my stay from June, 1927, to April of the next year, in spite of its being so common in the summer of 1929. Secondly, this district of

England is the first port of Europe touched by steamers coming from America. It is possible that its appearance in Plymouth Sound was due to its being carried by a steamer from its native country. Of course, it is probably not simply carried by adhering to the bottom of a ship, but the latter would first be covered by some hydroids including Obelia, to which the Syllid attaches itself secondarily.

III. *Proceræa picta* Ehlers and *Stephanosyllis scapularis* Claparède.

This Syllid described by E. Ehlers (1864, p. 587) under the title of "Proceræa picta" is most easily distinguished from other forms of the same type of animal by its characteristic pigmentation. The dorsal surface is covered with a deep deposit of black or dark brown pigment, with the exception of a mid-dorsal longitudinal line, which is free of pigment and hence appears white, and a series of transverse bands free of pigment and hence also appearing white. The white bands are especially well marked after the 7th setigerous segment, developing between the following segments: 7 & 8, 9 & 10, 11 & 12, 13 & 14, 19 & 20, 22 & 23, 26 & 27, 30 & 31, 34 & 35, 42 & 43, 45 & 46, 48 & 49, 52 & 53, 56 & 57, 60 & 61, 64 & 65, 68 & 69, 72 & 73; they become gradually obscure towards the caudal extremity. The pigmentation is further complicated on each segment. By the white line in the middle, the coloured area is divided into left and right halves, which are further subdivided into several narrow bands. This part of the centre is fringed by a longitudinal stripe of especially deep pigment. The latter is restricted to narrow limits on each side of the segments but stretches continuously from just behind the head to the tail end, without being interrupted by the transverse white bands mentioned above. Anteriorly at the level of the 3rd setigerous segment the peripheral fringes of deep pigment come from each side to the middle and meet together between a pair of nuchal organs, which are also deeply pigmented. Sometimes, especially in large individuals, the pigmentation in front of the 14th setigerous segment is more or less different from that of the posterior part of the body, the former part being always much more intense than the latter. This fact is easily understood when the method of stolonisation of this Syllid is considered; those segments posterior to the critical position are separated at each time of stolonisation and the missing part is replaced by new segments.

P. Langerhans (1879, p. 578) state that "bei jungeren Individuen ist die Färbung einfacher, nur die beiden braunen Längsstreifen sind zu erkennen. Das bestimmt mich zwei junge Thiere von 1 cm. und 50 Segmenten, die ich in Funchal am Strande gefangen habe, hierher zu stellen. Sie hatte nur zwei dunkelbraune dorsale Längsstreifen, die sich über das

ganze Thier bis zum Analsegment erstreckten. Aber sie stimmten sonst ganz mit der picta überein. Namentlich hatte der Pharynx wie bei dieser 20 Zähne, 10 grössere abwechselnd mit 10 kleineren. Analcirren kurz." Unfortunately this statement cannot be applied to all small individuals of the so-called " Autolytus pictus " in the Plymouth district. There are plenty of specimens which measure even less than 1 cm. and consist of less than 60 segments, yet showing the special pattern of pigmentation detailed above, while on the other hand there are also nearly as many specimens whose pigmentation is indeed " einfach," without the transverse white bands. These worms are, however, by no means always smaller than those of the other type. On the contrary, they are sometimes as big as the largest worms of the other type, and have even been observed in the act of producing the stolon. It is almost certain, therefore, that we are dealing here with two different species or varieties at least and not two developmental stages of one and the same species. Ehlers (1864, p. 257) has mentioned the existence of some variations among his " Proceræa picta " : " Ein dritte Form ist diejenige, wo die gleichmässig gelb gefärbte Rückenfläche an den Kanten von einem braunen Längsstreifen eingefasst wird, wobei die Stirnfühler und Cirren des zweiten Segmentes braun, die das ersten und dritten Segmenten nur an der Spitze braun, sonst weiss waren." Such pigmentation may be well applicable to " Stephanosyllis scapularis " described by Claparède in the same year from Port-Vendres (Pyrénées Orientales).

The stolon of the so-called *Autolytus pictus* was first shown by Saint-Joseph (1886, Figs. 102–105). It represents the male individual of the type " picta," while as to the other sex Saint-Joseph states, " Je ne vois jamais de Sacconereis se détacher ; je constate seulement que la tête en est semblable à celle figurée par moi pour la Sacconereis de *l'Autolytus ornatus*." In his monograph on " The British Annelids " McIntosh (1908, Pl. XLVII, Fig. 1) has figured a young Polybostricus of the same type. Now it might be asked whether this banded type of the Autolytus in question is not the male producing animal, and the other non-banded simply pigmented type the female producing one. Actually among Mrs. E. W. Sexton's sketches of the Plymouth Polychætes (unpublished and preserved in the Laboratory) there is a Sacconereis certainly belonging to the latter type. This consists of 28 setigerous segments in addition to the head and tail ones, differentiated into 6 unmodified, 13 modified, and 9 unmodified. However, there is also a female stolon of the banded type in the same collection of sketches. Therefore, sexual dimorphism cannot be applied here to explain the colour differences of the Autolytus in question. At any rate, to settle the problem definitely I cultivated the banded and non-banded animals separately to see what kind of stolons come out. As a result each type was found to produce both male and female stolons

independently, and those stolons well preserve their original pattern of pigmentation even after being separated from the anterior part.

Stolonisation, either in the banded or in the non-banded type, takes place quite easily even when the animals are confined in a finger-bowl filled with sea-water during the warmer season from June to August, while the stolons are most abundant in the plankton from April to June. A quite astonishing fact is that after September, in spite of its being still quite warm in Plymouth, the animals cultivated *in vitro* never produce any more stolons, although some of them are full of green eggs or milky-white spermatozoa. Apparently stolonisation in nature also stops after the summer season, just as in culture experiments. At about the same time we find no more stolons in the plankton, although there are still plenty of asexual individuals among the dredgings. Among the latter there are also specimens whose body segments are filled with sexual products. Claparède (*l.c.*, p. 108) observed in his " Stephanosyllis scapularis " the eggs contained up to the 10th setigerous segment, without, however, any sign of stolonisation. Langerhans (*l.c.*, p. 579) has also mentioned a similar case of sexual maturity in *Proceræa aurantiaca* : " Ich habe nur einmal bei dem grössten meiner Exemplare im December vom 16 Segment an Ei gefunden, ohne Anzeigen einer Knospenbildung." Since such specimens are obtained mostly in the winter season, it may be supposed that the stolonisation of Proceræa and its allied species would depend upon the temperature of the sea-water. However, examining Mrs. Sexton's drawings of Plymouth Polychætes again I find an example of *Autolytus prolifer*, which is full of ripe eggs and yet without any indication of forming a stolon. It was captured, according to a note attached, at Millbay pit on July 1st, 1914. In July the sea-water at Plymouth is by no means cold. As has been mentioned already, stolonisation in both *Proceræa picta* and *scapularis* stops nearly at the same time, about the end of August, while sexual individuals are quite abundant in the plankton in April. The temperature of the sea-water at Plymouth in September is never lower than in April, so that stolonisation of these Autolytids at least could not be simply due to the temperature of the external medium, but must be inherent and due to some other factors.

The regeneration of *Proceræa picta* is most interesting to study. As I have already shown in a former publication (1929, p. 560) if we cut the anterior segments, the posterior piece almost invariably regenerates the head up to about the level of the 42nd setigerous segment. But the regenerative power is not the same throughout the body. From the head to the end of the 5th setigerous segment the number of new segments almost always corresponds to that of the missing ones. Behind this level the number of regenerated segments is more or less smaller than the original number, the maximum number being still, however, the same as

the missing. Posterior to this level but up to the end of the 7th segment, the same maximum regeneration cannot as a rule exceed 4 setigerous segments in addition to the head ; and this 6-segmental recovery holds to the end of the 13th segment. Between the 14th and the 42nd setigerous segment, the regeneration is quite isopotential, only the head plus one setigerous segment being produced before sexual maturity, and only the head part in the sexually matured animal. Moreover, beyond the level of the 13th setigerous segment there is absolutely no stomodeal invagination in regenerated segments, and the cut end of the intestine opens directly to the exterior as a mouth. However, as I have mentioned before, "this interesting result that there is so distinctly regional difference in regeneration, cannot be extended and applied to the body of other Syllids, even within the bounds of the same genus." So far as my experiments are concerned only *Proceræa scapularis* presents the same regional difference in regeneration according to the point at which the cut is made.

Fragmentation is not a characteristic phenomenon in these species of Autolytids, but it has been well investigated in them. There are two methods of provoking artificial fragmentation, viz. dilution of sea-water with fresh or distilled water (Allen's dilution method) and employing a solution of KCl. As has been explained, the fragmentation due to KCl solution depends upon a muscular action, while the same phenomenon in diluted sea-water is due to the osmotic changes in the intestine. According to my former experiment almost no effect is produced by dilution until the degree of 60% (not 6% as printed in the former publication, Okada, 1929, p. 586) of distilled water in sea-water is reached. Proceræa can live quite normally in such a medium. Nevertheless, if we cut or injure any part of the body with the exception of the extreme anterior or posterior portion, fragmentation takes place even in such a low degree of dilution. In *Proceræa picta* two consecutive united groups of segments at each white band separate first on the dorsal surface, a transverse crack appearing in the middle of the white band. *Proceræa scapularis* has no transverse bands, but fragmentation of segments takes place exactly in the same manner as in the preceding case. The external and internal changes of the segments, which are observed in this case of fragmentation, have been described in the former paper. They are also illustrated here by the three microphotographs in Figure 5.

It was stated that "the swollen intestine is generally coloured brown, while in its normal condition it is almost without colour or at the most pale yellow." This change of colour in the intestine is found to be closely related to the change in the chemical nature of the granules contained in the intestinal cells. The granules in the normal specimens are slightly stained by eosin or other acid dyes, but not at all by Heidenhain's iron

hæmatoxylin, while the same granules in the fragmenting or fragmented specimens are highly stainable by the last-mentioned stain.

The structure of the pharynx, especially the dentation, is the most important clue for the identification of these Syllids. Ehlers (*l.c.*, p. 260) mentions that "am vorderen Eingange ist der Rand dieser Cuticula so

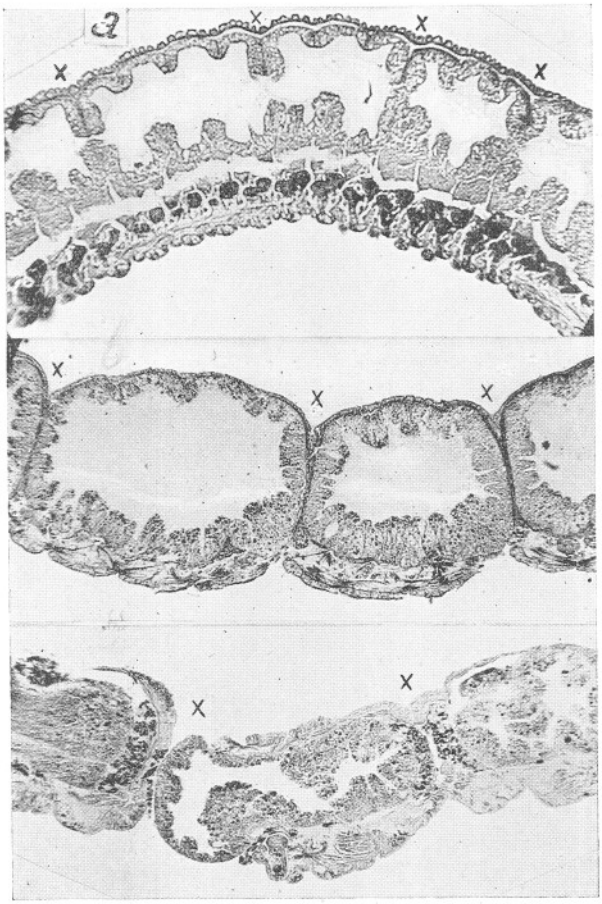

FIG. 5.—(*a*) Longitudinal section of *Proceræa picta*; (*b*) same of fragmenting, and (*c*) fragmented specimens, x indicating positions of macrosepta.

eingeschnitten, dass etwa 10 kleine Zähne, welche schräg nach vorn und gegen die centrale Längsaxe convergiren, die Eingangsöffnung umgeben und verkleinern." Claparède (1868, p. 221) states that "la cuticule de la trompe s'épaissit en avant pour former un cercle d'une dizaine de dents un peu crochues." Langerhans (*l.c.*, p. 577) describes the "trépan" a

little more precisely: "Pharynx mit 20 Zähne, 10 grössere, 10 kleine Zähne." This number of 20 of two kinds of larger and smaller teeth disposed alternately is also given by Saint-Joseph (1886, Fig. 101, also P. Fauvel, 1923, p. 316, Fig. 121b). However, it is doubtful whether these authors really counted all the teeth carefully or whether they counted only one side of the trépan and doubled the number. There are just 5 larger and 5 smaller teeth on one side of each trépan when we count them without moving the screw of the microscope. But if we count all

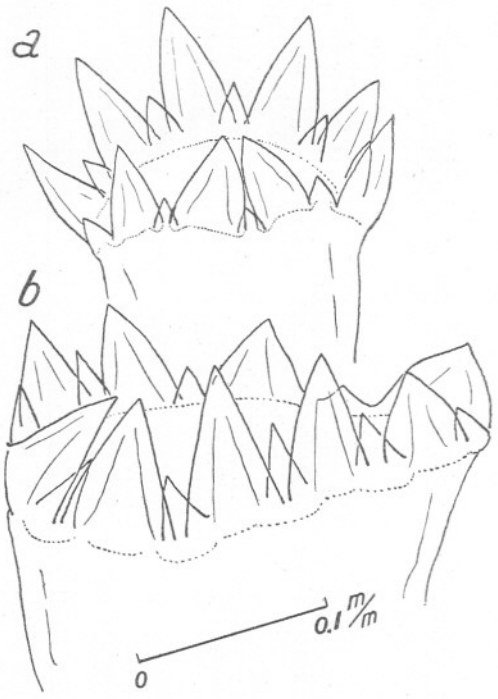

FIG. 6.—Trépan of *Proceræa picta* (*a*), and *scapularis* (*b*).

the teeth with a little more patience, we find the number is 18 instead of 20; 9 larger teeth are disposed alternately with 9 smaller teeth forming a circle (Fig. 6). In *Proceræa picta* the difference in size between the larger and smaller teeth is great. They are, however, of the same size and shape among those of the same category. On the other hand, the smaller teeth are much developed in *Proceræa scapularis*, and the difference in size between them and the larger teeth is accordingly reduced. Moreover, in the latter species the larger teeth are not uniformly shaped, some being broader than others, while the latter are more sharply pointed and longer than the former. Although this character is not very constant, yet it

is never found in the trépan of *Procerœa picta*. It cannot be considered teratological, since the structure is met with in too many cases. On account of the different dentation, as well as the difference in the colour pattern, I propose to revive the name *Procerœa scupularis* to be applied to the so-called " Autolytus pictus " with non-banded simple pigmentation and purple tentacles and cirri.

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