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OBSERVATIONS ON THE STRUCTURE AND LIFE HISTORY OF *AUTOLYTUS PROLIFER* (O. F. MÜLLER)

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(Text-figs. 1–3)

Introduction

All the specimens of *Autolytus prolifer* (O. F. Müller) described here were gathered from colonies of the hydroid *Obelia flabellata* Hincks, growing on pebbles in a shallow creek in the intertidal zone of the Chalkwell mud flats, on the north side of the Thames estuary. The syllid was found to be very plentiful on this hydroid, living in semi-transparent tubes attached to the stem, but was not found elsewhere.

The specimens agree well with previous descriptions of *Autolytus prolifer* in the number and arrangement of the pharyngeal teeth, and in the chaetae; but some of the other anatomical features show similarities with other species of *Autolytus* Grube.

Records of the occurrence of this species are scanty, due, no doubt, to lack of observation. Nevertheless, published descriptions have frequently been based on a few or even on single specimens, while here it may be pointed out that a relatively large number of worms of all ages were collected and examined.

In this paper the terms 'male form' and 'female form', or simply 'male' and 'female', have been used in place of the older terms, '*Polybostrichus*' and '*Sacconereis*' respectively.

The formation of stolons and the resulting female and male stages have been described by several previous authors (Slabber, 1778; O. F. Müller, 1788; Bruguière, 1791, table 56, figs. 8–15; Krohn, 1852; Max Müller, 1855; Keferstein, 1862; Greeff, 1866; St Joseph, 1887; McIntosh, 1908; Fauvel, 1923; de Vos, 1936; Thorson, 1946; Wesenberg-Lund, 1947), while a more general account is given by Potts (1911). Apart from de Vos, these authors appear to agree that, in the male form, only the first three segments behind the head are without natatory chaetae, whereas in the few males collected at Chalkwell six such undifferentiated segments separated the head from the metamorphosed segments. De Vos found the number of segments behind the head without natatory chaetae to be variable.

It is likely that the habit of living in tubes on hydroids is widespread among autolytoids. Wesenberg-Lund (1947) has found *Autolytus prolifer* on *Lafoëina maxima* Levinsen. McIntosh (1908) records *A. prolifer* from

shells and other debris brought up by the deep-sea lines of fishermen at St Andrews (Scotland), and in tough translucent tubes under stones near low-water mark. These worms have also been found on seaweeds (McIntosh, 1908; Thorson, 1946).

The larval development of this species has not hitherto been described, though sketches of larvae attributed to *A. prolifer* are scattered through the literature. Some of these resemble the corresponding stages described here, but others are very different. Most of the work on autolytoid development has been done on other species, e.g. Agassiz (1863) on *A. cornutus*, and Malaquin (1893) on *A. edwardsi*.

The syllids were easily collected by gathering the *Obelia* colonies. On placing these in glass dishes, most of the worms deserted their tubes and aggregated on the side of the dish nearest the light, and were then easily removed with a small brush. Some of the youngest stages obtained, however, were collected later, for although these were not found to be living in tubes, they nevertheless adhered strongly to the surface of the perisarc.

Drawings have been made with the aid of a camera lucida, and with the exception of Fig. 1 from narcotized specimens. Details were checked from material fixed in 2% formalin in sea water, after narcotizing with 8% magnesium sulphate, and mounting in benzyl alcohol or euparal, either unstained, or stained with borax carmine.

Collections were made on 1, 6 and 21 June 1949.

Identity and Structure

The ordinary non-reproductive stages ('*animal surculare*') resemble *A. prolifer* (O. F. Müller) in the following features: (i) two pairs of eyes with lenses, and one pair of lateral eyespots; (ii) most (but not all) individuals with an S-shaped pharyngeal curvature; (iii) pharynx always provided with ten, equal, teeth; (iv) oblong proventriculus; (v) coloration; (vi) chaetae.

In some other characters, however, these specimens differed from the published descriptions and figures of *A. prolifer* (O.F.M.), and in some features resemble *A. auriantiacus* Clap. These differences are: (i) the median head tentacle is invariably longer than the two lateral tentacles, and may be twice as long; (ii) dorsal cirri much shorter; (iii) male form with three regions behind the head—first with six anterior segments without natatory chaetae, second with about eighteen segments with natatory chaetae, third with about six undifferentiated terminal segments; (iv) smaller size (non-reproductive form 3–7 mm., cf. Fauvel (1923), 5–15 mm.); (v) some specimens show a looped pharyngeal curvature.

Most previous authors agree that the male form has only three undifferentiated anterior segments lacking natatory chaetae (Keferstein, 1862; Malmgren 1867; Langerhans, 1879, 1880; St Joseph, 1887; McIntosh, 1908; Fauvel, 1923; Wesenberg-Lund, 1947), and that the segments bearing natatory chaetae

extend to the pygidium, although St Joseph notes that the terminal chaetigerous segment has shorter natatory chaetae than the others. De Vos, however, found between three and six such anterior segments, followed by twenty to twenty-seven segments bearing natatory chaetae, and that the female also varied in a similar way. On the other hand, the sexual phases described by Wesenberg-Lund all have three such anterior segments, and although the non-reproductive stages are similar to the Chalkwell specimens, the male is different in some respects. Wesenberg-Lund does not mention eye-spots (as distinct from lensed eyes), and unfortunately makes no reference to the pharyngeal armature.

The stock differs little from the drawing by Thorson (1946), except in the longer prostomial tentacle, and the much shorter parapodial cirri, but does not bear a close resemblance to drawings made by earlier workers on autolytoids ascribed to this species (Keferstein, 1862; McIntosh, 1908). Stoloniferous forms were found with a single male stolon, and forms with up to four female stolons. A single free male form was found on the hydroid, but no ripe female stages were found unattached. A specimen with a single male stolon is shown in Fig. 1A, and a dorsal view of one of the parapodia from the differentiated region in Fig. 1B. The dorsal cirrus will be seen to be much shorter than those figured by all previous authors. As well as showing the more obvious differences already described, Keferstein's male does not show a pair of anal cirri, which are clearly visible in the Chalkwell worms.

If these Chalkwell specimens are regarded as belonging to a new species, then they can only definitely be separated from *A. prolifer* (O.F.M.) by the sexual phase, unless the much shorter length of the dorsal cirri is regarded as a constant feature of taxonomic importance. This cannot be decided until the real affinities of the males with only three anterior segments without natatory chaetae ascribed to *A. prolifer* has been proved, but from the observations of de Vos (1936) it would appear that the number of segments behind the head without natatory chaetae is variable, and cannot therefore be regarded of taxonomic importance. This applies equally well to other species.

If, on the other hand, these worms are regarded as belonging to *A. prolifer*, then the pharyngeal armature alone supplies reliable separation from closely allied species such as *A. auriantiacus* Clap. It may be added that the teeth are difficult to see in *A. prolifer*, even in fixed and cleared material, and Johnston (1845, p. 146, pl. IX, figs. 3, 4; 1865, p. 192, pl. XV*a*, figs. 3, 4) thought that there were no teeth.

Other characters are variable, especially the length of the median head tentacle (Figs. 1, 3D–F). Claparède (1868), McIntosh (1908), and Fauvel (1923) all show the median tentacle to be the same length as the lateral tentacles, as in *A. brachycephalus* Mar. (Marenzeller, 1874), but Viguier (1886, p. 429, pl. XXVI, figs. 13–15; pl. XXVII, fig. 1) shows the median tentacle as being slightly longer, but not as long as in the specimens described here.

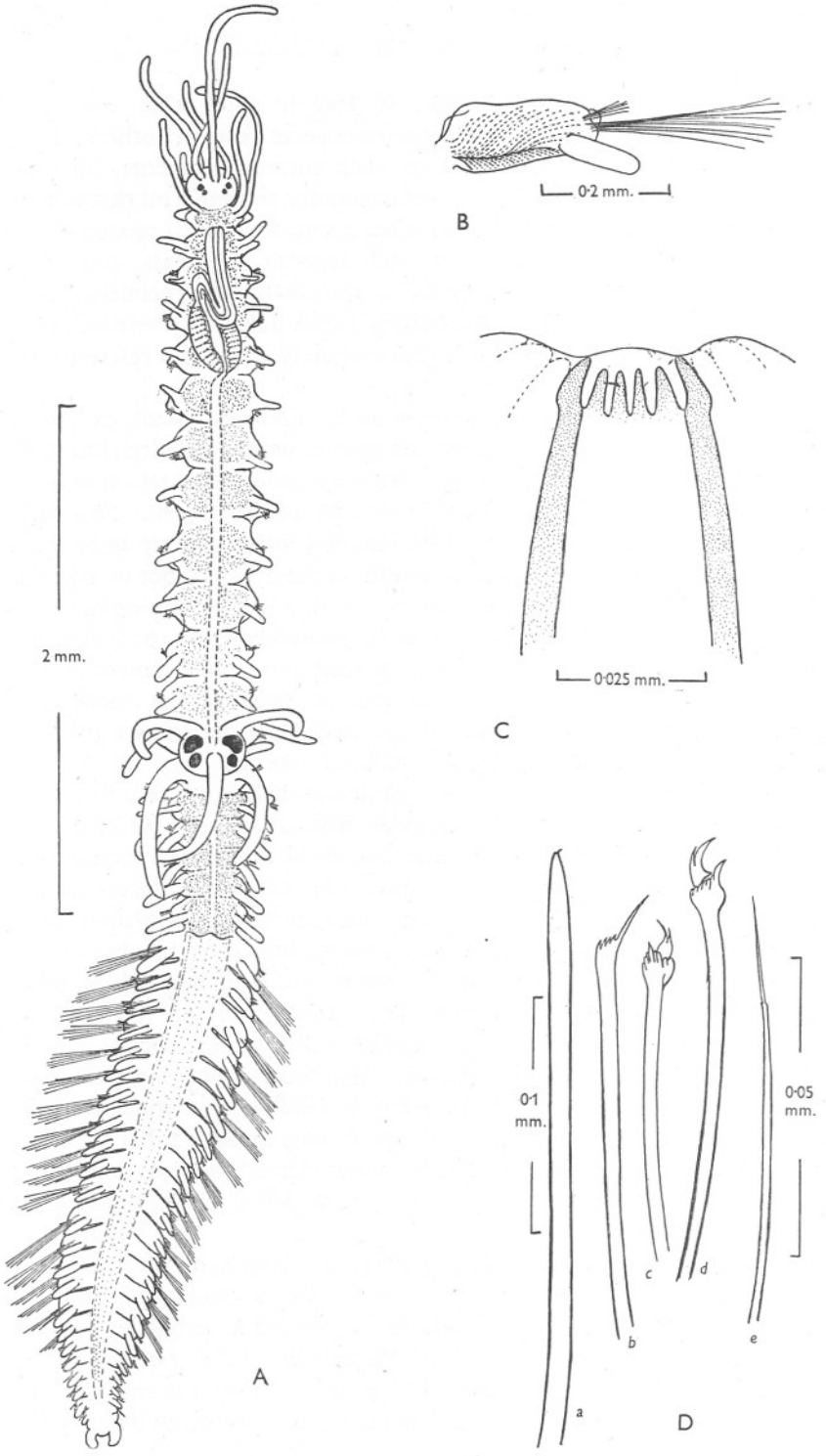

Fig. 1. *Autolytus prolifer*. A, stock with a single male stolon (dorsal view); B, dorsal view of a right parapodium from the differentiated region of the male form; C, pharyngeal armature; D, chaetae. *a*, distal half of a natatory chaeta from a male; *b–e*, chaetae from non-reproduction phase.

The looping and coiling of the pharynx has also been regarded as a character of taxonomic importance, but in several dozen adults examined at random for this feature, it was found to be variable. Fauvel (1923) states that *A. prolifer* has an S-shaped pharynx, while that of *A. auriantiacus* is completely coiled. In the Chalkwell worms, the length of the pharynx varied, and consequently although an S-shaped loop was usually formed when the proboscis was retracted, several specimens showed a complete coil as in *A. auriantiacus* (Fauvel, 1923, p. 313, fig. 120*a*; Marenzeller, 1874, Taf. VI, fig. 1), and it may be noted that *A. auriantiacus* itself is variable, since Claparède (1868) gives a drawing with a pharynx showing a double coil (pl. 15, fig. 1). In Chalkwell worms, also, the proventriculus was situated more anteriorly than segments 7–9, but this may be correlated with the somewhat smaller size of the adults (about 5 mm., see Fig. 3F).

Representative chaetae are shown in Fig. 1D. They resemble chaetae previously figured for *A. prolifer*, but many of these drawings might equally well be attributed to other species, so that no really significant conclusions may be drawn from this character. Fauvel states (1923, p. 312), that the capillary chaetae (Fig. 1D, *e*, in this paper), occur singly in all segments posterior to the third chaetigerous segment, but in the Chalkwell worms they were found to occur singly in every parapodium in larvae and young worms, but were often missing from older individuals. The type shown in Fig. 1D, *b* was never found in young stages, but was fairly common in older worms, and in the ventral bundles of the parapodia in the males.

McIntosh (1908) gives the rather lengthy synonomy of *A. prolifer*, but in the light of the present work it is doubtful how many of the descriptions do, in fact, refer to this species.

Reproduction and Development

The pelagic female of *A. prolifer* has already been described and figured by previous authors (Slabber, 1778; Krohn, 1852, 1855; Max Müller, 1855; Malaquin, 1890, 1893; McIntosh, 1908; Fauvel, 1923; Thorson, 1946).

There seems to be no fixed breeding season (Jensen, Johansen & Levinsen, 1904, pp. 286, 296; McIntosh, 1908, 1927; Allen, 1915; Thorson, 1946), although a spawning maximum probably occurs in late spring and early summer, as many of the records of the occurrence of specimens in the plankton refer to the period between April and July. At Chalkwell, stoloniferous forms, pelagic forms, and larvae were all found during June.

A few descriptions and figures of the larvae ascribed to *A. prolifer* are also scattered through the literature. Max Müller (1855) figures larvae from the egg-sac, and gives the size of the ripe egg as 50 μ, and a young achaetous larva with two segments as about 200 μ in length. McIntosh (1908) gives a figure of a larva which could refer to almost any syllid, and his later drawings (1927) do

not in the least resemble the larvae described here. Okada (1929), however, figures a larva rather more than 100 μ long, only slightly less advanced than the youngest stage found at Chalkwell, and although the smallest stage found here was about 300 μ in length, it showed only one more segment delimited. Okada's general remarks on the structure of syllid larvae apply to these larvae of *A. prolifer*.

It may be concluded that the eggs are small (100 μ or less in diameter) and develop into young achaetous larvae while still in the egg-sac suspended from the ventral surface of the female. Their pelagic life is probably not very long, and although they appear to undergo no great morphological differentiation during this period, they increase greatly in size and may treble their length. Martinus Slabber (1778) figures larvae emerging from the egg-sac of a female, and these larvae are already composed of head, pygidium, and two achaetous segments, and correspond with the youngest stage described here. On settling, they are still achaetous, and are about 300 μ in length (Fig. 3A). The body consists of a head region formed from a prostomium bearing an akrotroch anterior to two red eye spots, and a prominent prototroch posteriorly, which apparently corresponds to the buccal segment containing the pharynx. Okada (1929) could not distinguish these two parts of the head (prostomium and buccal segment), but they were clearly visible in the Chalkwell larvae. The pharynx lies entirely within the buccal segment, and does not project backwards into the peristomial segment which remains achaetous throughout life, and at this stage bears a prominent ciliary band (Okada's 'interparatroch'). The peristomial segment is followed by the future first chaetigerous segment, in which the chaetae may be seen developing internally (Fig. 2C), and which also bears a ciliary band. A further, relatively undifferentiated segment may be seen between this and the pygidium. A telotroch is not present, and does not develop until later, but the whole of the ventral surface is clothed with short cilia. Before the chaetae have been erupted from the first chaetigerous segment, two pairs of eyespots have been formed (Fig. 3), and a third pair, the most lateral in position, which remain without lenses, are added when three or four chaetigerous segments have been formed.

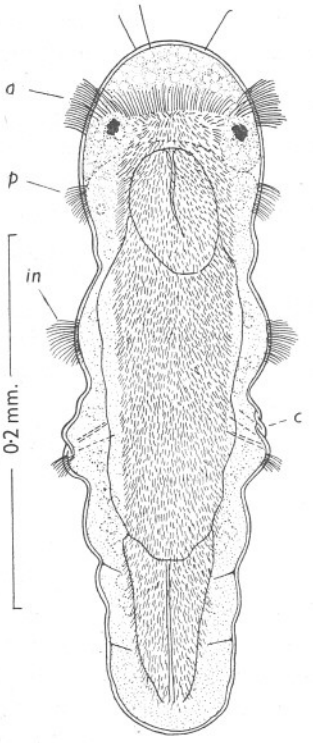

Fig. 2. *Autolytus prolifer*, young achaetous larva (ventral view) *a*, akrotroch; *in*, interparatroch; *p*, prototroch; *c*, first chaetigerous segment (chaetae not yet erupted).

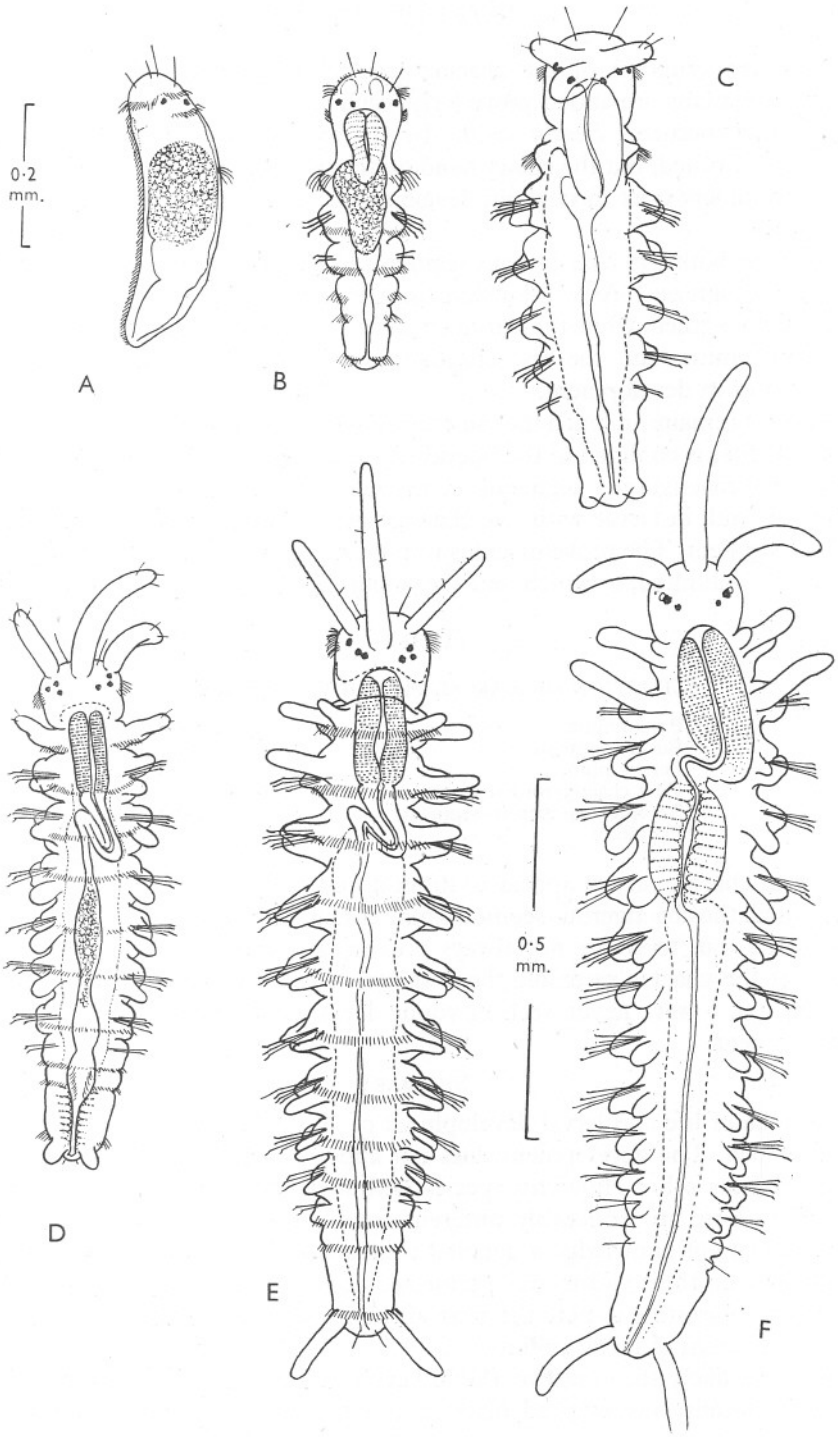

Fig. 3. *Autolytus prolifer*. A, a slightly later stage than in Fig. 2, seen in side view, showing two pairs of eyespots, and the ventral ciliation; B, larva with two chaetigerous segments (dorsal view); C, larva with five chaetigerous segments (dorsal view); D, young *Autolytus* with seven chaetigerous segments (dorsal view); E, a slightly older stage with nine chaetigerous segments (dorsal view); F, young *Autolytus* with thirteen chaetigerous segments, showing the proventriculus (dorsal view).

After the eruption of the chaetae from the first chaetigerous segment, further segments are added posteriorly, each segment bearing a ciliary band. A telotroch becomes clearly visible by the time two chaetigerous segments have been formed, but the ciliary band on the peristomial segment remains the most prominent tract throughout development. The ciliation is summarized in Table I.

In larvae with two chaetigerous segments (Fig. 3B), the prostomial tentacles may be recognized. As will be seen from Fig. 3B–F, the prostomial tentacles gradually lengthen, while the dorsal cirri and the supplementary tentacles from the peristomium and the first chaetigerous segment gradually lengthen out rather later in development.

The gut remains in much the same condition for some time, but the pharynx, which at first is confined to the buccal segment, extends backwards. In larvae with two chaetigerous segments it extends into the achaetous peristomial segment, and, in larvae with five chaetigerous segments, into the first chaetigerous segment. The proventriculus is not formed until ten or eleven segments have been delimited, by which time the young *Autolytus* is over 1 mm. in length.

TABLE I

CILIATION OF LARVAL *AUTOLYTUS PROLIFER*

Head	Prostomium	Akrotroch
	Buccal segment	Prototroch
	Peristomium	Interparatroch
	First chaetigerous segment	Ciliary band
	Second chaetigerous segment	Ciliary band
	Pygidium	Telotroch

Larval chaetae do not appear to differ appreciably from those of the adult. At first, all the chaetigerous segments may contain a chaeta of the type shown in Fig. 1D, *e*, but these are not always present, and are often, apparently, lost. Most of the chaetae resemble those shown in Fig. 1D, *c*, *d*, but those similar to Fig. 1D, *b* were never seen in young larvae, and appear to arise later in development.

SUMMARY

The mode of life and larval development of *Autolytus prolifer* (O. F. Müller) is described. The development does not appear to differ markedly from that described for other *Autolytus* species, although the larvae which have been described here are noticeably different from those of other species. In the present state of knowledge a detailed comparison is impossible. Most of the work done on these worms was performed about 50 to 100 years ago, and it is therefore interesting to note the general confirmation of the views of Okada on the constitution of larval syllids.

It seems likely that most of the life cycle is normally passed on a hydroid —in the locality investigated on a species of *Obelia*. There is probably no

specific relationship, since these worms have been found on seaweeds and other objects.

Mucous glands are well developed, and the young larvae adhere strongly to the perisarc of the hydroid, even when unprotected by a tube. These tubes, which ramble amongst the branches of the host colony, are semi-transparent, straw coloured, and unbranched, and may be inhabited by several animals. During the winter when the hydroids die back, the worms presumably hide under stones or migrate to deeper water.

In the adults, anatomical features such as the form of the pharynx, position of the proventriculus, the relative lengths of the prostomial tentacles, and the number of segments in the male without natatory chaetae, all usually considered of taxonomic importance, have been found to be variable. Apart from the coloration, which is lost on preservation in alcohol, the number of the pharyngeal teeth alone distinguishes the species from *A. auriantiacus* Clap.

The male form collected from Chalkwell has six segments without natatory chaetae, behind the head. It is likely that the number varies between three and six.

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