

THE ANATOMY OF THE BODY WALL AND
APPENDAGES IN *ARENICOLA MARINA* L.,
ARENICOLA CLAPAREDII LEVINSEN AND
ARENICOLA ECAUDATA JOHNSTON

By G. P. Wells

Department of Zoology, University College, London

(Text-figs. 1-21)

CONTENTS

	PAGE
Introduction	1
Methods	3
The main regions of the body	5
The body wall and appendages	9
The general structure of the body wall	9
The middle region ('trunk')	14
The anterior region ('head')	25
The posterior region ('tail')	37
Summary	41
References	42
Appendix: list of abbreviations used in the text-figures	44

INTRODUCTION

The anatomy of *Arenicola* has often been monographed. The best-known works are those of the series with which the names of Gamble and Ashworth are associated (Gamble & Ashworth, 1898, 1900; Ashworth, 1904, 1912). Unfortunately, these accounts are not fully satisfactory. They are sometimes incorrect; they omit all reference to many points of considerable functional interest; and they lack descriptive rigour (for example, although Gamble & Ashworth, 1900, point out that the blood vessels of *Arenicola* are arranged on an obvious segmental plan, none of these works attempts to bring out the fact by adopting a nomenclature based on serial homology). Now the lugworm is an excellent laboratory polychaete, and, because of its size, abundance and hardiness (at least during the cooler months), affords suitable material for many researches. A revision of its general anatomy is therefore desirable. The following account of the body wall and appendages was undertaken as a contribution to this end; a study of the internal anatomy is in preparation.

My first intention was to limit the description to *A. marina*, the commonest species around Great Britain and the one with which I am most familiar. On reflexion, however, the decision was taken to include two other species as well. The family Arenicolidae consists (according to Ashworth, 1912, with whose classification subsequent authorities are in substantial agreement) of two

genera only, *Arenicola* and *Branchiomaldane*. The first is made up of eight species, to which Berkeley & Berkeley (1939) have subsequently added a ninth; they fall quite clearly, from an anatomical point of view, into three groups. The second consists only of a single species of small and aberrant animals. Now to describe only *Arenicola marina* would result in a work of very limited usefulness, more particularly as the species is restricted to the cooler shores of the northern hemisphere; on the other hand, by including the three species *marina* L., *claparedii* Levinsen¹ and *ecaudata* Johnston, each representing one of the sections into which the genus naturally falls, an idea can be given of the general organization and also the range of variation found in this world-wide group. I hope later to publish notes on the other species; briefly, *grubii* most nearly resembles *ecaudata*, *assimilis* is most closely related to *claparedii*, though differing from it in several important points, and the rest group themselves with *marina*.

The descriptions are based mainly on material collected by myself—*marina* at Plymouth, at Bangor, North Wales, and at Thorpe Bay on the Thames Estuary; *claparedii* at Naples, where my expenses were partly defrayed by a grant from the Challenger Society; and *ecaudata* at Plymouth. I have also a small number of *claparedii* from the Pacific Coast of U.S.A., sent, very ill-preserved, by an American dealer. By the courtesy of Mr H. W. Parker I have been allowed to examine the collection of Arenicolidae in the British Museum (Natural History); this remains, with a few additions, substantially as catalogued by Ashworth (1912).

The following study is concerned with gross morphology, not histological detail. As far as possible, some indication will be given of the functional significance of the structures described. With *marina*, the habits of the worm are well known and such interpretations can often be made. This species lives in great numbers in muddy sand flats, where the piles of sandy cylinders, its faeces, and the saucer-shaped or funnel-shaped depressions, caused by its eating away the sand below, are familiar to everybody. It sometimes occurs in less typical habitats, for example, in gravel or among stones, provided there is a certain amount of muddy material to eat. Under favourable conditions, it inhabits the same burrow for weeks or even months at a stretch, swallowing the sand at one end of the burrow and depositing it as faeces at the other. The form of the burrow, and the behaviour of the worm, have been described in detail elsewhere (Wells, 1945, 1949*b*, 1950; Newell, 1948).

¹ *A. claparedii* Levinsen is probably identical with *A. pusilla* Quatrefages. The original definition of the latter species is inadequate and conflicts with the characters of the type specimen. The type was examined by Ashworth, who identified it as an incomplete specimen of *claparedii*, atypical as to the number of nephridia. He therefore merged both species under the older name of *pusilla* (Ashworth, 1912). The great majority of later writers term it *claparedii*, and Fauvel (1927) explicitly rejects Ashworth's proposal, not denying the identity of the two species, but because of the inadequacy of the definition of *pusilla* and the aberration of the type specimen.

Of *claparedii*, Ashworth (1912) wrote: 'The general habits of this species, which the writer had an opportunity of observing in Naples for some weeks, are similar to those of *A. marina*. Examples taken by Prof. A. D. Howard in Puget Sound were found generally in ordinary sandy beaches, but two larger specimens were burrowing in a coarse gravelly and rocky beach.' Describing the occurrence of *claparedii* on Vancouver Island, Berkeley & Berkeley (1932) write: 'It evidently occurs over large stretches of the sand exposed at low tide at Long Bay, judging by the enormous number of casts to be found.' Takahashi (1934) describes it as living in U- or V-shaped burrows, of depth 15-25 cm., the openings 3-10 cm. apart; in certain bottoms, the burrows of *marina* may be very like this (Wells, 1945). Now *claparedii*, while resembling *marina* in its general structure, differs in two points that one would expect to be of great functional importance; it lacks statocysts, and it lacks giant nerve fibres. The similarity of its way of life to that of *marina*, which the above citations suggest, makes these differences the more surprising. The breeding habits of *claparedii* are rather different in Canada and in Japan, according to the accounts of Guberlet (1934) and Okuda (1938).

For *ecaudata*, we have the following account by Ashworth (1912): 'It occurs in the littoral zone but chiefly in sandy, gravelly or muddy material among stones, or in clefts at the base of the rocks in the debris formed by the breaking down of the latter. A considerable amount of organic matter is generally present in the material in which the worm lives. The burrows of *A. ecaudata*...are oblique or sinuous cavities, lined with a fair amount of mucus, and situated a few inches below the surface in gravel or between rocks and stones. The castings of the worm, being composed of coarse material having little coherence, soon fall apart. The well-known signs—the sand-ropelike heap of castings and the funnel-like depression in the sand—which indicate the presence of *A. marina* on countless sandy beaches, have no good counterparts in the case of the ecaudate species, in which both the castings and the mouth of the burrow are inconspicuous among their surroundings.' Fauvel (1899*a*) comments on the occurrence of *ecaudata* in black, often foetid, sandy material between rocks at Cherbourg; the galleries are more or less sinuous and often horizontal; their walls are never yellow, as those of *marina* are. The worms are found at Plymouth in just such situations as these authorities describe, and it appears that the striking differences of structure between *marina* and *ecaudata* are paralleled by equally striking differences of habit.

METHODS

Preparation of worms for dissection

Ashworth (1904) recommends that lugworms should be killed with chloroform and dissected fresh, under sea water, 'as soon as possible after they are taken from the sand'. I find that formalin material, dissected within a week or

so of killing, is very much better. Fresh worms bleed easily and freely, while in formalin material the blood sets into a firm, uniform gel, so that such operations as the removal of the whole or part of a ventricle can be performed with ease. Moreover, the septa and other membranes of fresh worms are so transparent that their relations are hard to make out. The slight cloudiness which appears in formalin material is a great improvement.

The animals used in the present study were killed in either of two attitudes, 'relaxed' or 'distended'.

Relaxed worms. The worms are narcotized by immersion in a large volume of $7\frac{1}{2}\%$ $MgCl_2$. The time taken varies with the size of the worm; *marina* about 10 or 15 cm. long is fully relaxed in $3\frac{1}{2}$ or 4 hr. They are then transferred to a bath of $7\frac{1}{2}\%$ $MgCl_2$ containing 4% formaldehyde. At this stage, they may show slight movements, so it is as well to do the killing in a rectangular tank, and, if necessary, to straighten the worms against the side with a glass rod. They die in a very natural configuration. The body is straight (except for a slight ventral curvature of the first few segments). The proboscis is generally withdrawn. The worms can be stored in formalin until required. The organs usually retain quite a lot of their colour for some days, and even after months of preservation, such material is easy to dissect.

Distended worms. The worms are narcotized as above, then distended, one by one, in the following way. A cannula is connected by rubber tubing to a funnel; the whole is filled with the Mg-formalin mixture, and the tubing is closed with a screw clamp. The level of fluid in the funnel should be 15–20 cm. above the bench. The cannula is then tied into the tail, pointing forwards; it must go into the coelome, not the gut, and the way to ensure this is to insert it into an incision made in the lateral aspect of the tail. The worm is then tumbled into a long tank of the Mg-formalin mixture, and immediately distended with the same solution, by opening the screw clamp. A surprising degree of stretch is produced, and although the resulting attitude is highly unnatural, the distension straightens out the septa and other organs and greatly facilitates the study of their relationships. The proboscis is fully extruded.

Preservation for museum purposes

As many of the specimens to be found in museum collections are ill-preserved, and in very distorted attitudes, so that even their external characters are hard to make out, it may here be pointed out that worms killed in the 'relaxed' attitude, as directed above, are very suitable for museum purposes. Alcohol makes the worms rather hard, and they may easily break on handling.

Serial sections

Before sectioning, the worms were killed in Mg-formalin in the relaxed attitude, then at once transferred to Susa. The following techniques were found useful:

(i) 15 μ paraffin sections, stained with haematoxylin-eosin or Hansen's trioxyhaematin followed by Mallory's phosphomolybdic acid-aniline blue-orange G mixture, and mounted in balsam.

(ii) 100 μ celloidin sections, very lightly coloured with haematoxylin and orange G, and mounted in balsam without removal of the celloidin.

(iii) 300 μ celloidin sections, mounted unstained in glycerine jelly without removal of the celloidin.

In general, and especially when dealing with the front end of the worm, the horizontal plane is more useful than the sagittal.

Special methods

Polarized light is invaluable for working out the arrangement of the muscles. It can be used on sections, or on such objects as pieces of the body wall of distended worms, spread out flat and cleared. To avoid the necessity of turning the slide on the stage, which makes the working out of complicated muscular networks rather tricky, I have mounted two Polaroid disks, 7 in. in diameter, on a common vertical axle. One goes above, and the other below, the stage of my binocular microscope; by turning the axle, the plane of polarization of the light can be rotated without disturbing the specimen.

Spectacular preparations of the vascular system can be made by choosing unpigmented or lightly pigmented worms, distending them, then rapidly dehydrating the whole worms and clearing them in benzyl alcohol, in which they are kept.

When studying the movements of living worms, they should be placed in glass tubes; a suitable arrangement for this purpose was described elsewhere (Wells, 1945).

THE MAIN REGIONS OF THE BODY

Arenicola shows very clearly the tendency, which generally appears in sedentary polychaetes, to differentiate the chain of fundamentally similar segments, of which their body consists, into distinctively specialized regions.

The common lugworm, *A. marina*, has 19 segments with parapodia (rarely 20), and, although these segments show certain local specializations (gills restricted to segments vii-xix, nephridia restricted to iv-ix, etc.),¹ they are all built on a very evident metameric plan. These 19 segments together occupy the middle of the body and form a comparatively unspecialized region from which the two extremities stand out in marked contrast. Anterior to the first chaetigerous segment, there is a short, bluntly conical region, composed of the prostomium and one or two segments which have lost their appendages—one according to Lillie (1905), and two according to Ashworth (1904, 1912). The whole of this region is welded into a functional and structural unit, mainly in connexion with proboscis activity, and its metamerism is hard to make out.

¹ Roman numbers are used to identify particular segments.

At the hinder end of the body is the conspicuous 'tail', again composed of segments which have lost their appendages, and apparently lengthening continually backwards; in young animals at least, from reserve segments at its base (Fig. 1 A). We may therefore describe the body of *marina* as differentiated

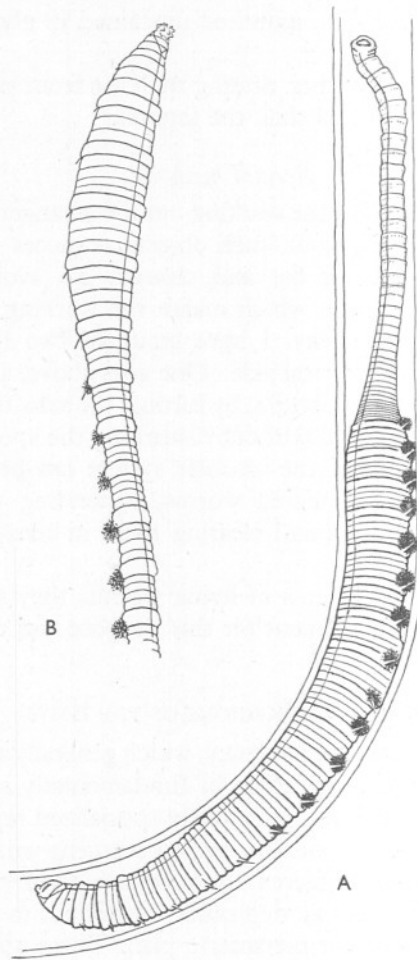


Fig. 1. *Arenicola marina*. A, a healthy individual lying, head downwards, in a glass observation tube. Most of the chaetigerous segments are pressed, laterally and ventrally, against the walls of the tube, but are separated from it by a narrow space on the dorsal side. Waves of swelling, which occlude this space, are travelling gently headwards and so driving water through the tube; one such wave is passing the 5th and 6th gills. B, the 'clubbed' attitude, which often appears in moribund specimens.

into three very distinct regions—an achaetous anterior region, or 'head', a chaetigerous middle region, or 'trunk', and an achaetous posterior region or 'tail'. The middle region shows various subsidiary differentiations, with

regard to the distribution of gills, nephridia, etc., among its component segments.

The body of *claparedii* resembles, in all the above respects, that of *marina*. In *ecaudata*, the differentiation between 'head' and 'trunk' occurs as in the other species, but the specialized third region appears, at first sight, to be lacking. The worm has a great number of segments and the parapodia and gills continue as far as, or nearly as far as, the hinder extremity. There are, however, indications of a differentiation corresponding to, though less profound than, that between 'trunk' and 'tail' in the other species (p. 37).

The above method of describing the regional organization of *Arenicola* differs from that generally adopted in the literature. Audouin & Milne Edwards (1834) wrote of *marina* as 'composé de trois portions assez distinctes: l'une antérieure, ordinairement renflée et ne portant pas de branchies, une moyenne, étroite et branchifère, et une postérieure, apode'. The anterior region, in this account, includes the 'head' and the first six chaetigerous segments. The majority of subsequent writers, down to the present day, have adopted this method of subdividing the worm. Ashworth (1904) instructs his students to 'note the shape of the worm; its division into an anterior abranchiate chaetigerous portion, middle branchiate chaetigerous region and posterior achaetous and abranchiate tail'. Fauvel (1927) describes *marina* thus: 'Région antérieure à 6 segments uncinigères abranches. Région abdominale à 13 sétigères, branchifères. Région caudale achète et abranche de longueur variable, fragile.' The gills have also been used to characterize the regions of *ecaudata*. 'Le corps', wrote Fauvel (1899*a*) of this species, 'se divise en deux parties: 1° la région antérieure ou thoracique qui comprend le prostomium, le segment buccal, un segment post-buccal achète et 15 ou 16 segments pourvus de parapodes et de tores uncinigères mais abranches; 2° la région abdominale dont tous les segments portent des parapodes et des branchies sauf parfois les 1 à 7 derniers qui sont abranches mais toujours sétigères.'

It seems to the writer, that the method of subdividing the body with reference to the gills is rather misleading. Of the various divergent specializations which differentiate the segments of *Arenicola* from each other, some are extremely constant and fixed in position, not only from individual to individual but also from species to species. Such, for example, are the persistence of septa i, iii and iv of the middle region as the well-known 'diaphragms', or the elaboration of the vessels of the (vanished) septum vii to form the ventricles, closely applied to the gut and separating its oesophageal from its gastric part. Others, on the other hand, fluctuate; for example, the nephridia are always restricted to a limited number of segments, but the number and position along the body of the segments concerned varies, not only from species to species but also to some extent from individual to individual. When seeking for criteria of regional differentiation, one should clearly choose characters of the former kind; yet the distribution of the gills, which so many

authorities use, is of the latter. In the 'caudate' species, i.e. in all those with an achaetous 'tail', the most anterior gill is typically on segment vii, and the division between abranchiata and branchiate regions therefore coincides with the position of the hearts and boundary between oesophagus and stomach. In the so-called 'ecaudate' species (*ecaudata* and *grubii*), the most anterior gill lies several segments farther back, though the cardiac and enteric differentiations remain at the same level as before. Even in the caudate species, including *marina*, 'the first gill is almost invariably small, and in a considerable percentage of examples, is reduced to minute proportions or is absent' (Ashworth, 1912). The same is true of *ecaudata*. Evidently, the boundary between abranchiata and branchiate regions is by no means a rigidly fixed one, and when more constant intersegmental differentiations are available, there is no justification for subdividing the body on the basis of the distribution of the gills. The division into 'head', 'trunk' and 'tail', described above, is undoubtedly the most profound of the local specializations exhibited by *Arenicola*, and is merely obscured by throwing together the 'head' and the first few 'trunk' segments into an 'anterior abranchiata chaetigerous portion'.

In conclusion, a word may be said about the 'renflée' and 'étroite' of Audouin & Milne Edwards' description, cited above. One sometimes finds lugworms in which the first half a dozen or so segments are distended and the rest of the trunk is narrowed by contraction of the circular muscles. The worm as a whole is therefore club-shaped (Fig. 1B). One never sees this attitude in vigorous, healthy worms, but only in dead or moribund specimens. It is very common in worms which have been badly collected, for example, in a hot, overcrowded jar. I believe its assumption to be an irreversible process, and a sign of approaching death; if any of the worms in my stock tanks exhibit it, they are thrown away before they die and foul the water.

The point would be hardly worth mentioning, were it not that 'clubbed' worms have appeared very often in the literature. The 'renflée' and 'étroite' in Audouin & Milne Edwards's description, together with their Pl. 8, fig. 8, show unmistakably that their worms were in the 'clubbed' attitude. Grube (1851) also refers to the anterior part of the body as 'mehr oder minder aufgebläht'. More recently, a beautifully drawn figure of a 'clubbed' worm was published by Cunningham & Ramage (1888) and reproduced in the well-known *Handbuch* of Kükenthal-Krumbach (Hempelmann, 1934, p. 191). A striking example is to be found in the *Cambridge Natural History* (Benham, 1896, p. 333). In healthy worms, however, or in those prepared by the Mg-formalin method, no trace of 'clubbing' can be seen. When we bear in mind, first, that the part of the body which distends in this abnormal attitude is also the pre-cardiac or 'anterior abranchiata' part, and, secondly, that many of the early authorities based their descriptions on specimens thus distorted, we may infer that the 'clubbed' attitude has some responsibility,

historically, for the idea that the boundary between abranchiate and branchiate regions represents a differentiation of major importance.

THE BODY WALL AND APPENDAGES

The account of the body wall follows the division of the body as a whole into three regions, as explained in the last section. The general plan of the body wall, common to all the regions, will be described first.

THE GENERAL STRUCTURE OF THE BODY WALL

The body wall is divided externally into *annuli*, separated by *interannular grooves*. The position of the nerve cord is marked externally by a conspicuous, pale *ventral groove*, in *marina* and *claparedii* but not in *ecaudata*.

The body wall consists of the following layers: (i) epidermis, (ii) sub-epidermal connective tissue, (iii) circular muscle, (iv) a layer of intermuscular connective tissue, which is brought out prominently by the aniline blue of Mallory's triple stain, (v) longitudinal muscle, (vi) coelomic epithelium. A series of oblique muscles, of the usual polychaete type, is generally present (Fig. 2). The body wall is richly vascularized, and one can generally see in sections that the blood vessels lie in tubular spaces; these are extensions of the coelome, penetrating into the body wall.

The *circular muscle layer* is interrupted by a radial partition of connective tissue at each interannular groove (Fig. 5C-E, p. 17). According to Lillie (1905), the circular muscles develop very much later than the longitudinal in *A. cristata* Stimpson—a species very similar to *marina*.

If one takes a piece of body wall from a distended specimen, clears it, spreads it flat on a slide, and then examines it between crossed polaroids, rotating the slide relative to the plane of polarization, one finds that the whole of the musculature at any given point on the body wall, both circular and longitudinal, blacks out in the same position. This means that the musculature of the general body surface consists *only* of these two series of fibres, whose molecules are orientated truly at right angles to each other. There can be no diagonal or spirally running fibres, as occur, for example, in several Oligochaeta.

The fibres of the *longitudinal layer* are grouped, in *marina* and *claparedii*, into a great number of longitudinal columns; each covered by coelomic epithelium. These columns branch and anastomose with their neighbours, and form a conspicuous and characteristic background when one dissects either of these species (Fig. 3A-C). In *ecaudata*, on the other hand, the body wall presents a smooth appearance internally; the longitudinal layer is covered over by a continuous peritoneal sheet which is only occasionally perforated or grooved to accommodate a blood vessel (Fig. 3D).

In all species, certain *lines of separation* can be traced in the longitudinal layer, which are important anatomical landmarks. They are usually evident in

dissections, and are especially obvious in distended material. They appear, in *ecaudata*, as longitudinal clefts in the layer, and in *marina* and *claparedii* as deep grooves between adjacent muscle columns, across which anastomoses seldom or never occur. The lines are (Fig. 2): (i) the *ventral line*, in which the nerve cord (*n.c.*) lies; (ii) the *nephridial lines* (*neph.l.*), at the level of the nephridiopores; (iii) the *notopodial lines*, (*notop.l.*), through which the inner ends of the notopodia protrude into the body cavity; and (iv) the *dorsal line*

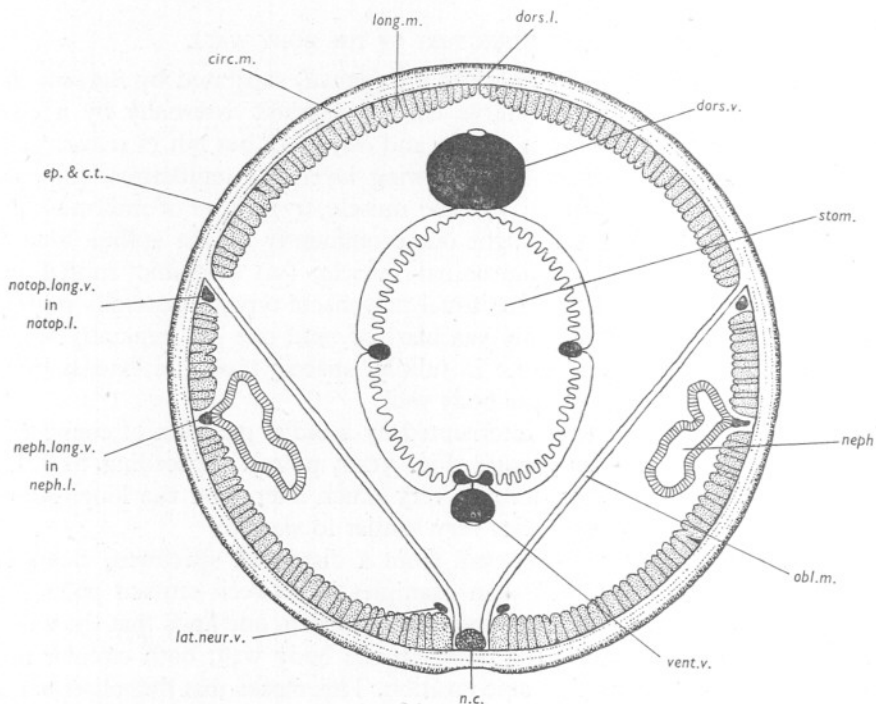


Fig. 2. *Arenicola marina*. Transverse section of an ordinary annulus, drawn from a section slightly anterior to the eighth chaetigerous annulus. For explanation of the lettering on the figures, see list on p. 44.

(*dors.l.*), into which the dorsal mesentery, where present, is inserted. The ventral, notopodial and dorsal lines are always present, and may perhaps divide the longitudinal musculature into functionally distinct fields. The nephridial lines are more variable; they are evident along the whole length of *ecaudata*, and in the trunk, but not the tail, of *marina*. In *claparedii*, they can be made out only in the immediate neighbourhood of the nephridia.

The *ventral nerve cord* is rounded in section and without segmental enlargements. It gives off a pair of interannular nerves in each interannular groove; these nerves run round the body to unite dorsally and so form a hoop enclosing

the body. They lie in the connective tissue partitions which divide the circular muscle layers in the interannular grooves (Fig. 5C-E, *interann.n.*). There is also a special outflow of nerves in each chaetigerous annulus, details of which have not yet been traced. The cord itself consists of a deep (dorsal) fibrous part and a superficial (ventral) ganglionic part. A giant fibre system is present in *marina* and *ecaudata*, but not in *claparedii*. Details of the giant fibre system

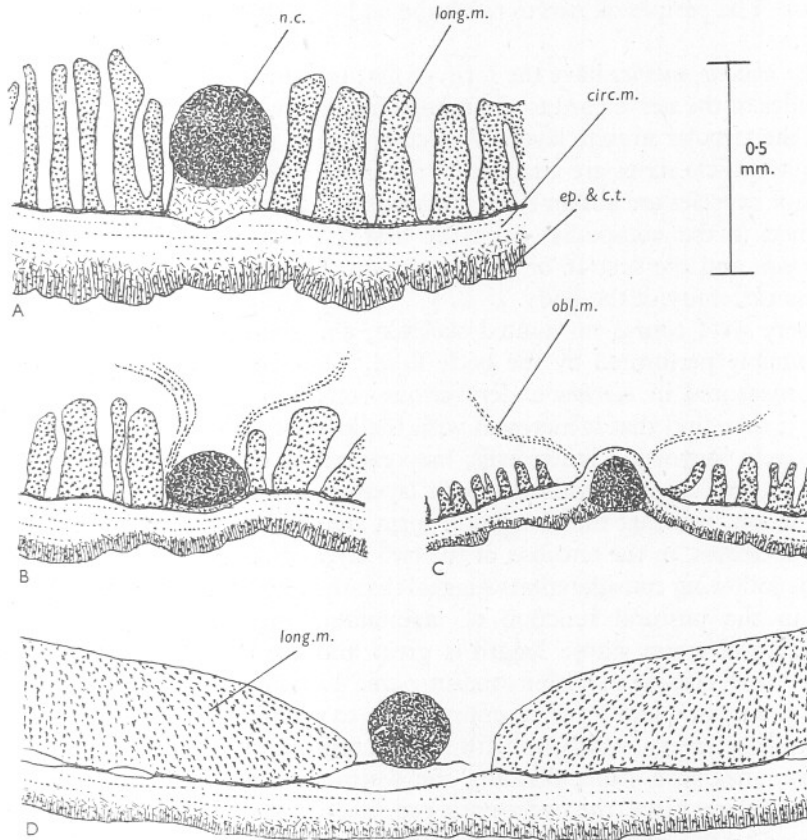


Fig. 3. Transverse sections through the body wall of ordinary annuli, in the region of the ventral nerve cord. A, *marina*, segment iii; B, *marina*, segment xviii; C, *claparedii*, segment xiv; D, *ecaudata*, segment xiii. Lettering as on p. 44.

are given by Gamble & Ashworth (1898, 1900), by Ashworth (1904) and by Nicol (1948).

The position of the nerve cord relative to the layers of the body wall varies from species to species. The most primitive condition is presumably that found in *claparedii*, where it lies superficial to the circular muscle layer and in intimate relation with the epidermis (Fig. 3C). In the other two species, the

cord lies deep to the circular muscle layer.¹ In *marina*, it is separated from the circular layer by a pad of connective tissue, staining conspicuously blue with the aniline blue in Mallory's triple stain, and thicker in the anterior segments of the body than farther back (Fig. 3 A, B). In *ecaudata*, this pad is absent, and an extensive coelomic space separates the cord from the circular muscle (Fig. 3 D). The cord is held in position by a membranous sheet running laterally to the longitudinal muscle layer, and perforated in many places to allow blood vessels to pass. The peripheral nerves reach the body wall by way of this membranous sheet.

The *oblique muscles* have the form of flat, translucent strips. They run from the sides of the nerve cord to the notopodial line, where their fibres enter, and join, the circular muscle layer. Particularly thin, thread-like members of the oblique muscle series are attached to the inner ends of most of the notopodia. Oblique muscles are absent from the heads of all species, and (except for those attached to the notopodia) from the first 3 trunk segments of *marina* and *claparedii* and the first 16 or 17 of *ecaudata*. Thereafter they continue to the hinder extremity of the body.

There is of course no jointed skeleton, and the main skeletal function is presumably performed by the body fluid. The pressure in the coelome has been measured in *marina* under various conditions by Chapman & Newell (1947); they find that it increases with the level of activity of the worms and, in actively burrowing individuals, may exceed 30 cm. of sea water. We may suppose that in active animals, both layers are in a state of sustained tonic contraction, and that the changes of form are produced by local increases, or local decreases, in the tensions of the two layers.

The following considerations suggest that the circular layer plays the greater part in the postural function of maintaining internal pressure. Suppose a cylindrical worm whose length is great and the thickness of whose body wall is small compared with its radius r cm. Let the pressure in its body fluid be P g. wt./cm.², and let it be entirely due to the tensions in the circular and longitudinal layers, which, as with surface tension, we call S_C , S_L g. wt./cm.

Now imagine a plane dividing the worm transversely. If no change of shape is taking place, the hydrostatic pressure acting over the area of section is balanced by the longitudinal muscle tension round the circumference, and we have

$$\pi r^2 P = 2\pi r S_L \quad \text{or} \quad S_L = \frac{1}{2} Pr. \quad (i)$$

¹ Ashworth (1904) writes of *marina*: 'In some specimens the cord in the tail and in the last chaetigerous segment lies only just below the epidermis.' I find, on examining serial sections of the tails of seven worms, that the cord lies deep to the circular muscles in all but one. In the single exception, the cord seems in some sections to lie as in *claparedii* while in others it is embraced by the circular muscle, the latter running both superficial and deep to it. This is much the smallest worm of the seven (tail diameter 1.1 mm.) so the appearances may represent a migration during development from the primitive to the final position. This specimen has the cord deep to the circular muscle in the chaetigerous segments.

Now imagine the worm divided by a longitudinal plane passing through its long axis. This time, the pressure is balanced by the circular muscles, and, if the length is l cm., we have

$$2rlP = 2lS_C \quad \text{or} \quad S_C = Pr. \quad (\text{ii})$$

Combining (i) and (ii)

$$S_C = 2S_L. \quad (\text{iii})$$

How far do these considerations apply to a real *Arenicola*? In the first place, the muscle layers have a measurable thickness; this is, however, not great compared with the radius and its effect will be to apply a small correction to the quotient 2 in equation (iii). Secondly, the oblique muscles may have a postural function; they are, however, very thin, and absent from a fairly considerable stretch of the body in *ecaudata*; and we may note, in passing, that septa and mesenteries are lacking over most of the trunk in all species. Thirdly, the body fluid is not the only skeleton. Isolated branchiate segments of *marina*, lying in a watch-glass of sea water, often undergo regularly rhythmical changes of shape, not perhaps very extensive but perfectly visible and corresponding in timing with the waves that traverse the body, when water is being pumped through the tube. This observation shows that there is a certain amount of elasticity in the body wall itself, though it seems probable that this factor plays only a minor role in the intact worm. Finally, there is the skeletal function of the surrounding mud. The movements of *marina* in glass tubes have been studied by various authors (Just, 1924; van Dam, 1937, 1938; Wells, 1944, 1945), and will be treated in a later section. For the present, we need only note that there appears to be an inverse relation between the degree of activity of the worm and the proportion of its surface which makes contact with the tube. At one extreme, it may be completely at rest: in this posture, the body is short and thick and presses against the tube with its whole surface; thus the relationships discussed above obviously do not apply. At the other, it is creeping actively forwards or backwards: the body is extremely elongated and at all points away from the tube, except that waves of swelling run along it, grip the tube, and so act as fixed points; here, as the waves follow each other fairly rapidly, the trouble lies in the assumption that no change of shape is taking place.

Evidently, equation (iii) is not to be taken as precise. It may, nevertheless, point in the right direction. Lugworms kept in glass tubes often show a regular alternation of rest and rhythmic activity. The resting worms are short and thick, and the onset of an activity outburst is accompanied by lengthening and narrowing of the body (Wells, 1949*a*). Spontaneous activity is also associated with an increase in internal pressure (Chapman & Newell, 1947). The phasic responses to stimulation are suggestive in this connexion. A nocuous stimulus may produce sudden shortening of the head or tail, or curving of the body (Just, 1924)—results evidently due, in the main, to

longitudinal muscle contraction. If a worm is creeping into a tube, and an attempt is made to pull it out backwards, it expands its front end very abruptly to grip the tube, a movement which suggests circular muscle inhibition. The data as a whole suggest that, in an active worm, the circular muscles are fairly highly contracted and the longitudinals less so; the phasic acts, whether reflexly or spontaneously produced, are mainly, at least, in the sense of longitudinal contraction and circular inhibition.

Fox (1949) has pointed out that the muscles of *Arenicola* contain haemoglobin, but does not discuss whether there is any inequality of distribution between the muscle layers. For the other pigments of the body wall, the works of Fauvel (1899*b*) and Lignac (1945) may be consulted.

The epidermis is richly provided with unicellular gland cells. The skin secretes mucus, which is used, in *marina*, to impregnate the wall of the burrow and keep it firm (Osler, 1826; Linke, 1939). The mucus of *ecaudata* is particularly copious, as anyone who has handled the living worm is aware. If specimens of *marina* are kept in the laboratory, the water comes to contain 'belts' of greyish mucus, of about the same diameter as the worms; these belts are sometimes seen round their bodies; they appear to be passed slowly headwards and to be a means of getting rid of such unwanted residues as the breakdown products of old chaetae. When handled, the lugworm produces a fluorescent, greenish yellow secretion, which stains the fingers and is also rather irritating.¹

THE MIDDLE REGION ('TRUNK')

As the middle region of the body is in many ways the least specialized of the three, it will be taken first.

Arenicola marina

The trunk of this species consists of 19 segments (in exceptional individuals, 20). They exhibit a certain amount of structural and functional divergence. Each segment includes several annuli, of which one, the *chaetigerous annulus*, is larger than the others and bears the parapodia and gills. The chaetigerous annuli are shown white in Fig. 4. The boundaries between segments are given internally by septa, or, where the septa have disappeared, by the septal blood vessels. The septal planes correspond approximately, though not quite exactly, to the second groove behind each chaetigerous annulus: in other words, the penultimate annulus of each segment is chaetigerous.

Typically, any two chaetigerous annuli are separated by 4 ordinary annuli, so that the number of annuli per segment is 5. In the first 3 segments, however, the number of annuli is reduced. The first has 2, the second 3 and the third 4, except that in a 'laminarian variety', described by Gamble & Ashworth (1898), the third has 3. The fourth, and all subsequent trunk

¹ The worm as a whole has a characteristic fragrance, especially when laid open. After he had worked on it for some years, it produced strong allergic symptoms in the writer (catarrh, asthma); this was put right by a course of injections.

segments, have 5 each. The rule, that the chaetigerous annulus is penultimate, holds for the anterior segments in spite of this reduction.

Ashworth gives no attention to the possible systematic usefulness of these numbers. It is true of all *Arenicola* species, that the majority of the trunk segments have 5 annuli, and that some degree of reduction occurs at the front

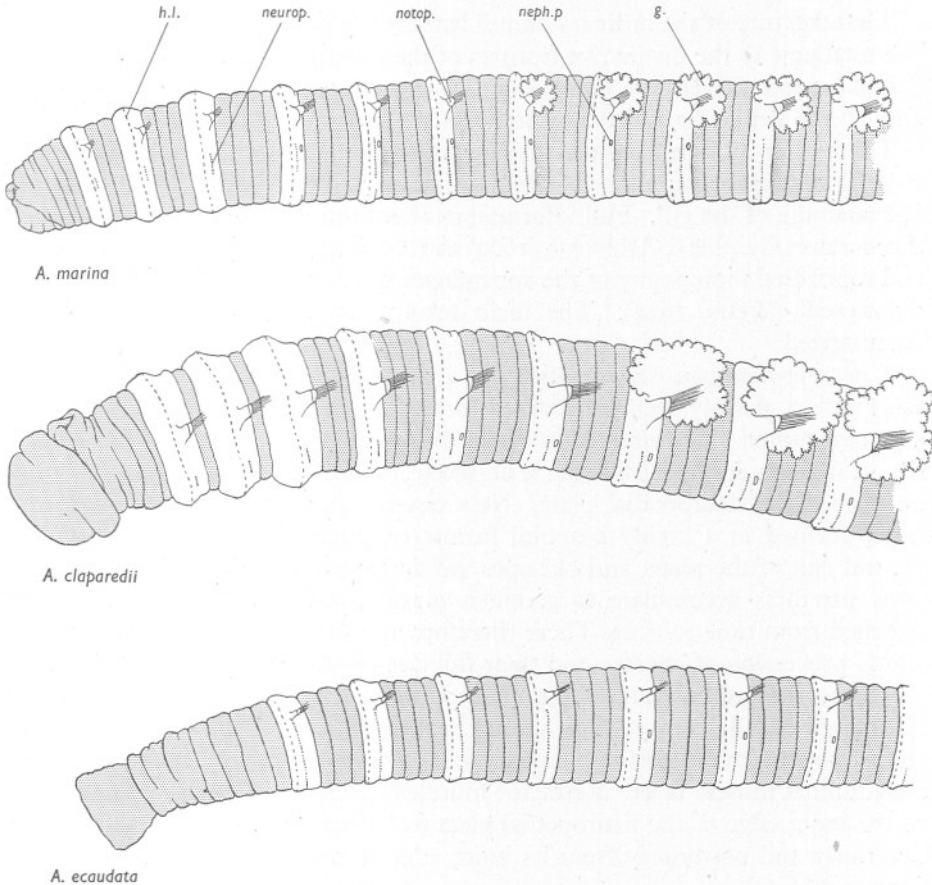


Fig. 4. Lateral views of the front ends of the three species, to show the annulation and the characters of the chaetigerous annuli and appendages (white). The proboscis is withdrawn in the *marina* and extended in the other two. Lettering as on p. 44.

end. The extent of this reduction is not always the same, and I find that each of the species now under examination has a fairly constant and characteristic annulation formula, which holds for all the range of material which I have been able to examine (p. 2).

The most convenient way of describing the reduction is to use serial Roman figures for the chaetigerous annuli, and to put between them, in Arabic

figures, the numbers of intervening ordinary annuli. Thus the typical formula for *marina* is:

i.2.ii.3.iii.4.iv.4.v ...

While the 'laminarian variety' is:

i.2.ii.2.iii.4.iv.4.v ...

The structure of the ordinary annuli has already been sufficiently described. We turn now to the distinctive features of the chaetigerous annuli. These are: (i) the neuropodia, (ii) the notopodia, (iii) the parapodial girdles, (iv) the gills, and (v) the nephridia and nephridiopores.

The earlier authorities were mainly interested in the characters supposed to be of systematic importance—the detailed form of the chaetae, and the mode of branching of the gill. Full information about these points is to be found in the works of Gamble & Ashworth (1900) and Ashworth (1912). The musculature and functional topography of the appendages were described, for *marina* only, by myself (Wells, 1944). The main results for that species will now be summarized.

A *neuropodium* consists essentially of a single dorsi-ventral row of chaetae, each with a sharply inclined rostrum projecting from the body surface and a gently curved shaft embedded in the body wall (Fig. 5A, B). Each chaeta lies in its own epithelial follicle. The whole row of chaetae and follicles may be termed the neuropodial plate. New chaetae and follicles are continually being formed in a highly basophil formative region (Fig. 5A, *form.*) at the ventral end of the plate, and old ones are destroyed at the dorsal end, where their products accumulate as greenish masses (*dest.*). These are somehow expelled from time to time. There therefore appears to be a continual dorsalwards procession of chaetae and their follicles along the neuropodial plate.

To see the musculature of the neuropodium, longitudinal sections, cut at right angles to the body surface, should be studied (Fig. 5C). The inner end of the neuropodium projects into a cavity, cut off from the general coelome by the longitudinal muscle layer. Retractor muscles run from the longitudinal layer to the outer edge of the neuropodial plate (*ret.m.neurop.*), and protractors run anteriorly and posteriorly from its inner edge to the neighbouring body wall (*prot.m.neurop.*).

The neuropodia of the more anterior segments are very short dorsi-ventrally, but they lengthen from segment to segment until, from segment x or xi backwards, they extend from a point slightly above the nephridial line to the side of the nerve cord (Fig. 4).

I know of no published description of the movements of the neuropodial chaetae. They could obviously be protracted to some extent by the protractors, and withdrawn again by the retractors, if the substance of the annulus is sufficiently flexible. I am, however, inclined to guess that another movement is more significant. Simultaneous contraction of the posterior protractors and

anterior retractors would tend to incline the chaeta as a whole, so that its inner end would move backwards relative to its outer; at the same time, owing to the form of the chaeta and the position in which it normally lies in the neuropodial plate, it would rotate so that the rostrum points forwards (Fig. 5A, B). Similarly, the anterior protractors and posterior retractors could turn the rostra backwards. The usefulness of this movement, in facilitating the ratchet or gripping function of the neuropodia when the worm is creeping along the tube, needs hardly to be stressed.

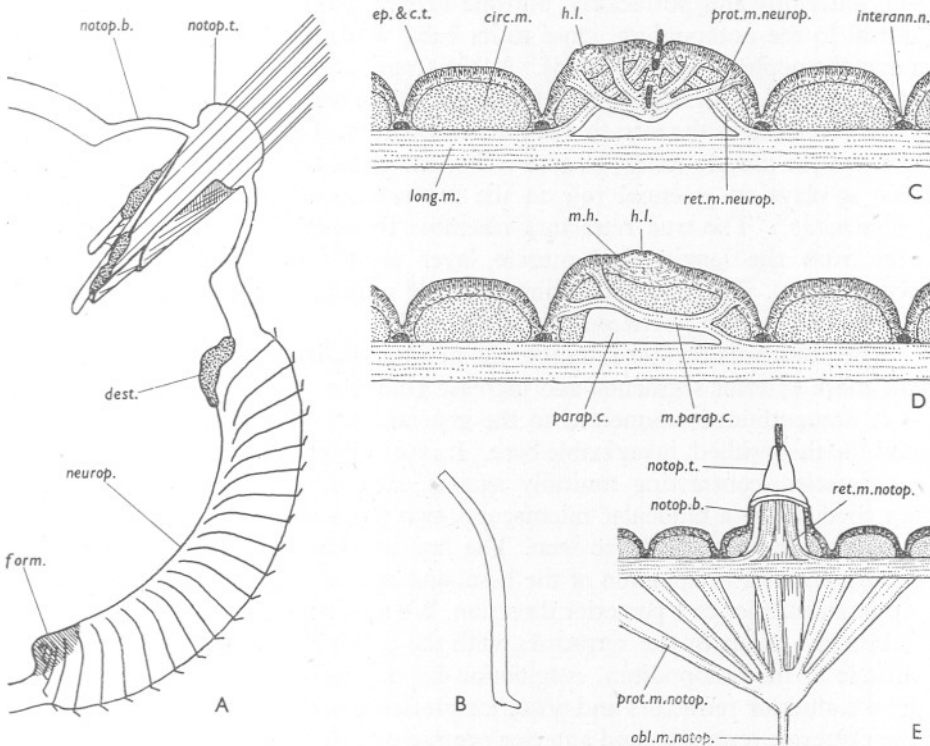


Fig. 5. *Arenicola marina*. Diagrams of the parapodia. A, the essential structure of a notopodium (above) and a neuropodium (below). B, a neuropodial chaeta. C, longitudinal section through one of the hinder neuropodia, at right angles to the body surface. Two ordinary annuli are also included. D, sagittal section through one of the first three chaetigerous annuli, near the mid-dorsal line. E, the muscles of a notopodium, exposed by a longitudinal cut through the body wall passing through its base. Lettering as on p. 44.

A *notopodium* can be regarded as a modified neuropodium. In external view, a dorsi-ventrally flattened tip (Fig. 5A, E, *notop.t.*) can be distinguished from a thin-walled, evaginable base (*notop.b.*). The chaetae are very long and emerge from the tip in two closely applied, parallel rows. To derive a notopodium from a neuropodium, the plate must be supposed to have duplicated itself into two plates lying close side by side like two leaves of a book, and then the inner

corners of the double plate to have been folded and rolled forwards, giving the inner end of the whole a somewhat scroll-like appearance (Fig. 5A). The resulting structure is complicated and not easy to visualize. Full details of the notopodium and its musculature were given elsewhere (Wells, 1944).

The inner end of the notopodium protrudes through the longitudinal muscle layer into the general body cavity. The protractor muscles radiate from this end to the surrounding body wall (Fig. 5E, *prot.m.notop.*). Most of these run anteriorly and posteriorly, but one or two are inserted on the body wall dorsal to the notopodium, close to its base, while others spread ventrally as far as the nephridial line (Fig. 6). A thin strand of muscle generally runs from the inner end of the notopodium to the side of the nerve cord, and this has often been described as the retractor of the notopodium. It is evidently a member of the oblique muscle series; and, as it is quite often absent, we cannot suppose that it plays an essential role in the movements of the podium. (Fig. 5E, *obl.m.notop.*). The true retractors resemble those of the neuropodium; they run from the longitudinal muscle layer to the notopodial tip (Fig. 5E, *ret.m.notop.*). There are also thin sheets of muscle sheathing the notopodial plates, and running between their inner ends.

The notopodia further resemble the neuropodia in that they are smallest in the more anterior segments, and increase gradually in size posteriorly.

A notopodium is connected to the general body wall only by the muscles and the thin-walled, invaginable base. It must therefore be held in position by its muscles, contracting tonically against each other. If a living worm is watched under a binocular microscope, two types of movement of the notopodium can very readily be seen. The first is retraction and protraction, i.e. invagination or evagination of the base, and the second is the direction of the tip in an anterior or a posterior direction. We may conjecture that invagination is brought about by the retractors, with the possible assistance of the oblique muscle of the notopodium, evagination by the protractors, anterior pointing by the anterior retractors and posterior protractors, and backward pointing by the posterior retractors and anterior protractors. A high pressure of the body fluid will tend towards evagination. From the arrangement of the muscles, it would also be possible to swing the tip dorsally and ventrally, and perhaps to rotate the podium on its own long axis, but I am not aware that such movements have been witnessed or described.

The *parapodial girdle* is a name now proposed to cover a group of special features of the chaetigerous annulus to which I drew attention elsewhere (Wells, 1944). These features are best seen in a sagittal section through one of the first three segments, somewhere near the dorsal line (Fig. 5D). The chaetigerous annulus stands out at once in such a section, because it contains a conspicuous cavity, the 'parapodial canal' (*parap.c.*). This canal runs right round the annulus, and is separated from the general body cavity by the

longitudinal muscle columns, and by a connective tissue sheet on which they rest. It communicates with the general cavity only at the notopodial, nephridial and ventral lines (Fig. 6). Outside the parapodial canal is a special longitudinally directed musculature, arching in the main from the front to the rear half of the annulus, but also running into the longitudinal layer posteriorly ('muscles of the parapodial canal', Fig. 5D, *m.parap.c.*). If now one looks at the surface of one of these annuli, one sees that it is girdled by a pale line, usually elevated as a slight ridge (Fig. 4, *h.l.*); this is the 'hinge line' and under it, in the subepidermal connective tissue, a series of fine, antero-posteriorly running muscles can be detected ('muscles of the hinge', *m.h.*). All of these structures run right round the annulus, except only for the ventral line, where it is crossed by the ventral groove.

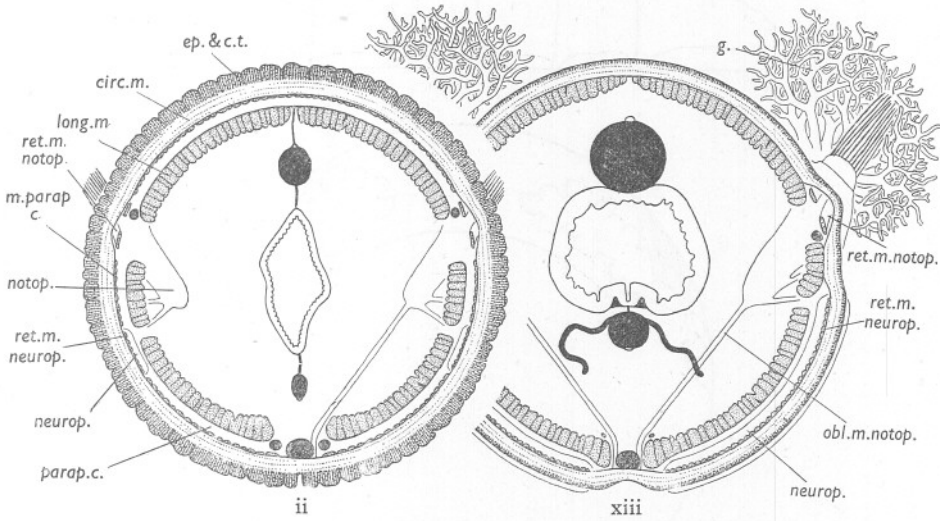


Fig. 6. *Arenicola marina*. Transverse section through chaetigerous annuli ii and xiii. The worm was transected in front of the appendages, and drawn with a binocular: the appendages are therefore seen just beyond the plane of section. Compare Fig. 2. Lettering as on p. 44.

We have already seen that the neuropodia and notopodia are small in the more anterior segments, and increase in size as one passes backwards. Just the opposite is true of the parapodial girdle (Fig. 4). The hinge line approaches more and more closely to the front of the annulus in segments iv-viii, and at the same time the parapodial canal and the two special musculatures decrease in importance and move with it. At first sight, each of these chaetigerous annuli looks rather like two; the front part is raised and swollen by the parapodial girdle, while the hinder part is flatter, like the rest of the body wall. Finally, from segment ix onwards, the parapodial girdle disappears altogether from the dorsal part of the annulus.

Now, on comparing C, D and E in Fig. 5, it will be seen that there is a considerable degree of resemblance between the musculatures of the notopodium, of the neuropodium, and of the parapodial canal. The two former can be regarded as derived, in part at least, from the latter. The cavity in which the inner end of the neuropodium lies is clearly a part of the parapodial canal (Fig. 6), and by analogy the invaginable notopodial base can also be so derived. In other words, the parapodial girdle persists in the hinder segments, but only in connexion with the notopodia and neuropodia. The hinge line can be seen, running down the front of the neuropodium, on many of the hinder segments, but it fades as one passes back, and is usually quite invisible on the last four or five.

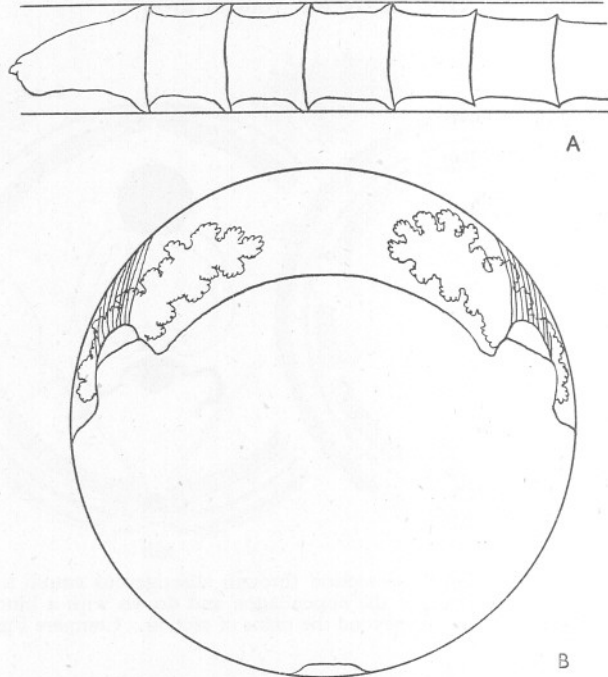


Fig. 7. *Arenicola marina*. A, the elevation of the anterior chaetigerous annuli. B, diagrammatic section of a worm circulating water through a tube, as in Fig. 1A.

There is no doubt at all about the importance of the parapodial girdle of the more anterior chaetigerous annuli as a motor apparatus. If a *marina* is put into a large funnel of sea water, with the lower end of the stem closed with rubber tubing and a clamp, the worm usually burrows down into the stem, and the movements of the more anterior chaetigerous annuli can then be watched. At one moment they lie flat; then they are suddenly raised, and apparently distended, into the form of sharp, backwardly directed flanges; then they drop again (Fig. 7A). The whole apparatus seems to act as a single unit, i.e. all of the 'parapodialized'

annuli, and the whole periphery of any one of them, rising and falling together, though the movements are most evident in the first three segments, in which the responsible structures are best developed. The movements are used in burrowing, to grip the sand and help to draw the worm in, and also, apparently, for certain other purposes, such as the drawing of surface sand down into the head end of the burrow (Wells, 1944).

The *gills* are hollow, branched, contractile outgrowths of the body wall, borne by the chaetigerous annuli just behind the notopodia, and present on every segment from vii onwards (Fig. 4). The most anterior gill is smaller than the rest and may be lacking altogether on one or both sides. For details of the mode of branching of the gills, the works of Ashworth (1904, 1912) may be consulted.

The sphinctered *nephridiopores* open just behind, and very slightly below, the upper ends of the neuropodia, on segments iv to ix inclusive. According to Goodrich (1946) the 'nephridium' of *Arenicola* is a nephromixium and includes an ectodermal component which should logically be described with the rest of the body wall; it will, however, be included with the internal anatomy, which the writer hopes to describe in a later paper.

We turn now from the various components of which the body wall of the trunk consists, to the plan of the region as a whole. It can be divided, on structural grounds, into the following three sections (Fig. 4):

(i) Segments i, ii, iii. Gills absent. Neuropodia and notopodia small and apparently unimportant. Parapodial girdles massively developed round the whole circumference of the chaetigerous annuli.

(ii) Segments iv to viii. Graded, transitional.

(iii) Segments ix onwards. Gills present. Neuropodia and notopodia well developed. Parapodial girdle absent, except in connexion with the neuropodia and notopodia.

Now this structural differentiation is very nicely paralleled by a physiological one. The movements of *marina* were first studied in detail by Just (1924), who pointed out that the first three or four segments (the boundary is not absolutely sharp) stand in functional contrast to the rest. His observations have been confirmed and extended by others (van Dam, 1937, 1938; Wells, 1944, 1945). In burrowing, in forwards or backwards creeping, and in the driving of water through the burrow, waves of swelling travel along the trunk. These waves may go in either direction and their form varies with the particular type of movement that is being carried out. At all times, however, they concern the hinder 15 or 16 segments, and (though the amount of worm they involve varies to some extent with the type and vigour of the movement) they are seldom, if ever, shown by the first three. Proboscis activity, on the other hand, is brought about by the integrated action of the proboscis itself, of the body wall of the head, and of the body wall of the first three trunk segments.

If a worm is watched quietly pumping water through a glass tube (Fig. 1), the ventro-lateral surfaces may be noticed, over most of the trunk, to be pressed tight against the tube; a space remains, however, between the dorsal surface and the tube, and the gills spread out into this space. Waves of swelling travel along the dorsal surface, occluding the space and so driving water through the tube; the gills contract as the waves approach and expand again as soon as they pass. A rather conjectural cross-section of a worm in the act of irrigation, based on watching worms in glass tubes from the side, is drawn in Fig. 7B. The problem at once arises, of how the close pressing of the flanks against the tube is achieved. The only possible answer, I think, is by means of the notopodial protractors. It will be seen from the drawing, that the contact could be maintained if the notopodia were pressing outwards and upwards. Meanwhile, the head and first few segments (which are not concerned in the irrigation waves, and in which the notopodia are poorly developed) arch away from the side of the tube (Fig. 1).

In active creeping, as Just (1924) described, the notopodia exert a ratchet action, being directed backwards for headward locomotion, and forwards for tailward locomotion. We may fairly safely guess that the neuropodial rostra play a similar role. When swimming, the worm travels tail first, with lateral waves of great amplitude travelling headwards along the body, while the notopodia are directed headwards and held close to the body surface. The podia are never used as oars or paddles, or even as punt poles; they are bracing and anti-slip devices.

It seems, then, that the neuropodia and notopodia are adapted to assist in those wave movements which are the concern of the hinder segments, and it is in those segments that they are best developed. The first few trunk segments are specialized, partly to help in the extrusion of the proboscis by driving their contained body fluid forwards (Just, 1924) and partly for the flanging movement described above. The great development of the parapodial girdles which the latter function involves appears to carry with it a reduction in the size of the neuropodia and notopodia, and the disappearance of the gills. It is indeed striking, in a view of the whole worm, that the gills appear just as the parapodial girdles leave the dorsal faces of the chaetigerous annuli (Fig. 4).

Arenicola claparedii.

The general organization of the body wall of the trunk is the same in the other two species as in *marina*; it is therefore only necessary to note divergences.

An immediately obvious feature of *claparedii* is the enormous development of the first three chaetigerous annuli (Fig. 4). In the living worm, the movements of these annuli are like those of *marina* in type, but very much more powerful and impressive. The anatomical features which distinguish these annuli are correspondingly well developed. At the same time, this expansion has entailed

a great reduction in the ordinary annuli of the anterior segments. I find the following formula, in my Neapolitan specimens:

i. 1. ii. 1. iii. 3. iv. 4. v. ...

The hindmost of the 3 annuli between iii and iv is generally much smaller than the others. Some of the American specimens at the British Museum have a second annulus between ii and iii; it is however always very small and may

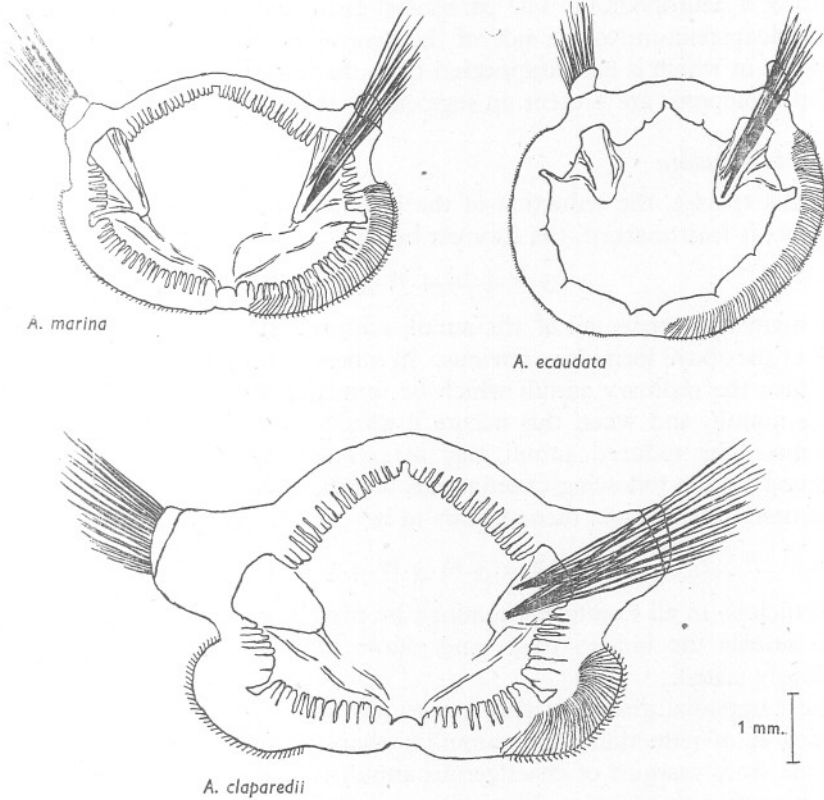


Fig. 8. Drawings, all to the same scale, of chaetigerous annulus xvi in each of the three species. Drawn from cleared specimens of the isolated annuli. The full extent of the chaetae is shown on the right, the projecting portions only on the left.

not extend round the whole circumference of the worm. In others, chaetigerous annulus iii hangs forwards in such a way that a minute ring might be present but hidden. We seem to be concerned here with an annulus in process of disappearance; and the variations described below for *ecaudata* support the idea that it is always immediately in front of the chaetigerous annuli that reduction occurs.

In a posterior direction the parapodial girdle is seen to leave the dorsal surface after segment vi—so, although the girdle is better developed than in *marina*, it embraces rather fewer segments.

The notopodia are more massive in *claparedii* than in *marina*, and so are the individual notopodial chaetae. The neuropodia are short in the more anterior segments and lengthen posteriorly, but they never approach the ventral line as closely as in *marina* (Fig. 8). Even in the hinder segments, the ventral ends of the neuropodia are separated by a distance about equal to the length of a neuropodium. The parapodial girdle extends from the lower end of the neuropodium to the side of the ventral groove, even in those hinder segments in which it has disappeared from the dorsal surface.

Nephridiopores are present on segments v to ix inclusive.

Arenicola ecaudata

In this species, the reduction of the ordinary annuli of the more anterior segments is least marked, the formula being:

$$i.3.ii.4.iii.4.iv.4.v \dots$$

In many specimens, all of the annuli are prominently developed, and the truth of the above formula is obvious. In others, however, there is a tendency to reduce the ordinary annuli which lie immediately in front of the chaetigerous annuli, and when this occurs it affects all of the first three or four segments. The reduced annuli may in extreme cases be so small, and so overhung by the following chaetigerous annuli, as to be invisible on surface inspection. The formula then appears to be:

$$i.2.ii.3.iii.3.iv.4.v \dots$$

Nevertheless, in all examples examined by myself, a sagittal cut with a razor blade reveals the hidden rings, and shows that the formula is in fact as previously stated.

The parapodial girdles of this species are rather poorly developed, as the low degree of reduction of the annuli perhaps suggests. The hinge lines lie near the front margins of chaetigerous annuli i—iii, instead of bisecting them as in the other two species. The various components of the parapodial girdle are all present, but they are small, and all localized in the front part of the annulus. In a posterior direction these structures get gradually less and less well defined, until they can no longer be made out on the dorsal surface, as from about segment xiv. In other words, although less well developed than in the other species, they concern about twice as many segments. Now the most anterior gill, in *ecaudata*, is typically on segment xvi; as in *marina*, this gill is generally small and sometimes absent. The whole arrangement evidently confirms the idea, already suggested by the other two species, that the gills and the parapodial girdles tend to exclude each other from the dorsal surface.

The notopodia are relatively smaller, and more dorsally placed, than in the other species (Fig. 8). The neuropodia are exceedingly long, extending from the side of the nerve cord to a point well above the nephridial line. In the more anterior segments, far from being short (as in *marina* or *claparedii*), the neuropodia of *ecaudata* are best developed, and reach from the ventral line to the bases of the notopodia (Fig. 4).

Nephridiopores are present on segments v to xvii.

THE ANTERIOR REGION ('HEAD')

The 'head' is the roughly conical region extending forwards from the anterior margin of the first chaetigerous annulus (Fig. 4). Its segmentation is largely obscured, in the adult, by its profound functional modifications. It consists of the prostomium and a second large portion which, to quote Ashworth (1912),

in most adult specimens of *Arenicola*, is divided by encircling grooves into three or four (or more) rings. There are good reasons for stating that this is composed of the peristomium and a body segment which is without chaetae in the adult. In post-larval stages of *A. marina* and *ecaudata*, the region between the prostomium and the first ordinary chaetiferous segment is subdivided by a groove into two parts. The anterior and usually rather smaller portion is undoubtedly the peristomium; it never bears chaetae, but the paired statocysts may be seen near its anterior margin. The posterior of the two parts is, in the post-larval stages which the writer has examined, achaetous, but a chaeta has been observed in this segment, in either *A. marina* or *A. ecaudata*, by Professors Ehlers, Benham, Mesnil and Fauvel, a fact which demonstrates that this is a true segment. Evidence confirmatory of this interpretation is afforded by the arrangement of the giant nerve cells. In later post-larval stages in which the annulation is making its appearance, the peristomium and the segment in question become subdivided into secondary rings... The composition of this region is probably constant throughout the family.

Except for the important study of the statocysts by Ehlers (1892), previous writers on this region have mainly confined themselves to cursory accounts of its external features, and discussions of its segmental homology. Many interesting features, especially the musculature, have received little or no attention. The following account omits the proboscis, and certain special structures (e.g. the retractor muscle) associated therewith. I hope to describe them, with the internal anatomy in general, at a later date.

Arenicola marina

Apart from the absence of parapodia, the most noteworthy specializations of the body wall of the anterior region may be grouped under the following headings: (i) the mouth, (ii) the prostomium and nuchal pouch, (iii) the central nervous system, (iv) the metastomial muscle, and (v) the statocysts.

At the *mouth*, which is terminal, the layers of the body wall continue on to the eversible proboscis. The latter organ is partly extruded in Figs. 9 and 10.

The *prostomium* may be completely withdrawn into the *nuchal pouch*, which lies behind it. The general relations of these structures can be seen in Figs. 9–13. The pouch (*nuch.p.*, Figs. 10B, 13) opens by a crescentic slit just above the prostomium (*prost.*); its roof is thin and flexible; its floor is the prostomium itself. The later organ, when fully exposed, has roughly the form of an

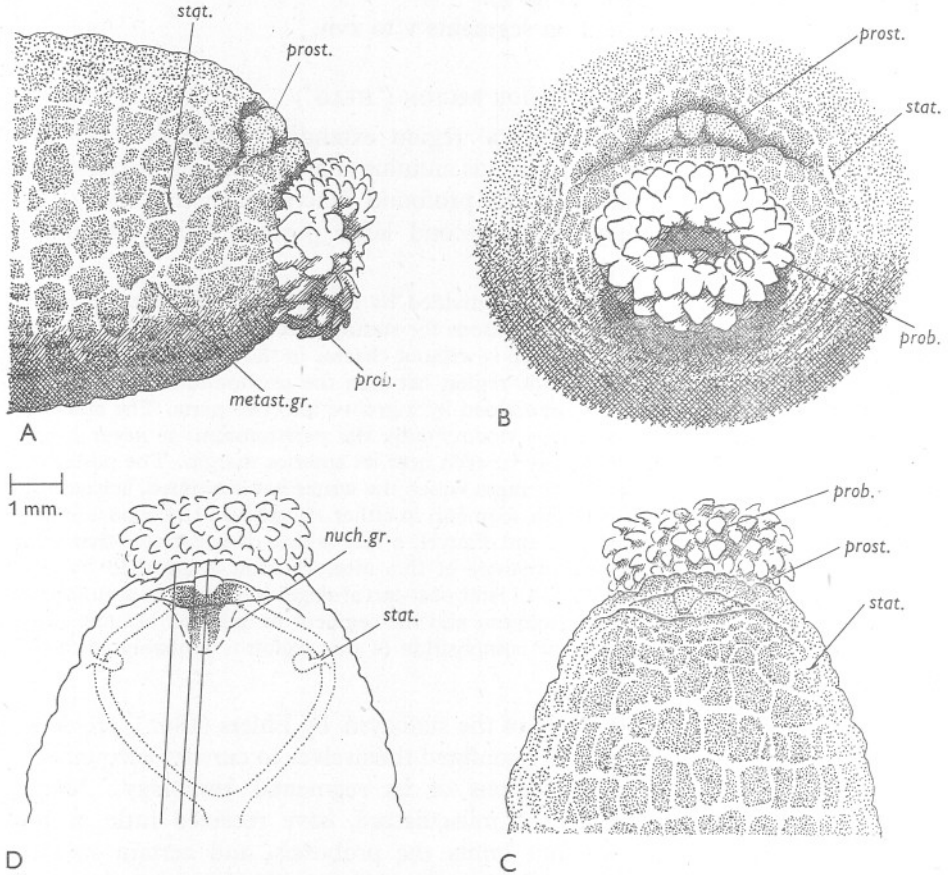


Fig. 9. *Arenicola marina*. Lateral view (A), anterior view (B) and dorsal view (C) of a specimen killed in the relaxed attitude by the Mg-formalin method. D, outline of the dorsal view, with the positions of the brain and oesophageal connectives included; that part of the brain which adheres to the dorsal surface of the prostomium is stippled; the nuchal groove is shown as a dashed line; the ruled lines give the positions of the sections in Fig. 12. Lettering as on p. 44.

isosceles triangle with its apex directed backwards; its dorsal face is impressed by a shallow Y-shaped groove (Fig. 10A). The worm must, however, be dissected if the whole prostomium is to be seen. In preserved material, it is always more or less completely overlapped by the dorsal lip of the nuchal pouch, so that one sees only its anterior margin; this is trilobed, owing to the

fact that the arms of the dorsal, Y-shaped groove continue down the anterior face of the prostomium. Between the prostomium and the mouth is a strip of body wall, which Ashworth (1912) terms the 'upper lip'.

The nuchal pouch as a whole may be regarded as a blind in-pushing of the epidermis and subjacent connective tissue, passing through the circular and longitudinal muscle layers. In sections, a large amount of transversely running muscle can be seen immediately ventral to the prostomium. Its position and course suggest that it is circular muscle; in fact, however, as will be shown below, it is made up of certain specialized muscles, derived, largely at least, from the longitudinal layer (the metastomial muscle, and the dorsal muscle of

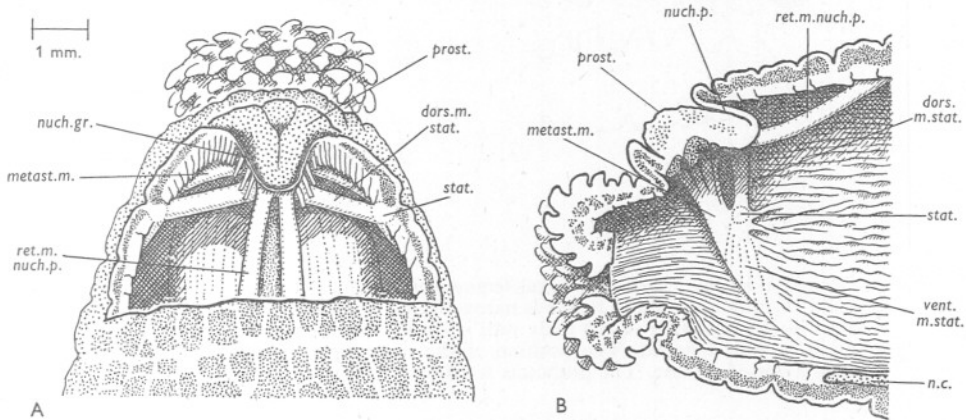


Fig. 10. *Arenicola marina*. A, dorsal dissection of the animal of Fig. 9; part of the body wall and the thin roof of the nuchal pouch have been removed. The front part of the dorsal vessel (stippled) can be seen between the retractors of the nuchal pouch. B, lateral dissection of another worm to show the coelomic aspect of the body-wall muscles of the right side; the animal has been bisected in the median plane and the gut and blood vessels have been removed. The ventral muscle of the statocyst is seen as a series of fine strands (dotted lines) running ventrally across the face of the metastomial muscle. Lettering as on p. 44.

the statocyst). The columns of the longitudinal layer pass by the sides of the nuchal pouch, and those immediately adjacent to it send slips which are inserted on its walls and help in its retraction. The chief part in retraction, however, is played by a paired muscle, the retractor of the nuchal pouch, clearly derived from the longitudinal layer, and running from the hind end of the pouch to a point on the body wall, about half way between the prostomium and the first chaetigerous annulus (Figs. 10 and 13, *ret.m.nuch.p.*).

My impression is that retraction of the nuchal pouch never occurs as an isolated act, but only when the anterior end as a whole is shortened and thickened, as part of the general movement. There are no protractor muscles. Extrusion of the proboscis is presumably due to the pressure of the body fluid, and occurs, I believe, whenever the head as a whole lengthens and narrows, and at no other time. Fig. 11, drawn from preserved specimens, illustrates

two configurations within the range that can be seen in the living animal. When the living worm assumes the extended attitude, the roof of the nuchal pouch evaginates and can be seen as a crimson transverse ridge, just behind the prostomium.

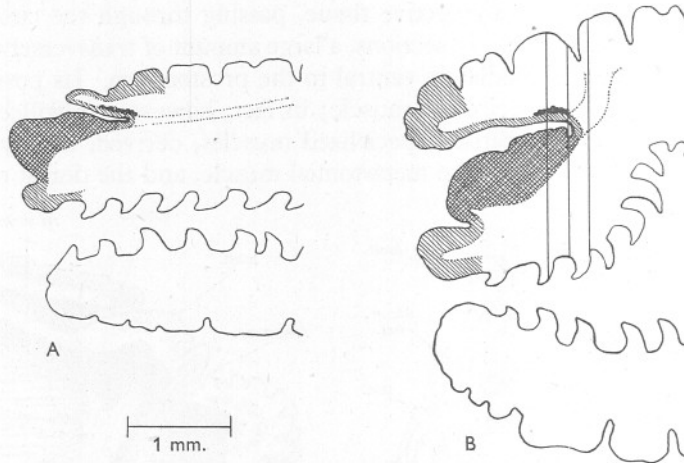


Fig. 11. *Arenicola marina*. Median sagittal sections of specimens killed as follows: A, in Mg-formalin; B, in Bouin without previous narcosis. The ruled lines in B give the planes of the sections in Fig. 13. Part of the body wall is shaded to show its thickness, and the prostomium is cross-hatched. The position of the retractor muscle of the prostomium is given as a dotted outline. The proboscis is fully withdrawn in both specimens.

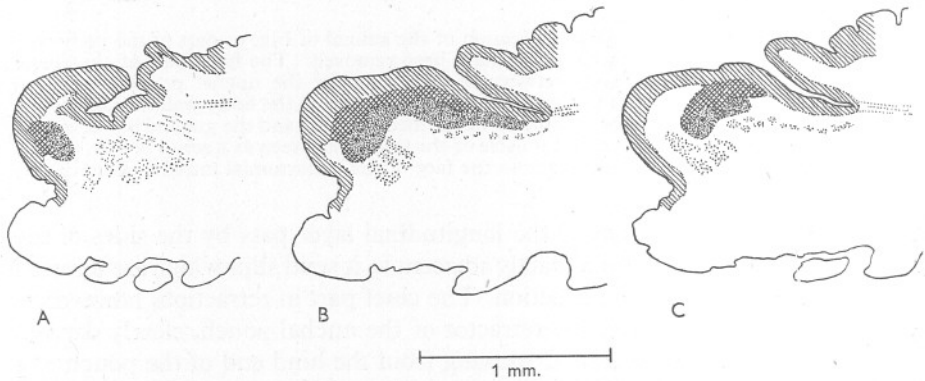


Fig. 12. *Arenicola marina*. Sagittal sections of a Mg-formalin specimen, corresponding approximately to the ruled lines in Fig. 9D. The proboscis is fully withdrawn. The superficial (ganglionic) part of the brain is cross-hatched, and the deep (fibrous) part is closely stippled. Section C is median.

The hinder part of the roof of the nuchal pouch bears a curious vascular plexus, shown black in Fig. 11. This marks what is evidently an important structural differentiation of the roof. In the region of the plexus, the roof consists of a very deep columnar epithelium without a subjacent muscular

layer. Elsewhere, it has a shallower epithelium and a thin circular muscle layer, continuous with the circular muscle layer of the general body wall. Now in the other two species, as we shall see, the prostomium cannot be retracted, and its hinder margin is marked by a nuchal groove, whose epithelium is very deep, ciliated and presumably sensory. This evidently corresponds to the hinder, vascular part of the roof in *marina*. The non-vascular part, present only in *marina*, is simply attenuated body wall, and it is this which converts the whole region into a pouch and makes retraction of the prostomium possible.

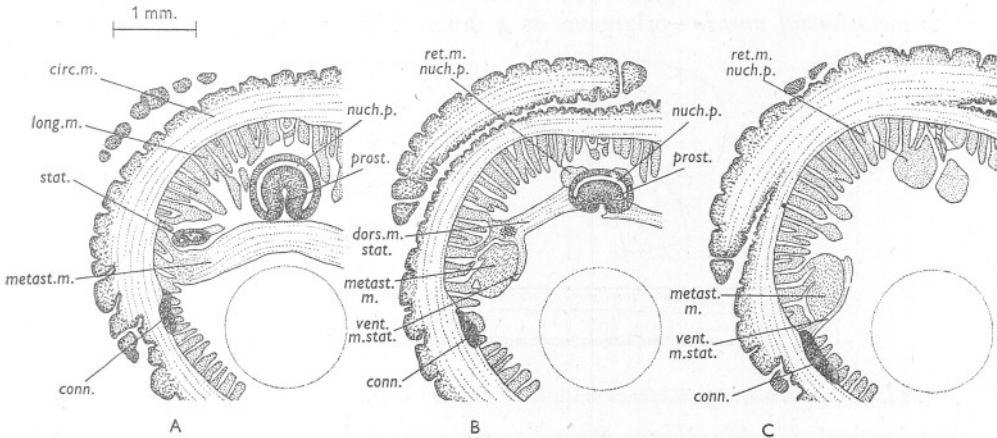


Fig. 13. *Arenicola marina*. Three transverse sections, corresponding approximately to the ruled lines in Fig. 11B, of a specimen killed in Bouin. The sections are equidistant and 0.2 mm. apart; the most anterior is on the left. The dotted circle gives the position of the gut. Lettering as on p. 44.

The general plan of the *central nervous system* of the head is shown in Fig. 9D. The ventral nerve cord continues forwards for a short distance on to the head; it then divides to give rise to the connectives, which run obliquely upwards and forwards to the prostomium. Just as the course of the ventral cord is marked externally by the ventral groove, so that of the connectives is marked by the more or less evident metastomial grooves (Fig. 9A, *metast.gr.*). The connectives resemble the ventral cord in consisting of a superficial ganglionic and a deep fibrous part, and in lying deep to the circular muscle layer (Fig. 13, *conn.*). When they reach the lateral corners of the prostomium, where the nuchal pouch pushes through the circular layer, the ganglionic part of the connectives enters into intimate relation with the epidermis. The nerves now expand somewhat and, remaining in close contact with the epidermis, pass up the front face of the prostomium to reach its dorsal side. Here they run backwards for a short distance to meet each other in the median plane. From their point of union, a pair of massive nerves runs back to the nuchal groove. That part of the central nervous system which lies in the prostomium,

in intimate relation with the epidermis, is generally termed the brain. Its form can be seen in Figs. 9D and 12. For the fine structure of the brain, see Gamble & Ashworth (1900).

The shallow grooves, which divide the anterior margin of the prostomium into three lobes and trace a Y on its dorsal face, give the line along which the brain adheres to the epidermis. The body wall is therefore thick under these grooves. At the sides of the prostomium, and in its median anterior lobe, the body wall is thin and the coelome comes near the surface (Fig. 12).

Immediately dorsal to the connectives, over the more ventral part of their course, lies the largest special muscle in the body wall of the worm. This—the *metastomial muscle*—originates as a union of contributions from all the

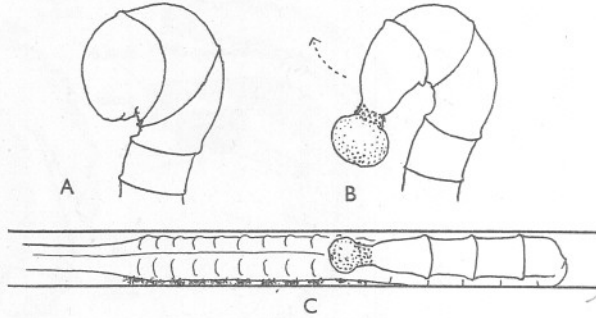


Fig. 14. *Arenicola marina*. Sketches to illustrate the process of reversing in the tube (see text).

longitudinal muscle columns ventral to the notopodial line. It runs forwards and upwards, following the general course of the connectives, until it reaches the level of the statocysts;¹ it then leaves the inner face of the longitudinal layer and crosses the body cavity, just below the brain, to continue into its fellow of the opposite side (Figs. 10, 13, *metast.m.*).

This muscle was first described by Ehlers (1892), who said that it was inserted on to the prostomium. It is briefly mentioned by Gamble & Ashworth (1898) and by Ashworth (1904), who regard it as a retractor of the prostomium. Its true anatomical relationships, however, show that it cannot play that role. Its actual function is quite different, and very important. The lugworm sometimes reverses itself, either in its own burrow or in glass observation tubes, by narrowing its body and then burrowing (with continual extrusions of the proboscis, and uprisings of the parapodial girdles) along its own ventral surface. In this way it can turn in a tube which, at other times, it seems comfortably to fill (Fig. 14C). The problem now arises, how does this performance start? Living worms, when watched,¹ can occasionally be seen to assume a remarkable

¹ To study the movements of the proboscis and head, it is convenient to tie the whole worm with fine string about at the level of chaetigerous annulus v, to cut away everything behind the ligature, and to put the isolated front end in sea water under a binocular microscope. The preparations stay active for hours, and frequently show the turning attitude described above.

attitude, in which the dorsal wall of the head and of the first two or three segments is greatly distended, while the ventral wall shows extreme longitudinal contraction (Fig. 14A). The prostomium and mouth are thereby come to be directed backwards: the attitude can be roughly imitated by 'burying one's chin in one's chest'. Now the assumption of this attitude always heralds an outburst of proboscis activity. The first extrusion begins while the worm is still in the attitude, and the proboscis therefore emerges in a tailward direction. As this extrusion completes itself, the whole anterior end assumes a more usual configuration. If the worm is lying in a dish of sea water, this results in a forward swing of the proboscis (Fig. 14B); but if the worm is in a tube, the forward swing cannot occur, and subsequent extrusions, made in the usual manner, will serve to pull the head farther and farther along the worm's ventral surface (Fig. 14C). The metastomial muscle runs like a sling over the mouth, and, if it contracts simultaneously with the more ventral longitudinal columns from which it arises, will play an important and perhaps essential role in the assumption of the attitude of Fig. 14A.

The *statocysts*,¹ whose form was beautifully described by Ehlers (1892), are a pair of blind in-pushings of the epidermal layer of the body wall, which pass through the circular muscle layer (Figs. 9, 10, 13, *stat.*). Their openings are slit-like and dorsi-ventrally elongated. Each leads into a tube with a lumen of the same form, and which opens forwards at its deep end into a spherical bulb. The whole organ is therefore rather retort-shaped. It contains various foreign objects, such as quartz grains, fragments of spicules and diatom shells, etc., covered with more or less well-marked layers of a 'chitinoid' secretion (Ashworth, 1904).

The statocyst is provided with a rather complicated musculature, whose functions are obscure. The muscles are: (i) the dorsal muscle of the statocyst (Fig. 10B, *dors.m.stat.*), which runs dorsally and medially; its more anterior fibres continue into the corresponding muscle of the opposite side, while its hinder ones are inserted into the posterior end of the nuchal pouch, just below its retractor; (ii) a number of slips of muscle running back to the longitudinal columns adjacent to the statocyst; (iii) the ventral muscle of the statocyst (Figs. 10, 13, *vent.m.stat.*), which crosses the metastomial muscle, as a thin sheet or as a series of fine strands, to the tissue round the connectives. On the whole, it seems likely that the dorsal muscle of the statocyst is derived, as the metastomial muscle is, from the longitudinal layer; the anatomical relations of the ventral muscle, on the other hand, are consistent with its being a member of the oblique muscle series.

¹ The statocysts lie at the level of the notopodia; as they are invaginations producing a chitinoid secretion, and as the notopodial chaetae have sensory nerve endings round their bases (Retzius, quoted by Ehlers, 1892), it is tempting to think of them as the peristomial notopodia. The idea was discussed at length by Ehlers (1892), who decided against it, on the ground that certain polychaetes of other families have statocysts, neuropodia and notopodia in the same segment.

According to von Buddenbrock (1912, 1913), the statocysts of *Arenicola* are used to guide the worm when burrowing down into the mud.

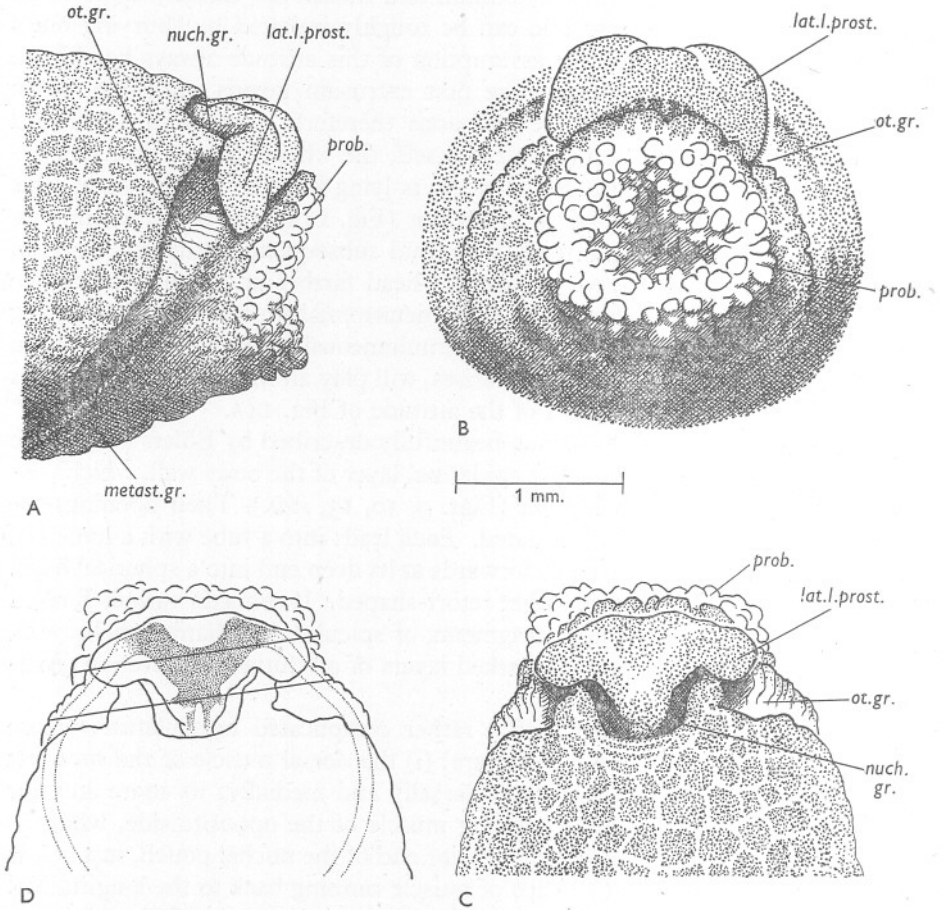


Fig. 15. *Arenicola claparedii*. Lateral view (A), anterior view (B) and dorsal view (C) of a Naples specimen killed by the Mg-formalin method. D, outline of the dorsal view with the brain and connectives given as in Fig. 9D; the ruled lines give the positions of the transverse sections in Fig. 17. Lettering as on p. 44.

Arenicola claparedii

The prostomium of *claparedii* differs in two important respects from that of *marina*. In the first place, it is prolonged laterally into two large, vertical flaps, the lateral lobes (Fig. 15, *lat.l.prost.*). In the second place, it is not retractile; nuchal pouch and retractor muscle are lacking (Fig. 16D). The nuchal groove lies, as in *marina*, round the sides and hind-end of the prostomium (Figs. 15, 17, *nuch.gr.*). It will be seen, on comparing Figs. 9 and 15, that the prostomium is relatively larger in the latter. This results, partly at

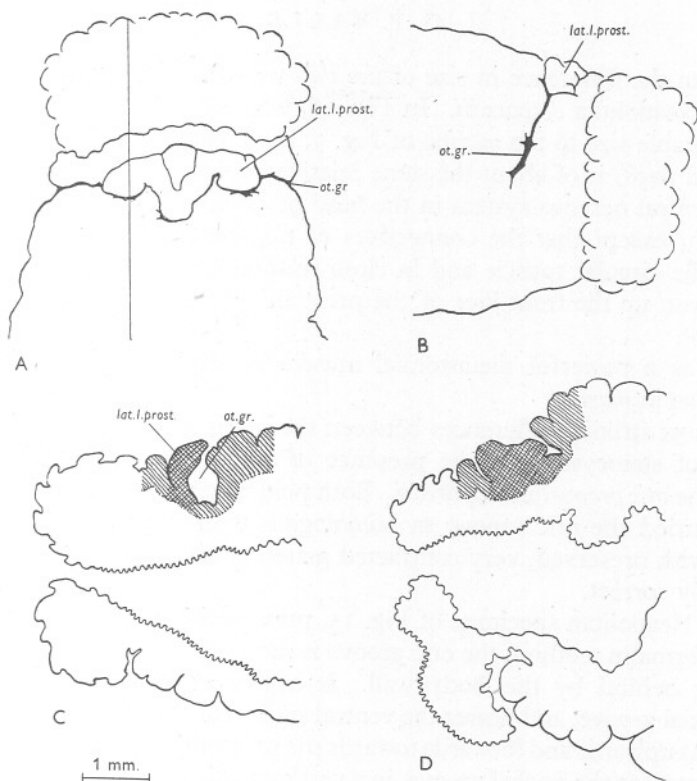


Fig. 16. *Arenicola claparedii*. American specimens, killed by means unknown to the writer. A, B, dorsal and lateral views of the same specimen. C, sagittal section of the same, cut along the ruled line in A, to show how the lateral wing of the prostomium (cross-hatched) overhangs the otic groove. D, median sagittal section of another specimen, for comparison with Fig. 11.

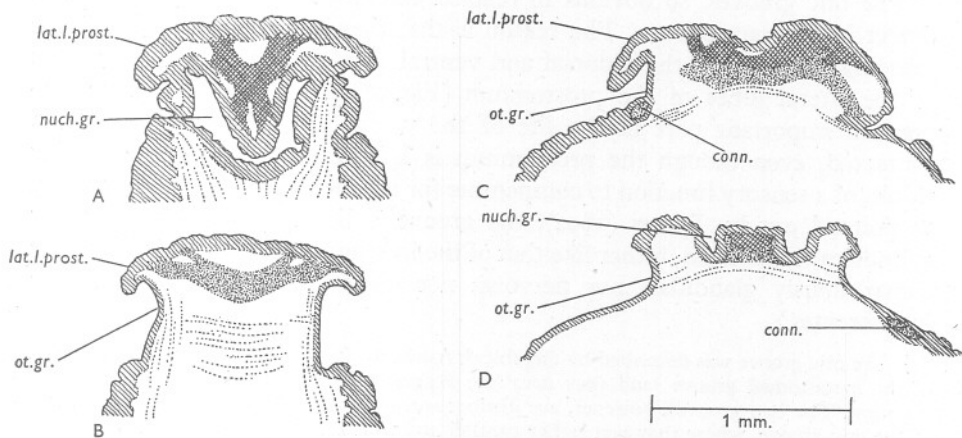


Fig. 17. *Arenicola claparedii*. Naples specimens, killed in Mg-formalin. A, horizontal section through the nuchal groove and the superficial part of the brain. B, horizontal section through the otic grooves and the deep part of the brain. C, D, transverse sections, corresponding approximately to the ruled lines in Fig. 15D. Conventions as in Fig. 12. Lettering as on p. 44.

least, from the difference in size of the two worms. Fig. 15 was drawn from a small, Neapolitan *claparedii*. In Fig. 16, which is from a Pacific specimen of comparable size to the *marina* of Fig. 9, the prostomium (after subtracting the lateral flaps) is of about the same relative size.

The central nervous system in the head of *claparedii* is very similar to that of *marina*, except that the connectives of *claparedii*, like its nerve cord, lie outside the circular muscle and in close relation to the epidermis. The connectives run up the front face of the prostomium, medial to the lateral lobes (Fig. 15D).

There is a powerful metastomial muscle in *claparedii*, having the same relations as in *marina*.

The most striking differences between the heads of the two species are the absence of statocysts, and the presence of a new structure, which will be termed the *otic groove*, in *claparedii*. Both points were noted by Ehlers (1892), who regarded the otic groove as homologous with the statocyst; but as he worked with preserved, very contracted material, his account of the groove is not wholly correct.

In the Neapolitan specimen of Fig. 15, preserved in the relaxed attitude by the Mg-formalin method, the otic groove is seen as a large, open shelf, slightly overhung behind by the body wall. It begins at a point just above the metastomial groove, and nearer the ventral surface of the worm than the dorsal, and it runs upwards and forwards towards the prostomium.¹ It ends, lateral and rather ventral to the nuchal groove, in a vertical wall (Figs. 15A, 17). Strands of muscle run across, below the brain, from the otic groove of one side to that of the other; these are indicated in Fig. 17D; if the otic groove indeed represents the statocyst, they might be its dorsal muscle.

The otic grooves, so obvious in relaxed animals, may be very difficult to detect in contracted ones. The reason is that they are closed, partly by the pressing together of their dorsal and ventral borders, and partly by means of the lateral lobes of the prostomium (Fig. 16C). The groove appears to play an important part in the life of the worm, since its surface is thus protected, even though the prostomium is left exposed, and one naturally thinks of a sensory function to compensate for the lack of statocysts. However, as pointed out by Ehlers (1892), the groove is lined by an unusually low cylindrical epithelium, rather like that of the interannular grooves; it is neither conspicuously glandular, nor nervous, nor ciliated; in a word, 'ein sehr indifferentes'.

¹ The otic groove was described by Gamble & Ashworth (1900, p. 501) as 'an enlargement of the metastomial groove' and they deny the suggestion of Ehlers that it represents the statocyst. The two grooves, however, are distinct and easy to distinguish at the ventral end of the otic groove, where they run rather parallel and with the otic groove slightly dorsal to the metastomial.

Arenicola ecaudata

The general appearance of the head in *ecaudata* is different in many ways from that of *marina*. The nuchal groove is very long, resembling in shape a U whose vertical limbs have been bent outwards, their tips reaching more than half way towards the ventral line. The area between this groove and the mouth is divided more or less obviously by a transverse fold, which separates the upper lip in front from the prostomium behind. The latter is a flat area,

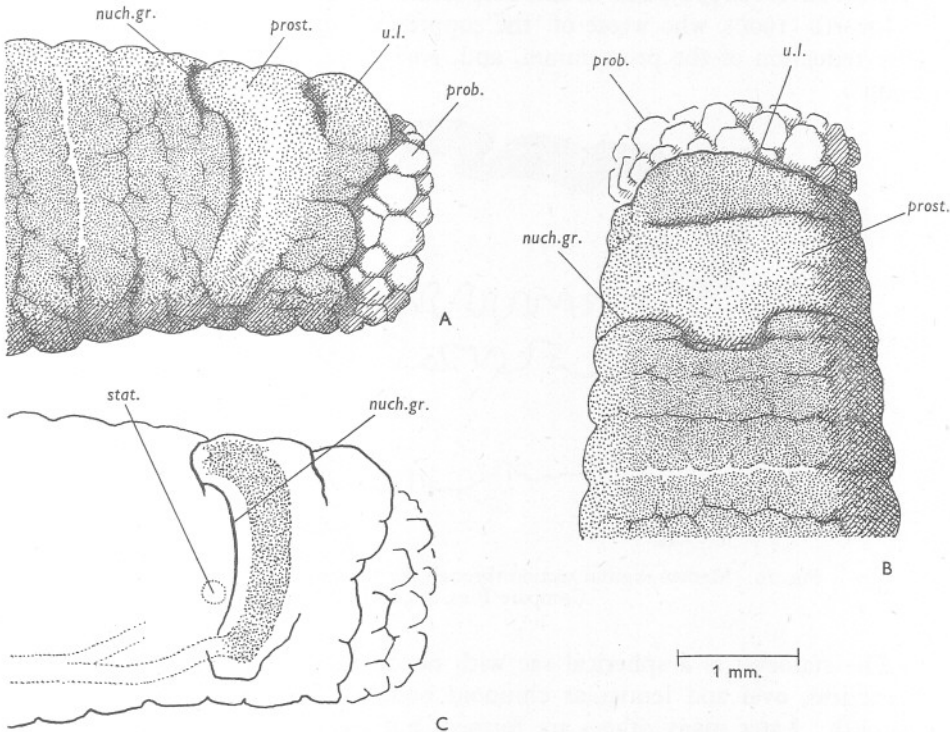


Fig. 18. *Arenicola ecaudata*. Lateral view (A) and dorsal view (B) of a specimen killed in Mg-formalin. C, outline of the lateral view, with the positions of the right statocyst and the central nervous system indicated; the part in relation with the epidermis is stippled. Lettering as on p. 44.

often hardly distinguishable from the general body wall; but in good specimens, a broad, rather smooth, very shallow depression, corresponding to the Y-groove on the prostomium of *marina* and indicating the position of the brain, can be seen; this depression is drawn pale in Fig. 18. The prostomium extends slightly farther ventrally than does the nuchal groove. There is no nuchal pouch, and the prostomium is obviously not retractile (Fig. 19).

The connectives resemble the nerve cord in lying deep to the circular muscle layer, from which they are separated by a coelomic space. On reaching the corners of the prostomium, they enter into close relation with the epidermis,

and proceed dorsalwards as the brain. This organ is dotted in Fig. 18C; its outlines are, however, rather ill-defined and it gives off numerous nerves to the nuchal groove and the anterior body wall.

The form of these structures in *ecaudata* can be derived from that in *marina* by supposing that the corners of the brain and prostomium are dragged for a great distance in a latero-ventral direction. It will be noted that the brain is relatively large. 'Le cerveau est relativement développé pour une Arénicole' wrote Fauvel (1899*a*), and in this respect he was more exact than Gamble & Ashworth (1900), who wrote of 'the suppression of the prostomium' and of 'the reduction of the prostomium, and, *pari passu*, the simplification of the brain'.

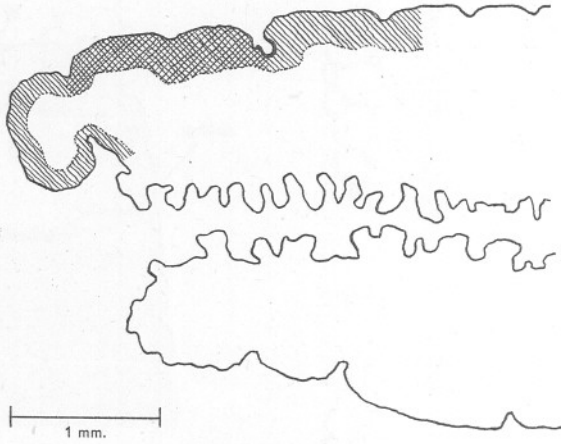


Fig. 19. Median sagittal section through the head of *Arenicola ecaudata*. Compare Figs. 11, 16D.

The statocyst is a spherical sac with no duct to the exterior; it contains 'spherical, oval and lenticular chitinoid bodies...there is at first only one statolith. Later many others are formed, but the original one remains conspicuous by reason of its larger size' (Ashworth, 1912). It corresponds in position with the statocyst of *marina*, and lies on the superficial face of, and partly embedded in, the longitudinal muscle layer. It receives a nerve from the connective, shortly before the latter enters the brain.

Owing to the smooth face which the longitudinal layer presents to the coelome in this species, the special muscles of the head are hard to make out in dissections. However, examination of the cleared and flattened body wall with polarized light shows that a metastomial muscle exists, having essentially the same relations as in *marina* or *claparedii*.

and proceed dorsalwards as the brain. This organ is dotted in Fig. 18C; its outlines are, however, rather ill-defined and it gives off numerous nerves to the nuchal groove and the anterior body wall.

The form of these structures in *ecaudata* can be derived from that in *marina* by supposing that the corners of the brain and prostomium are dragged for a great distance in a latero-ventral direction. It will be noted that the brain is relatively large. 'Le cerveau est relativement développé pour une Arénicole' wrote Fauvel (1899*a*), and in this respect he was more exact than Gamble & Ashworth (1900), who wrote of 'the suppression of the prostomium' and of 'the reduction of the prostomium, and, *pari passu*, the simplification of the brain'.

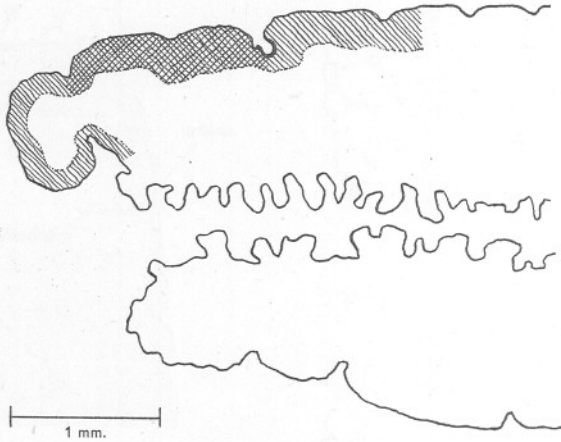


Fig. 19. Median sagittal section through the head of *Arenicola ecaudata*. Compare Figs. 11, 16D.

The statocyst is a spherical sac with no duct to the exterior; it contains 'spherical, oval and lenticular chitinoid bodies...there is at first only one statolith. Later many others are formed, but the original one remains conspicuous by reason of its larger size' (Ashworth, 1912). It corresponds in position with the statocyst of *marina*, and lies on the superficial face of, and partly embedded in, the longitudinal muscle layer. It receives a nerve from the connective, shortly before the latter enters the brain.

Owing to the smooth face which the longitudinal layer presents to the coelome in this species, the special muscles of the head are hard to make out in dissections. However, examination of the cleared and flattened body wall with polarized light shows that a metastomial muscle exists, having essentially the same relations as in *marina* or *claparedii*.

THE POSTERIOR REGION ('TAIL')

For many decades, the genus *Arenicola* has been divided into 'caudate' and 'ecaudate' sections. All the species have a head, whose characters have already been noted. This is followed, in the 'caudate' species, by a number of trunk segments with parapodia, and in which all the septa, except the first, third and fourth, have practically disappeared; and this again by the tail, in which appendages are lacking but the septa persist. The number of trunk segments varies, in different 'caudate' species, from 16 to 20. The 'ecaudate' division consists of two species, *ecaudata* and *grubii*. In *ecaudata*, the head is followed by a trunk region resembling in many points that of the 'caudate' species; for example, it lacks septa except for i, iii and iv; the vessels of septum vii are specialized to form the hearts; and so on. The first gill, however, is rather farther back; on chaetigerous annulus xv instead of vii. There follows a rather gradual transition (through segments xvii to xix) to a region in which the septa persist, and which is externally distinguishable from the trunk.¹ In the trunk segments, the four annuli that separate any two chaetigerous annuli are very equal in size and pigmentation; in the tail, on the other hand, the second (and sometimes the third) of the four is rather larger and more deeply coloured than the others; this gives the tail as a whole a banded appearance, except in the darkest specimens. It seems clear enough that a differentiation exists, corresponding to, though less profound than, that of the 'caudate' species. A similar differentiation, a couple of segments farther forwards, is traceable in *grubii*. However, it is with *marina* and *claparedii*, in which the tail is most distinctively specialized, that we shall now be concerned.

Arenicola marina

The fact that the tail segments of *marina* are short at its base and lengthen towards the tip, is suggested by surface inspection and established by dividing the tail horizontally (Fig. 20). The fact is interpreted by Ashworth (1912) as follows: 'During development, new chaetiferous segments are formed immediately in front of the terminal segment or pygidium. In the ecaudate species all the segments are produced in this growing zone, the activity of which becomes exhausted at about the end of the post-larval stage. In the caudate species, after the full number of chaetiferous segments has been formed, new segments are evidently produced at the anterior end of the tail; for in this region each segment is short from before backwards, while in the middle and posterior regions of the tail the segments are longer, and, in adult or late post-larval specimens, are subdivided into annuli. . . . In *A. marina* there may be 60 to 70 tail segments, though usually there are fewer owing to losses posteriorly.'

Now horizontal sections, either of large or small *marina*, never show a new segment in the act of formation at the base of the tail. The animal of Fig. 20 is

¹ This distinction is clearer in preserved than in living worms.

typical; even the shortest tail segments have a definite and uniform length (in this case, of 3 annuli), and the foremost of all is rather longer than those which follow it. Having examined many specimens, I do not believe that there is any formation of new segments at the tail base.

Fig. 21 gives the number of annuli per segment in three worms of different size, and affords a representative picture of the mode of growth of the tail. The counting of the annuli was not always exact, because it is sometimes doubtful whether an incipient annulus, in process of formation, should be counted or not: the use of smoothed curves is therefore legitimate. As the worms grow, the segments evidently lengthen; segment xv, for instance, has 2, 6 and 12 annuli in the three worms; and this growth becomes more rapid tailwards.

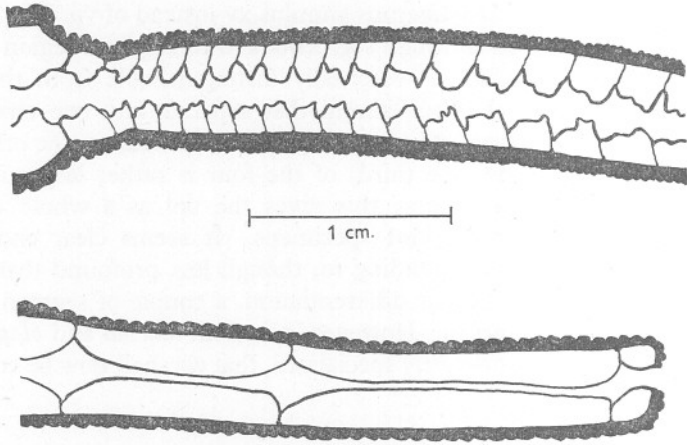


Fig. 20. Horizontal sections through the base and tip of the tail of an *Arenicola marina* of overall length 140 mm.

The following interpretation is suggested. The pygidial growth zone first lays down the trunk segments, then a great number of tail segments; these are at first very short and serve as a reserve stock; then they lengthen, the hinder ones more rapidly than the front. The graph clearly shows that losses from the hind-end must occur, not only as accidents but of necessity, as the hinder segments would otherwise become impossibly long. The worms in the graph had 44, 28 and 18 tail segments, in ascending order of size.

The reason for this fountain of tail production is not obvious at first sight. The hinder segments may be nearly 2 cm. in length; if the largest worm of Fig. 21 started with the '60 to 70 tail segments' which Ashworth gives as the maximum for this species, it has clearly lost about a metre of tail or potential tail; more than five times its overall length at death. The method adopted by *ecaudata*, of growing a tail of appropriate length and tolerating such losses as may occur, would seem more economical. 'Adult specimens of this species',

wrote Ashworth (1912) of *ecaudata*, 'seldom exhibit as many segments as they possessed at the end of the post-larval stage, but occasionally an unabbreviated example is met with, in which case the number of segments is about 60 to 64.

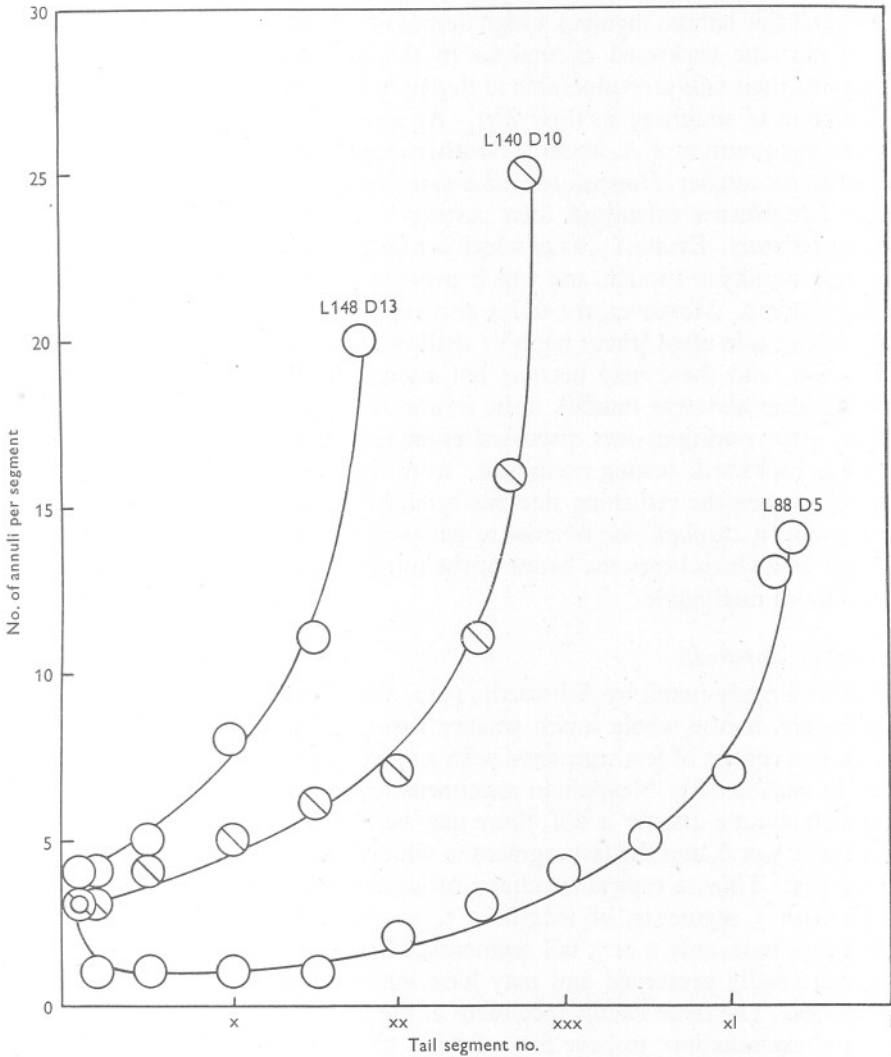


Fig. 21. The number of annuli per tail segment in three specimens of *Arenicola marina*. The total length, and trunk diameter, are given, in mm., by the graph of each specimen.

There are about 45 to 50 segments in average specimens.' These figures include trunk segments. An average *ecaudata*, then, starts with 60-odd segments, of which it loses 20 or 25%; a large *marina* has lost more than 50% of

its initial 80 or 90; and the lengthening of the segments in *marina* makes its losses the greater in proportion.

As already noted, *marina* generally lives on muddy sand flats, while *ecaudata* is found in sandy material among stones or the breakdown fragments of rocks. The sand-flat habitat involves a high degree of exposure of the tail. Lugworms make periodic backward excursions to the surface to defaecate, at which moments their tails are vulnerable to those predators which do not resent a high proportion of roughage in their diet. At low tide, sea birds may intervene. Stach (1944) writes of *A. loveni*, a Southern species very similar to *marina*, that 'The oyster catcher (*Haematopus fuliginosus*) was often observed to peck off the tails of lugworms extruding their castings'. High tide will doubtless bring other predators. Evidently, a tail which contains no very essential organs, which shortens rapidly at a touch, and which grows from reserve segments at the base, is appropriate. Moreover, the tail is also exposed to physico-chemical assault. The falling tide often leaves pools or shallow sheets of water over the burrows of *marina*, and these may become hot enough in bright sunshine, or dilute enough after a violent rainfall, to be injurious to the worms. Their behaviour under such conditions was discussed elsewhere (Wells, 1949*a*). They appear to make backward 'testing excursions' from time to time towards the surface, and only when the returning tide has brought cooler or more saline water do they pump it through the burrow to get the oxygen they need. Once again, it is the tail which bears the brunt of the injurious conditions, and its renewal is the more intelligible.¹

Arenicola claparedii

It was already noted by Ashworth (1912) that Neapolitan specimens of this species are on the whole much smaller than Pacific ones. In both, the tail appears to consist of few segments, with a much less well-marked size gradient than in *marina*. My Neapolitan specimens are mostly 40–60 mm. in length, of which about a quarter is tail; there may be 12 tail segments, but usually the number is 5 or 6, and the last segment is seldom much more than twice as long as the first. Thus, a typical specimen measures overall 41 mm.; this includes a tail with 5 segments, of lengths 1.7, 2, 2.3, 3 and 3.6 mm. My Pacific specimens have only 2 or 3 tail segments, all of about equal length; they are, however, badly preserved and may have autotomized some tail segments in the process. The three Pacific specimens at the British Museum all appear (from external examination) to have few—from 5 to 7—tail segments.

All of these specimens are adult, and it is difficult to discuss the significance of their tail numbers without information about the post-larval stages, which

¹ The tail is also specialized with regard to its movements. The irrigation waves, by which water is driven through the tube, typically start at the junction of trunk and tail in *marina* and move forwards. If reversed (tailward) irrigation is in progress, they die out at the junction. In *ecaudata*, on the other hand, they run forwards from the hindmost end of the body. It appears likely that the tail of *marina* is responsible for the very rapid ejection of the faecal cylinders.

does not appear to be available. Similar tails occur in *A. cristata* Stimpson, at Wood's Hole, and for this species the development is known. Ashworth (1912) writes of adult American *cristata*, that the tail usually consists of 7-10 segments. By the kindness of Prof. Ritchie, of the University of Edinburgh, I have been allowed to dissect one of Ashworth's largest specimens; its overall length is 434 mm., and it has 7 tail segments, measuring, from base to tip, 12, 16, 17, 18, 19, 23 and 31 mm. Now the development of *cristata* was described by Lillie (1905), and the post-larva is figured by Ashworth (1912). The pygidial growth zone forms about 40 tail segments before its activity ceases, and, in the post-larva, these show a beautiful size gradient, as in adult *marina*. Apparently *cristata* resembles *marina* in the essential mechanism, but its reserve is smaller, and is often more completely spent. The same may be true of *claparedii*.

SUMMARY

Worms for dissection, or for museum preservation, should be prepared by the magnesium-formalin method, of which two modifications are given in the text.

The body of *Arenicola* is differentiated into: (a) an achaetous 'head', comprising the prostomium and a small number (probably two) of subsequent segments, (b) a 'trunk', composed of a number, varying somewhat with the species, of chaetigerous segments, and (c) a 'tail', which may or may not be chaetigerous according to the species. The method of subdividing the body according to the distribution of the gills, so often met with in the literature, is misleading because it conceals the very fundamental differentiation between 'head' and 'trunk'.

The main layers of the body wall are described. There are grounds for supposing that the circular muscle layer plays a greater part than the longitudinal in the maintenance of a postural fluid pressure in active worms.

The parapodial derivatives are the neuropodia, the notopodia, and the parapodial girdles; details of all three, and especially of their musculatures and movements, are given in the text. The extent to which these structures are developed varies from species to species, as well as from segment to segment within a species; the latter differentiation (at least in *marina*) corresponds to functional differences in the attitudes and movements of the segments. *Claparedii* differs from *marina*, chiefly in the great development of the parapodial girdles of the more anterior trunk segments, with concomitant reduction of the intervening ordinary annuli, and in the comparative shortness of the hinder neuropodia. *Ecaudata* is especially distinguished by the slight development of the parapodial girdles and the length of the neuropodia, especially in the more anterior segments.

The head is the roughly conical region extending forwards from the anterior margin of the first chaetigerous annulus. All species have a metastomial

muscle, derived from the longitudinal layer, and playing an important part in the process of turning in the tube. The chief special sense organ appears to be the nuchal groove. The main differences between the three species are as follows: *marina* has a nuchal pouch into which the prostomium can be retracted; *claparedii* lacks statocysts and has, instead, a large and rather complex otic groove of unknown function; *ecaudata* has a nuchal groove and brain which extend for a great distance towards the ventral line.

The tail of *ecaudata* bears parapodia and gills; it differs from the trunk in having well-developed septa and in respect of the external annulation. The tail of *marina* is achaetous and grows backwards from reserve segments, laid down early in life, at its base. The rate of tail production in this species is great, and probably related to the hazards which the sand-flat habitat involves for the tail. The tail in adult *claparedii* has few segments. It is compared in the text with that of *A. cristata* Stimpson; and the conclusion is drawn that in both species the facts are essentially as in *marina*, but the reserve is smaller and soon exhausted.

REFERENCES

- ASHWORTH, J. H., 1904. *Arenicola*. *Liverpool Marine Biology Committee Memoirs*, Vol. XI. London.
- 1912. *Catalogue of the Chaetopoda in the British Museum*. A. Polychaeta. Part I. Arenicolidae. London.
- AUDOUIN, A. & EDWARDS, H. MILNE, 1834. *Recherches pour servir à l'histoire naturelle du littoral de la France*. Tome III: Annélides, première partie. Paris.
- BENHAM, W. B., 1896. *Polychaete Worms*. In *Cambridge Natural History*, Vol. II. London.
- BERKELEY, E. & BERKELEY, C., 1932. On a collection of littoral Polychaeta from the West Coast of Vancouver Island. *Contrib. Canad. Biol., Fisheries*, Vol. VII, pp. 309-18.
- 1939. On a collection of Polychaeta chiefly from the west coast of Mexico. *Ann. Mag. Nat. Hist.*, Vol. XI, pp. 321-46.
- BUDDENBROCK, W. VON, 1912. Über die Funktion der Statozysten im Sande grabender Meerestiere (*Arenicola* und *Synapta*). *Biol. Zbl.*, Bd. 32, pp. 564-85.
- 1913. Über die Funktion der Statozysten im Sande grabender Meerestiere, II. *Zool. Jb., Abt. Allg. Zool. Physiol.*, Bd. 33, pp. 441-82.
- CHAPMAN, G. & NEWELL, G. E., 1947. The role of the body fluid in relation to movement in soft-bodied invertebrates. I. The burrowing of *Arenicola*. *Proc. Roy. Soc. B*, Vol. 134, pp. 431-55.
- CUNNINGHAM, J. T. & RAMAGE, G. A., 1888. The Polychaeta Sedentaria of the Firth of Forth. *Trans. Roy. Soc. Edinb.*, Vol. 33, pp. 635-84.
- DAM, L. VAN, 1937. Über die Atembewegungen und das Atemvolumen von *Phryganea*-Larven, *Arenicola marina*, und *Nereis virens*, sowie über die Sauerstoffausnutzung bei *Anodonta cygnea*, *Arenicola marina* und *Nereis virens*. *Zool. Anz.*, Bd. 118, pp. 122-8.
- 1938. *On the Utilisation of Oxygen and Regulation of Breathing in some Aquatic Animals*. 143 pp. Groningen.
- EHLERS, E., 1892. Die Gehörorgane der Arenicolen. *Zeitschr. wiss. Zool.*, Bd. 53, Suppl., pp. 217-85.

- FAUVEL, P., 1899*a*. Observations sur l'*Arenicola ecaudata*. *Bull. Soc. Linn. Normandie*, 5e Sér., T. II, pp. 64-93.
- 1899*b*. Sur le pigment des Arénicoles. *Compt. Rend. Acad. Sci., Paris*, T. 129, pp. 1273-5.
- 1927. Polychètes sédentaires. *Faune de France*, Vol. 16. 494 pp. Paris.
- FOX, H. MUNRO, 1949. On chlorocrourin and haemoglobin. *Proc. Roy. Soc. B.*, Vol. 136, pp. 378-87.
- GAMBLE, F. W. & ASHWORTH, J. H., 1898. The habits and structure of *Arenicola marina*. *Quart. Journ. Micr. Sci.*, Vol. 41, pp. 1-42.
- — 1900. The anatomy and classification of the Arenicolidae, with some observations on their post-larval stages. *Quart. Journ. Micr. Soc.*, Vol. 43, pp. 419-570.
- GOODRICH, E. S., 1946. The study of nephridia and genital ducts since 1895. *Quart. Journ. Micr. Sci.*, Vol. 86, pp. 113-393.
- GRUBE, A. E., 1851. *Die Familien der Anneliden*. Berlin.
- GUBERLET, J. E., 1934. Observations on the spawning and development of some Pacific annelids. *Proc. 5th Pacific Sci. Congress (Canada, 1933)*, Vol. v, pp. 4213-20.
- HEMPELMANN, F., 1934. Archannelida und Polychaeta. *Kükenthal-Krumbach, Handb. d. Zool.*, 2. II. Berlin.
- JUST, B., 1924. Über die Muskel- und Nervenphysiologie von *Arenicola marina*. *Zeits. vergl. Physiol.*, Bd. 2, pp. 145-54.
- LIGNAC, G. O. E., 1945. About Arenicochrome and its possible significance as a mesocatalyst. *Proc. Koninkl. Akad. Wetensch.*, Vols. XLVI-XLVIII, pp. 406-10.
- LILLIE, RALPH S., 1905. The structure and development of the nephridia of *Arenicola cristata* Stimpson. *Mitt. Zool. Sta. Neapel.*, Vol. 17, pp. 341-405.
- LINKE, O., 1939. Die Biota des Jadebusenwattes. *Helgol. wiss. Meeresunters.*, Bd. 1, pp. 201-348.
- NEWELL, G. E., 1948. A contribution to our knowledge of the life history of *Arenicola marina* L. *Journ. Mar. Biol. Assoc.*, Vol. 27, pp. 554-80.
- NICOL, J. A., 1948. The giant axons of annelids. *Quart. Rev. Biol.*, Vol. 23, pp. 291-323.
- OKUDA, S. 1938. Notes on the spawning habit of *Arenicola claparedii* Levinsen. *Annot. Zool. Jap.*, Vol. 17, pp. 577-80.
- OSLER, E., 1826. On burrowing and boring marine animals. *Phil. Trans. Roy. Soc.*, Part III, p. 342-71.
- STACH, L. W., 1944. Ecology of the sand flats at Moreton Bay, Reevesby Island, S. Australia. *Trans. Roy. Soc. S. Australia*, Vol. 68, pp. 177-82.
- TAKAHASHI, K., 1934. Contributions to the study of Japanese *Arenicola*. I. Notes on the habits and distribution of *Arenicola* in Japan. *Sci. Repts. Tokyo Bunrika Daigaku*, Sect. B, Vol. 1, pp. 271-9.
- WELLS, G. P., 1944. The parapodia of *Arenicola marina* L. *Proc. Zool. Soc.*, Vol. 141, pp. 100-16.
- 1945. The mode of life of *Arenicola marina* L. *Journ. Mar. Biol. Assoc.*, Vol. 26, pp. 170-207.
- 1949*a*. Respiratory movements of *Arenicola marina* L.: intermittent irrigation of the tube, and intermittent aerial respiration. *Journ. Mar. Biol. Assoc.*, Vol. 28, pp. 447-64.
- 1949*b*. The behaviour of *Arenicola marina* L. in sand, and the role of spontaneous activity cycles. *Journ. Mar. Biol. Assoc.*, Vol. 28, pp. 465-78.
- 1950. Spontaneous activity cycles in polychaete worms. *Symposia of the Society for Experimental Biology*, no. IV. Cambridge, 1949.

APPENDIX

Reference letters used in the text-figures

<i>circ.m.</i>	circular muscle	<i>notop.b.</i>	notopodial base
<i>conn.</i>	connective nerve	<i>notop.l.</i>	notopodial line
<i>dest.</i>	destruction zone	<i>notop.long.v.</i>	notopodial longitudinal vessel
<i>dors.l.</i>	dorsal line		
<i>dors.m.stat.</i>	dorsal muscle of the statocyst	<i>notop.t.</i>	notopodial tip
<i>dors.v.</i>	dorsal vessel	<i>nuch.gr.</i>	nuchal groove
<i>ep. & c.t.</i>	epithelium and connective tissue	<i>nuch.p.</i>	nuchal pouch
		<i>obl.m.</i>	oblique muscle
<i>form.</i>	formative zone	<i>obl.m.notop.</i>	oblique muscle of the notopodium
<i>g.</i>	gill	<i>ot.gr.</i>	otic groove
<i>h.l.</i>	hinge line	<i>parap.c.</i>	parapodial canal
<i>interann.n.</i>	interannular nerve	<i>prob.</i>	proboscis
<i>lat.l.prost.</i>	lateral lobe of the prostomium	<i>prost.</i>	prostomium
		<i>prot.m.neurop.</i>	protractor muscle of the neuropodium
<i>lat.neur.v.</i>	lateral neural vessel		
<i>long.m.</i>	longitudinal muscle	<i>prot.m.notop.</i>	protractor muscle of the notopodium
<i>metast.gr.</i>	metastomial groove		
<i>metast.m.</i>	metastomial muscle	<i>ret.m.neurop.</i>	retractor muscle of the neuropodium
<i>m.h.</i>	muscles of the hinge		
<i>m.parap.c.</i>	muscles of the parapodial canal	<i>ret.m.notop.</i>	retractor muscle of the notopodium
<i>n.c.</i>	nerve cord	<i>ret.m.nuch.p.</i>	retractor muscle of the nuchal pouch
<i>neph.</i>	nephridium		
<i>neph.l.</i>	nephridial line	<i>stat.</i>	statocyst
<i>neph.long.v.</i>	nephridial longitudinal vessel	<i>stom.</i>	stomach
		<i>u.l.</i>	upper lip
<i>neph.p.</i>	nephridiopore	<i>vent.m.stat.</i>	ventral muscle of the statocyst
<i>neurop.</i>	neuropodium		
<i>notop.</i>	notopodium	<i>vent.v.</i>	ventral vessel