

DIRECT PERISTALTIC PROGRESSION  
AND THE FUNCTIONAL SIGNIFICANCE OF THE DERMAL  
CONNECTIVE TISSUES DURING BURROWING IN THE  
POLYCHAETE *POLYPHYSIA CRASSA*  
(OERSTED)

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INTRODUCTION

Since the classical analyses of worm locomotion by Gray and his colleagues (Gray 1939; Gray & Lissmann, 1938; Gray, Lissmann & Pumphrey, 1938) many studies have been made of behaviour, hydrostatic skeletal function and muscle activity patterns on a variety of worm-like burrowing invertebrates (Chapman, 1958; Clark, 1964; Trueman & Ansell, 1969; Seymour, 1971 *a*). In most marine groups with soft-bodied burrowing members (Anthozoa, Annelida, Mollusca, etc.) penetration, after initial entry into the substratum, is achieved by forceful protrusion or eversion of a proboscis or other terminal part of the body. The animal then moves forward into the cavity so formed by one of several methods: undulatory movements, e.g. *Nephtys* (Clark & Clark, 1960), or by utilizing the dilated proboscis or physa, etc. as a 'terminal anchor' upon which the body can pull, e.g. *Arenicola* (Trueman, 1966), *Peachia* (Ansell & Trueman, 1968). The animal advances into the cavity and the cycle is begun again by the body forming one or more 'protrusion anchors' or *points d'appui* which act as a fixed base for eversion or protrusion of the terminal anchor. The body is usually cylindrical in soft-bodied non-septate burrowers, and circular and longitudinal muscles oppose each other by means of a hydrostatic skeletal fluid system (Chapman, 1958). Locomotion frequently involves the use of peristaltic waves which may be direct (waves travel in the same direction as the animal) or retrograde (waves travel in the opposite direction to the animal) (Seymour, 1971 *b*) and progression of the whole body is cyclical (Clark, 1964; Trueman, 1968).

The polychaete *Polyphysia crassa* (Oersted) burrows by a somewhat different mechanism. Instead of thrusting a proboscis forward into the substratum *Polyphysia* employs prostomial horns to scrape the substrate out to the sides. The head end of the animal progresses in a continuous, non-cyclical way into the substratum while the rest of the body advances by means of direct peristaltic waves. The structure of the body wall is highly modified (Elder, 1972) apparently to enable the animal to accomplish the latter type of locomotor pattern, which involves simultaneous contraction of circular and longitudinal muscles. The present paper is an analysis of the burrowing mechanism and of the body-wall configurations adopted as the direct peristaltic wave passes along the body.

## MATERIALS AND METHODS

Animals were obtained from the Scottish Marine Biological Association, Millport, Isle of Cumbrae, and were kept until required, in breffits of mud and sea water at 6 °C in the dark. The sea water was aerated and changed as necessary. By this method the worms could be kept alive and active for several weeks.

Observations on burrowing worms were made in three ways: in breffits almost full of mud with about 2 in of sea water above the surface, in a layer of wet mud between glass sheets, and in trays with a shallow layer of mud (about 1½ in) under about 1 in of sea water. For analysis of the locomotor movements electronic flash photographs were taken, mainly of worms burrowing into the mud in the open trays. In order to standardize the photographs the single-lens reflex camera was set at a fixed focal distance and focusing was conveniently achieved by moving the hand-held camera. All prints were made at the same enlargement.

For histological examination animals were relaxed in 0.15% propylene phenoxetol in sea water (Owen, 1955), and fixed in Bouin's fluid, or placed directly in fixative without prior relaxation. Specimens were then embedded in Ester wax (B.D.H. Ltd) and cut at 5–8 µm. Sections were stained for connective tissue with Heidenhain's Azan or with spirit blue and alcoholic picrofuchsin (Elder & Owen, 1967).

## RESULTS

*Tentacular excavation*

The polychaete *Polyphysia crassa* (Scalibregmidae) is found in soft, flocculent, sublittoral muds. The family is related to the Arenicolidae and the anatomy, with thick cylindrical body, non-septate coelom apart from four anterior septa and a series of posterior septa in about the last eight segments, and reduced parapodia (Elder, 1972) is in many respects similar to the latter family, especially the tail-less members. The proboscis is eversible but opens on the ventral surface of the head and the prostomium carries a pair of stubby horns or tentacles (Text-fig. 1). *Polyphysia* does not appear to utilize its proboscis at all in burrowing. Instead, the head is moved from side to side and the prostomial horns displace the mud laterally.

The head and anterior trunk segments (nos. 1–5) act as a unit and display a locomotor pattern quite distinct from the rest of the body. Anatomically this region is distinguished internally by having complete septa between segments 2 and 3, 3 and 4, 4 and 5 and 5 and 6; the probable significance of this local septate condition is discussed below. For these reasons and to avoid possible confusion when referring to the locomotor activity patterns of other trunk segments the term 'head region' will be used in the following account to include the first five setigerous segments in addition to the head *sensu stricto* which, as in other polychaetes, consists of prostomium and peristomium.

A healthy worm placed on the surface of the mud in a sea-water-filled container immediately attempts to burrow into the substratum. The head region and anterior trunk segments are elongated and flexed in the dorso-ventral plane, thus arching the body of the worm and bringing the prostomium of the worm into contact with the mud surface at a steep angle (Pl. 1a). The head is moved from side to side and the prostomial

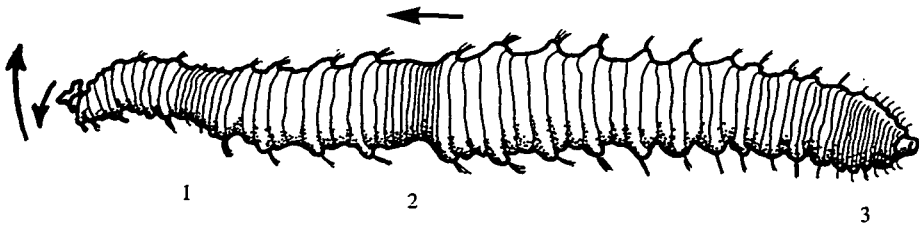


Fig. 1. Drawing made from photographs of *Polyphysia* burrowing into the surface of the substratum. The lateral sinusoidal motion of the head region and the scraping action of the prostomial horns are indicated. At 1 the anterior trunk segments are slightly contracted, allowing for hydraulic extension. A peristaltic constriction is seen travelling anteriorly at 2 and a new constriction is forming in the tail segments, 3. Protrusion of the backwardly directed fans of setae in the dilated trunk and tail segments and in those segments of the head region at the crests of the sinusoidal wave is apparent.

horns perform lateral scraping movements. The lateral head movement is produced by a direct sinusoidal wave which starts at about the posterior end of the 'head region' and travels forward with increasing amplitude to the head (Text-fig. 1). The frequency of this direct undulatory wave is usually less than 1 per sec (i.e. for the complete cycle, say left to right to left again). At the same time the direct peristaltic waves of contraction, which constitute the principle locomotor mechanism and are analysed below, commence to press the body of the worm forwards. If successful entry into the substratum is made, the worm burrows at a steep angle to the mud surface (Pl. 1 *d*).

#### *Direct peristaltic locomotion*

While burrowing excavation is primarily achieved by tentacular scraping, locomotion of trunk and tail is achieved by means of a direct peristaltic wave which involves simultaneous contraction of both circular and longitudinal muscles of the body wall. In order to describe and quantify the changes in the segmental body-wall configuration during the passage of a peristaltic wave photographs of actively burrowing worms were taken using electronic flash (Pl. 1). From suitable frames measurements were made of the length and diameter of segments in both the contracted and the extended states in a number of worms. Only photographs of worms burrowing into the surface mud in open trays were used since accurate measurements of segmental dimensions could not be obtained from photographs of worms completely buried in the substratum as they burrowed alongside glass 'windows'. Observations by the latter method, however, suggest that the type of locomotion employed by the animals is similar whether the body is burrowing into the surface or enclosed in a burrow. Only photographs taken when the camera was at right angles to the long axis of the worm were used in the analysis.

Table 1 gives the dimensions, from five worms, of ten pairs of adjacent segments in which one segment is in the contracted state while its neighbour is in the extended state. The odd-numbered pairs are from the anterior of the advancing rings of constriction and the even-numbered pairs from the posterior margins. From the means in Table 1 it can be calculated that, during the passage of a ring of contraction, segments constrict to approximately 80% of their expanded diameter (expanded to

Table 1. *Segmental dimensions (mm) measured from flash photographs of burrowing Polyphysia during the passage of a peristaltic wave*

Worm no.	Margin of peristaltic constriction	Segmental Pair no.	Dilated segments		Contracted segments	
			Diameter	Length	Diameter	Length
I	Anterior	1	6.3	3.7	5.8	1.1
	Posterior	2	7.5	3.4	5.8	1.2
II	Anterior	3	6.4	3.0	5.3	1.5
	Posterior	4	7.5	2.2	5.4	1.5
III	Anterior	5	7.8	3.4	6.7	1.1
	Posterior	6	8.4	2.9	6.6	1.2
IV	Anterior	7	7.5	2.5	6.3	1.2
	Posterior	8	7.9	2.5	6.3	1.1
V	Anterior	9	6.0	3.8	5.4	1.2
	Posterior	10	8.1	3.5	5.4	1.2
		Mean	7.34	3.09	5.90	1.23
		± s.e.	± 0.25	± 0.17	± 0.16	± 0.04

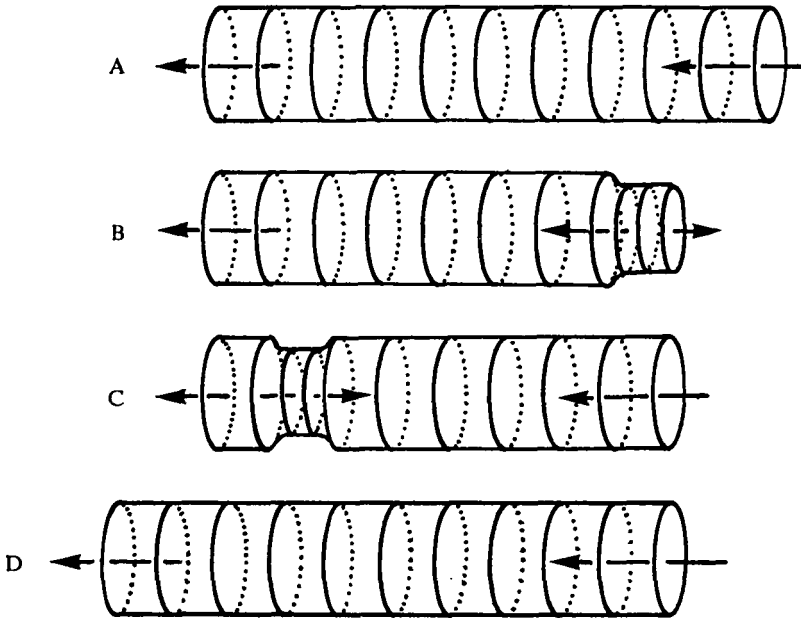


Fig. 2. Diagram illustrating the method of progression involving direct peristaltic constriction in the mid-trunk segments. The head is to the left. In A coelomic fluid is moving anteriorly, displaced by a forming constriction in the tail region. In B and C the arrival and passage of a constriction advances the segments and locally displaces fluid posteriorly; some anterior displacement continues. By D the cycle is completed with the passage of the constriction to segments in front.

contracted width is 7.34:5.90) and shorten to approximately 40% of their extended length (expanded to contracted length is 3.09:1.23). The peristaltic constriction begins at the posterior end of the worm with contraction of circular and longitudinal muscles of several segments (Text-fig. 1). An obvious and well-demarcated ring of constriction, involving some three segments, then travels forwards towards the head region. As the advancing wave first reaches a particular segment of the trunk or tail,

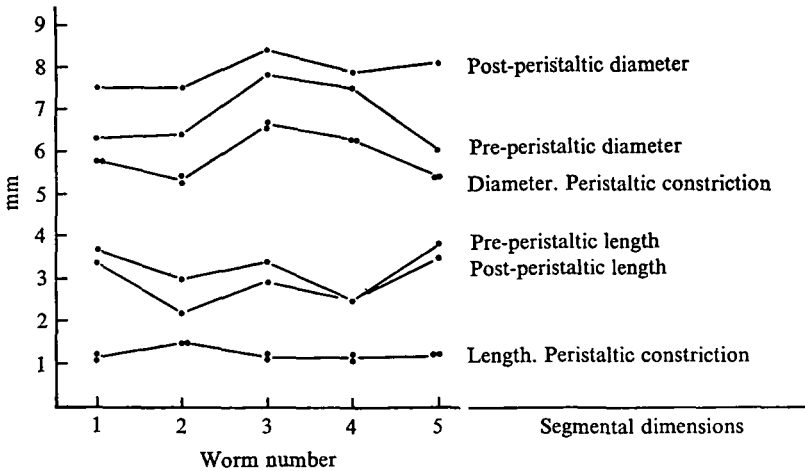


Fig. 3. The data of Table 1 have been replotted to separate the dimensions of pre- and post-peristaltic segments. It can be seen that postperistaltic segments are consistently wider and shorter than preperistaltic segments, at least in worms crawling on the surface.

contact with the substratum (or burrow wall in the case of a buried worm) is lost due to the contraction of the circular muscles, and the segment shortens due to the contraction of the longitudinal muscles. The now contracted segment continues to advance as the peristaltic constriction reaches and shortens the segments immediately anterior to it. Since the ring of constriction involves some three segments, and each may shorten to approximately 40% of its extended length, the distance by which a peristaltic wave advances a segment may be almost the length of two dilated segments (Text-fig. 2). As the constriction advances past a segment the muscle layers relax and contact is again made with the substratum or with the burrow wall in the case of submerged worms. Using the method of Gray (1968) it can be shown that the relative amount by which the body of the animal is advanced by the passage of one peristaltic wave may be as much as one-fifth of a wavelength in animals exhibiting the shortest wavelengths observed (10–11 segments) during locomotion over the surface of the substratum. This is closely comparable to the advancement of one-fifth to one-seventh of the wavelength per cycle which may be estimated from Fig. 1 of Gray & Lissmann (1938), for the earthworm.

The lateral scraping movements of the prostomial horns and the forward progression of the body by means of direct peristaltic waves are shown by fully buried animals, but there are also differences. Thus worms which are almost submerged in the substratum are observed to perform strong periodic contractures of the longitudinal muscles during which the tail is pulled down into the burrow. Such 'thrusts' appear to alternate with periods of peristaltic progression and are followed by relaxation and re-emergence of the tail from the burrow. It seems possible that these thrusts serve to dilate the burrow and to consolidate the walls with mucus in much the way that Seymour (1971*b*) has described for *Arenicola*.

While the direct peristaltic waves appear to be similar whether the animal is lying on the surface or submerged in a burrow, it is probable that the configuration of

distended segments varies between that photographed in Pl. 1 *a-d* and that of worms enclosed in a burrow. Thus it was frequently observed in worms crawling on the surface or commencing to burrow into it that the segmental diameter was greatest immediately following the peristaltic ring of contraction. The segmental diameter gradually diminishes as the next ring of constriction advances and although there is still a definite transition from the dimensions of preperistaltic contraction to those of the ring as the wave reaches a segment, the most abrupt change in the cycle is at the emergence of a segment from the tightly contracted ring to the dilated configuration which immediately follows. This is apparent in Pl. 1 *d* and is shown in the analysis of five rings of peristaltic contraction in Table 1. The data of Table 1 are replotted in Text-fig. 3 which shows that segments immediately following the ring of contraction are consistently shorter in length but of greater diameter than those immediately prior to the ring. The tone of the circular muscles in segments immediately following the ring of constriction is probably less than at any other phase of the locomotor cycle but the degree of dilation seen in such segments in worms crawling on the surface may not be possible in animals within the restriction of a burrow.

Since both circular and longitudinal muscle layers contract during the passage of a peristaltic wave it follows that the volume of the segment will be much reduced at this time. Assuming that the volume of the body wall tissues and other organs remains constant there must therefore be considerable coelomic fluid displacement as the wave passes. That this is so can readily be seen in gravid female worms; the bright yellow ova accumulate in the coelom and can be seen through the body wall moving forwards and then backwards again in the coelom as a peristaltic wave passes along the body.

#### *Continuous head progression*

During burrowing it is observed that the head end of the worm is continuously pressed forwards against the mud as the prostomial horns sweep from side to side. The cyclical advance of trunk and tail segments by means of the peristaltic waves must therefore be converted into a non-cyclical progression at the head region. The obvious ring of contraction can be observed to travel along the body of the worm from its point of origin in the tail segments to the anterior trunk region where it fades out about the 6th to 8th setigerous segments. The arrival of the wave at the anterior trunk region places the segments of that region in a shortened state, with a consequently reduced coelomic volume. When a new ring of constriction starts to travel forwards coelomic fluid is displaced posteriorly to distend segments immediately behind. The posterior segments, however, almost immediately begin to contract in a steady and progressive manner until a new ring of circular and longitudinal contraction is ready to travel forward. During locomotion the posterior tail region is therefore almost always in a contracted or partially contracted state. Such initiation of a new peristaltic wave by progressive constriction of the most posterior body segments must displace coelomic fluid steadily towards the anterior end, and it is probably this hydraulic force which maintains the forward pressure on the head end while distending the anterior trunk segments once more. The arrival of another wave of contraction at the anterior trunk region will complete the cycle by reducing the volume of the segments in that region and displacing the coelomic fluid posteriorly again. The anterior trunk segments in the region of the 6th to 8th segments therefore, like the posterior tail

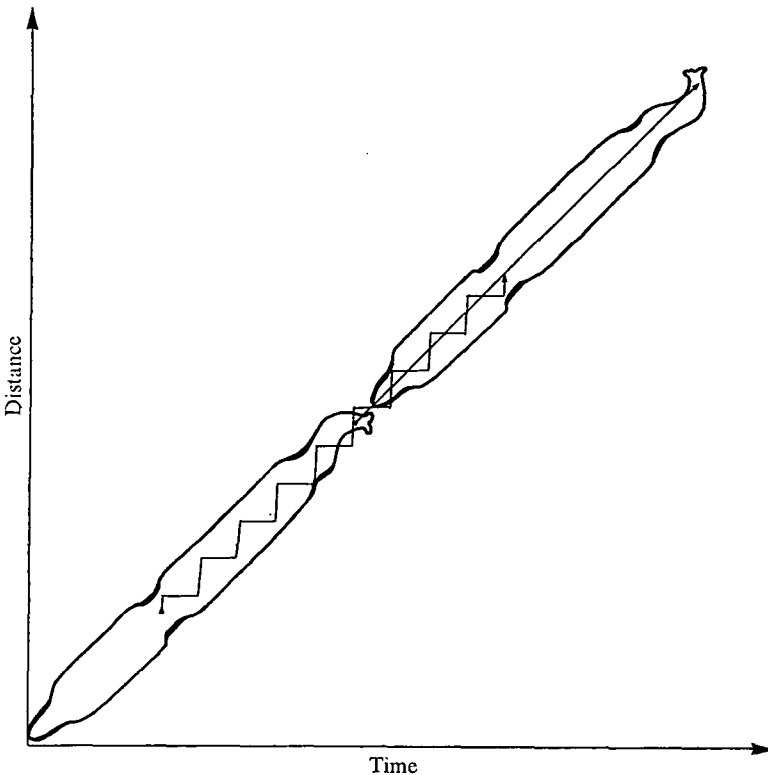


Fig. 4. Diagram illustrating the periodic progression of segments in the mid-trunk region; and, in contrast, the continuous progression of the head region. See text for further details.

segments, are maintained in a contracted or partly contracted state for most of the locomotor cycle, although the anterior trunk segments are gradually distending while those of the posterior tail are gradually contracting. In contrast to the segments of these two regions, all the intervening segments in the trunk and tail region exist in the extended phase for most of the locomotor cycle, contracting only briefly as a peristaltic ring passes. During the locomotor cycle coelomic fluid is slowly and progressively displaced anteriorly through the whole length of the tail and trunk from contracting tail segments to the extending anterior trunk region and is rapidly and locally transferred posteriorly again by the passage of the peristaltic ring of constriction. The cyclical advance of the trunk and tail segments is thus reconciled with the steady progression of the head region into the substratum. The situation can be diagrammatically represented as in Text-fig. 4.

While the maintained pressure from the rear probably plays the major role in keeping the prostomial horns pressed against the anterior face of the burrow it is probably not the only factor. The direct sinusoidal wave which arises in the setigerous segments of the head region and the backward thrust of the posteriorly directed fans of fine setae on these segments have been described above. The effective stroke of these parapodia probably serves two functions, first to help push the mud, scraped by the prostomial horns, laterally and posteriorly, and secondly to advance the head region

thus augmenting the forward thrust generated by the hydrostatic pressure of the trunk and tail region.

In Text-fig. 5 some differences are summarized between the mechanism of locomotion by direct peristaltic waves of constriction, as described above for *Polyphysia*, and aspects of the better known locomotor mechanisms of the earthworm (Gray & Lissmann, 1938), a septate crevice burrower (Roots & Phillips, 1960; Seymour, 1970), and the non-septate *Arenicola* during tailward creeping in its burrow (Wells, 1961).

#### *Body-wall configuration*

Hydraulic deployment of body fluids is well known in a wide range of soft-bodied invertebrates (Chapman, 1958; Clark, 1964). The features which distinguish the direct peristaltic locomotor wave of *Polyphysia* are the degree of simultaneous longitudinal and circular muscle contraction and the sharpness of the transition from the constricted to the dilated state. If the segments are regarded as being cylindrical in shape and over short lengths of the trunk region as being of comparable dimensions in the narcotized animal it can be calculated from the means in Table 1 that the total segmental volume is reduced to approximately one-quarter of the dilated volume during the passage of a peristaltic constriction. The coelomic fluid displacement which results from this has been noted above. On the assumption that the volume of the body-wall tissues remains constant it also follows that the thickness of the body wall must increase significantly during these changes in segmental dimensions.

In histological preparations thickness variations of up to fourfold have been encountered in comparisons of the body wall between constricted and extended segments of the same animal (H. Y. Elder, in preparation). Although these configurations may not be related to the dimensional changes involved in locomotion they do show that the body wall is capable of extensive deformation, a property conferred by the elaborate three-dimensional collagen system and integrated elastic fibre network of the thick dermal connective tissue layer (Elder, 1972).

#### *Dimensions of the direct peristaltic wave*

Calculations based on the data in Table 1 from photographs of burrowing animals and histological methods can be used to estimate the degree of change in the body-wall dimensions during the passage of a peristaltic wave. The shape of each segment is regarded as being that of a hollow cylinder. All calculations assume that the volume of tissue in the body wall remains constant during configurational changes and take no account of the corrugations of the cuticle or the existence of the parapodia.

If cylinder 1 in Text-fig. 6 represents the mean dilated segmental dimensions, the diameter ( $D_1$ ) and the length ( $L_1$ ) are known from Table 1. If the assumption is made that the body-wall thickness in a narcotized worm is similar to that of an extended segment of an active worm then  $T_1$  the body-wall thickness may be obtained from histological sections from narcotized worms.  $r_1$  is obtained as  $R_1 - T_1$  and the total volume ( $V_1$ ) and the coelomic volume including viscera, ( $v_1$ ) may be readily calculated. The difference between  $V_1$  and  $v_1$  gives the volume of the body-wall tissues ( $V_{BW}$ ). If cylinder 2 in Text-fig. 6 represents the mean contracted segmental dimensions the total volume ( $V_2$ ) is again obtained from the means in Table 1. The coelomic volume ( $v_2$ ) is given by  $V_2 - V_{BW}$ . The radius of the coelomic space ( $r_2$ ) may therefore be



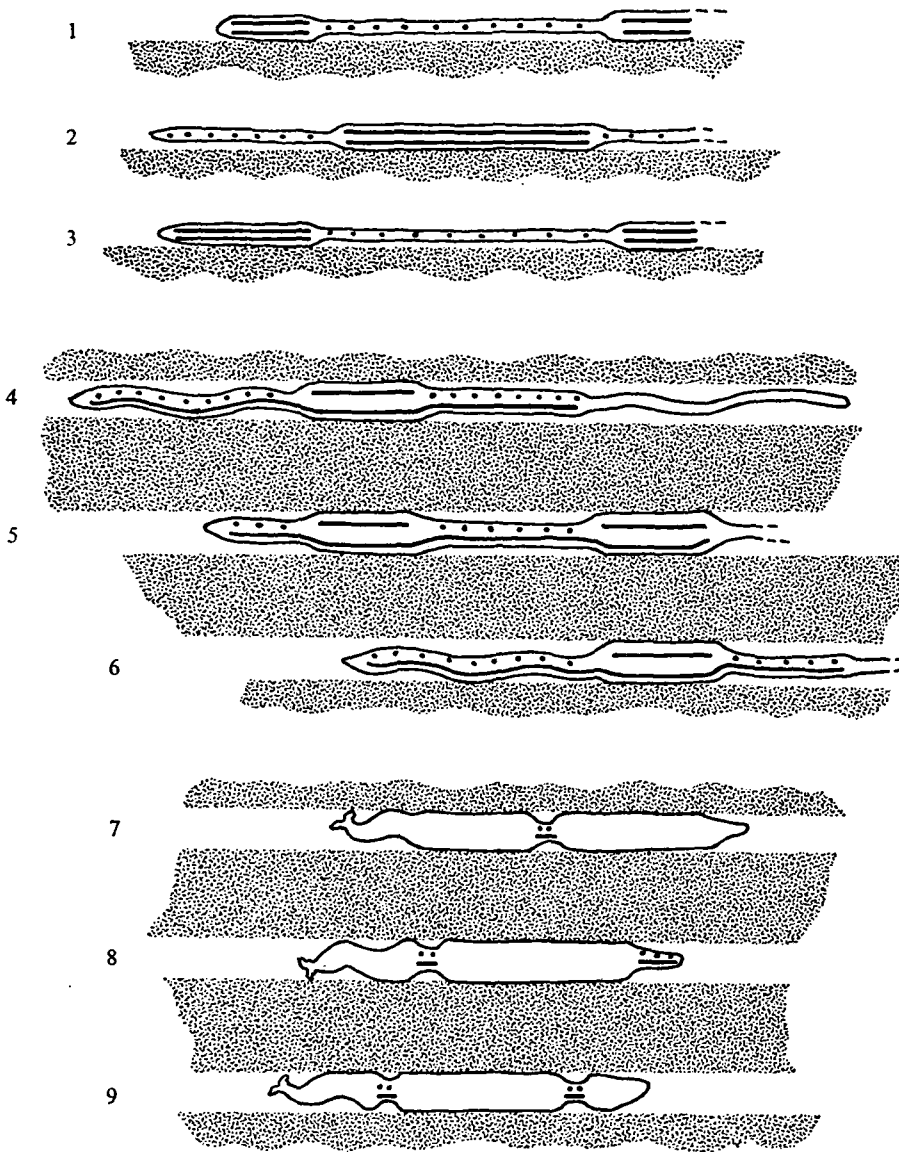


Fig. 5. Diagram comparing some aspects of the locomotion in *Lumbricus*, *Arenicola* and *Polyphysia*; the head is to the left in each. The muscle layer, longitudinal —, or circular ·····, predominantly contracted in any region is indicated. In *Lumbricus*, 1-3 (after Gray & Lissmann, 1938) the waves are retrograde, the animal is septate and the relation between circular and longitudinal muscle contraction is largely reciprocal. The *points d'appui* move relative to the ground and the direction of movement is opposite to that of wave travel. 4-6 illustrate 'tailward creeping' in *Arenicola* (after Wells, 1961). The trunk coelom is not compartmented and the waves are again retrograde, i.e. in the opposite direction to travel. The *points d'appui* are stationary relative to the substratum and are regions of relative relaxation of circular muscle. 7-9 illustrate forward progression in *Polyphysia*. The trunk and tail segments are not compartmented. The peristaltic waves are direct, *points d'appui* move relative to the substratum and are regions of relative relaxation of circular and longitudinal muscles.

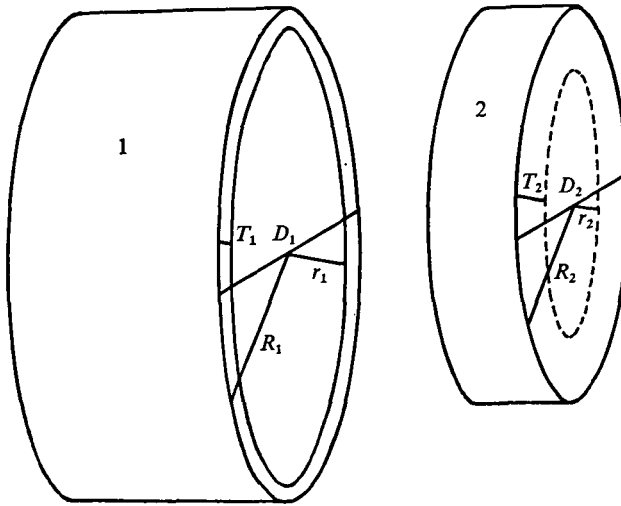


Fig. 6. Diagram illustrating the methods of estimating the increase in the thickness of the body wall during the passage of a peristaltic constriction. See text for further details.

calculated and the value of  $T_2$  may be obtained from  $R_2 - r_2$ . Calculations from two worms for which histological data were available (narcotized segmental diameters of 7320 and 5610  $\mu\text{m}$  and body-wall thickness of 390 and 220  $\mu\text{m}$  respectively) gave values for the expected increase in body-wall thickness ( $T_2/T_1$ ) during the passage of a peristaltic wave of 4 and 3.7 respectively.

The above method is circuitous and depends upon the availability of histological data. A more rapid method, involving an approximation but having the advantage of requiring only data from the flash photographs of active worms, was utilized. The derivation of the approximation

$$\frac{T_2}{T_1} \approx \frac{L_1 D_1}{L_2 D_2},$$

where  $T_1$ ,  $L_1$ ,  $D_1$  and  $T_2$ ,  $L_2$  and  $D_2$  are the body-wall thickness, segmental length and diameter of the dilated and contracted segments respectively, is given in Appendix 1.

The method was applied to the ten pairs of measured segments from the five worms in Table 1. The results are set out in Table 2 from which it can be seen that the body wall is estimated to increase in thickness by a factor from just over 2 to almost 4.4, with a mean of 3.17. Estimates of the error involved in the approximation (see Appendix 1) suggest that the actual increase in thickness should be some 20% more than the method indicates.

All of the methods of estimating the variation in radial dimension of the body wall are subject to error, but the methods of calculation based upon photographs of active animals indicate that the increase in thickness during the passage of a peristaltic constriction may be of the order of three- to fourfold and histological examination confirms that the body wall can change in dimension by this amount. Text-fig. 7 illustrates diagrammatically a fourfold increase in the thickness of the body wall while the outer diameter of the constricted segment (B) has decreased to 80% of the

Table 2. Ratios of the body-wall thickness in the constricted state ( $T_2$ ) to the distended state ( $T_1$ ) calculated by the approximation method for the segmental pairs of Table 1

Segmental pair no.	$T_2:T_1$	Mean $\pm$ S.E.
1	3.65	3.17 $\pm$ 0.22
2	3.66	
3	2.42	
4	2.04	
5	3.60	
6	3.06	
7	2.48	
8	2.85	
9	3.52	
10	4.38	

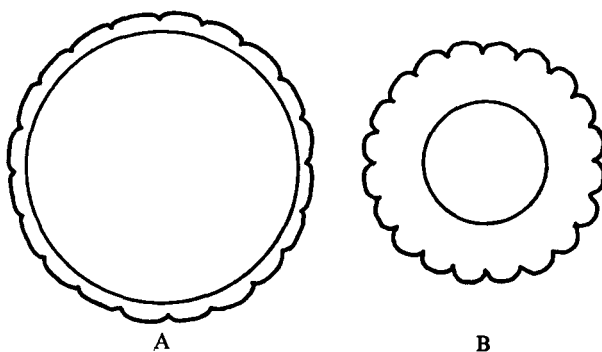


Fig. 7. Diagram illustrating the change in dimensions of a cross-section of *Polyphysia* during the passage of a peristaltic constriction. In the contracted state, B, the total diameter has decreased to approximately 80% of the distended dimension, A, and the body-wall thickness has increased fourfold. The outer (cuticular) circumference has been kept constant in both by increasing the degree of corrugation in B.

value of the distended configuration (A) as observed above. The ratio of the body-wall thickness to the total diameter in A is approximately that measured in histological sections of narcotized animals. Cuticular circumference has been kept the same in both segments by increasing the degree of corrugation in B.

With this estimate of the degree of change in the radial dimension of the body wall the volume of coelomic fluid displaced during the passage of a peristaltic wave can readily be shown to be approximately 90% of the distended volume. Histological evidence suggests that the volume of the gut and other organs within the coelomic cavity, though variable, may be significantly greater than 10% of the distended volume. Thus either the degree of reduction calculated above for the coelomic cavity could not occur, or the gut would be compressed. In either event it seems likely that virtually the total volume of coelomic fluid would be displaced. Moreover, the constrictions may play a role in the propulsion of blood in the peri-intestinal haemal sinuses and in the movement of the gut contents.

## DISCUSSION

*Basic burrowing mechanism*

Analysis of the burrowing activity of *Polyphysia* reveals a mechanism which departs from the generalized scheme suggested by Trueman (1968) and Trueman & Ansell (1969) for soft-bodied burrowing animals. The body of the worm does form a penetration anchor in the sense that it provides a firm and continuously advancing base from which the terminal portion can obtain the purchase necessary to excavate the burrow. The anterior end, however, achieves penetration of the substratum by scraping the mud laterally rather than by exerting thrust along the long axis of the body and against the 'penetration anchor', and at no time does a terminal anchor form. This means that the trunk region cannot pull upon a distal *point d'appui* but must effect its own advance by means of the trains of direct peristaltic locomotor waves.

It is probably best to regard the special features of the locomotor pattern of *Polyphysia* not as a breach of the concept of the basic mechanism but as a specialized derivation. On a temporal basis other soft-bodied burrowing animals alternate penetration phases with body progression, while in *Polyphysia* during periods of active burrowing the head region of the worm progresses steadily into the substratum, although the advance of the trunk and tail segments is periodic. On the other hand, from the functional morphological viewpoint all soft-bodied burrowing animals including *Polyphysia* possess a terminal region specialized for substrate penetration and a region adapted to form the penetration anchor. Burrowing excavation by means of lateral scraping is found in several soft-bodied burrowers and is the rule in burrowing forms with hard skeletal parts, e.g. many burrowing crustaceans, the xiphosuran, *Limulus*, and the spatangoid sea urchins. In other groups of the echinoderms the starfish *Astropecten* utilizes tube feet for scraping the sand laterally from beneath its arms and, most significantly, the worm-like holothurian, *Leptosynapta*, excavates its burrow by the lateral scraping action of the circum-oral tentacles (Elder, 1973). The polychaete *Aphrodite* excavates, mole-like, by scraping the substrate laterally with its chaetae. Future work will probably reveal further examples of soft-bodied burrowing animals which employ lateral scraping rather than a longitudinally protruded terminal anchor, and though instances of scraping excavation are of less importance than the latter they should not be overlooked in attempts to define a uniform burrowing mechanism. Certainly generalizations such as that in Clark (1964) that 'Direct locomotory waves, in which the *points d'appui* occur where the underlying longitudinal muscles are relaxed, are obviously inappropriate for animals living in burrows...' require modification, as Mettam (1969) has pointed out. Trueman & Ansell (1968) draw attention to the use of peristaltic locomotory waves for movement along a burrow in *Arenicola* and in the anthozoan *Peachia*. During burrowing and locomotion along the surface *Polyphysia* provides a clear example of direct peristaltic progression in which the longitudinal muscles of the *points d'appui* must be under less tension than those involved in the peristaltic constriction.

*Direct peristaltic progression*

It was originally shown by Gray (1939) that waves of muscular activity passing either from tail to head or from head to tail in worm-like animals could be used in locomotion. The direction of locomotion produced either by peristaltic or by undulatory waves depends upon both the direction of the propagated wave and the phase of the cycle at which the segments attach to the ground (Gray, 1968). Considering peristaltic locomotion, in both septate and non-septate worm-like animals, Mettam (1969) examined the possible mechanisms which would result in forward locomotion, namely retrograde waves in septate animals, of constriction with circular muscle contraction or of dilation with longitudinal muscle contraction and, in non-septate animals, the additional possible mechanisms involving direct waves of constriction with both longitudinal and circular muscle layers contracted or of dilation with relaxation of both circular and longitudinal muscle layers. The literature provides examples of three of these types of mechanism (Mettam, 1969), but until the present account there have been no examples of worm-like animals utilizing direct waves of pronounced simultaneous circular and longitudinal muscle contraction.

A less pronounced and less obvious direct peristaltic wave than that described here for *Polyphysia* but also involving a region of simultaneous longitudinal and circular muscle contraction has been documented in the studies by Wells (1949), Trueman (1966) and Seymour (1971*b*) on *Arenicola*. This pattern of muscle activity is possible only in an animal without watertight septa and allows coelomic fluid pressure generated by segments contracting in one region of the body to be deployed at another (Chapman, 1958, 1967). A similar hydraulic function of the coelomic fluid occurs in the trunk and tail of *Polyphysia*. During the phase of formation of a ring of constriction fluid is slowly and steadily transferred forwards from the tail region to extend the anterior trunk segments (6–8), enabling them to provide a firm and steadily advancing base for the activities of the head region. The coelomic fluid is locally more rapidly returned, segment by segment, as a peristaltic constriction travels headwards along the body.

*Role of the septa*

The series of four complete septa in the head region probably serves to isolate the coelomic fluid of that region from the rest of the body cavity and to permit the sinusoidal movements observed in the head region since the parapodial power stroke (and probably also the lateral scraping action of the prostomial horns) is derived largely from the contralateral longitudinal muscles via the coelomic fluid (Gray, 1939, 1968). The simple strand-like form of the series of incomplete septa in the tail region of *Polyphysia*, unlike those of *Arenicola* which can be closed to isolate the region from the coelomic pressure peaks of the trunk coelom (Seymour, 1971*b*), precludes any hydrostatic isolation function. They may, however, serve to prevent rectal eversion during defecation, as Wells (1961) has suggested additionally for *Arenicola*.

*Function of the body-wall connective tissue*

Evidence for the existence of both collagen and a type of invertebrate elastic fibre in the body-wall connective tissues of *Polyphysia* (= *Lipobranchius*) was presented by

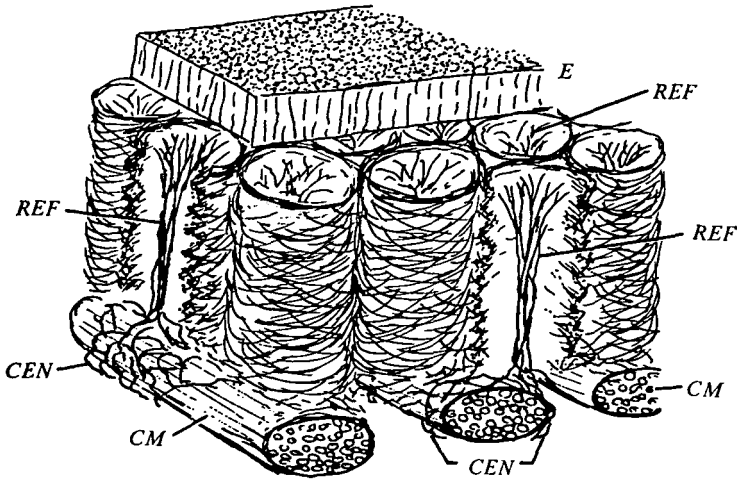


Fig. 8. Diagram illustrating the fibrous construction of the connective tissue layer in the body wall of *Polyphysia*. The radially oriented 'honeycomb units' of the three-dimensional collagen lattice are shown extending between the circular muscle layer (CM) and the epidermis (E). Radially oriented columns of elastic fibres (REF) extend from the coarse elastic network (CEN) around the muscle bundles, to the epithelial basement membrane. See text for further explanation. Modified after Elder (1972).

Elder & Owen (1967). The fibre organization in the thick dermal connective tissue layer has recently been described (Elder, 1972). Collagen fibres follow an essentially spiral course around the cylindrical body but are integrated in a three-dimensional lattice which is capable of extensive deformation in the radial plane as well as longitudinally or circumferentially. The elastic fibres on the other hand form a system of radially oriented columns traversing the connective tissue layer and linking the epidermal basement membrane with a coarse network of elastic fibres surrounding the circular muscle layer (Text-fig. 8).

In earthworm cuticles collagenous fibres are found in a secreted matrix (Watson, 1958; Coggeshall, 1966; Pikkarainen & Kulonen, 1972), and Clark (1964) points out that the relatively inextensible and inflexible annelid cuticle places limits on the deformability of the annelid body. Calculations suggest that the apparent surface area of the cuticle in *Polyphysia* decreases to one-third of its extended surface area during the passage of a peristaltic ring of constriction. Histological examination shows that the cuticle achieves flexibility by being very thin (approximately  $1.3 \mu\text{m}$ ) and extensibility by virtue of the longitudinal and circumferential folds into which it is thrown in constricted segments (Elder, 1972). The cuticular surface area may remain constant, although the apparent segmental surface area varies by a factor of at least three, and one function of the thick connective tissue layer would therefore be to accommodate the extensive folding of the cuticle and its underlying epidermis during simultaneous circular and longitudinal muscle contraction (Text-fig. 7).

On the assumption of a constant volume for the tissues of the body wall during configurational changes it was calculated above that the radial dimension may increase by a factor of 3 to 4 during the passage of a peristaltic constriction. The radial elastic fibre columns are extended during this phase of locomotion and their function may be

to control the folding of the epidermis and cuticle. The degree of deformability thus conferred is shown not only by the threefold variation in the effective cuticular surface area but also in the abruptness of the transition between the fully constricted and fully distended segmental configurations. The more gradual transition between contracted and extended configurations during the passage of a direct peristaltic wave in *Arenicola* (Seymour, 1971*b*), or even between shortened and lengthened segments in the earthworm (Gray, 1968), contrasts strongly with the transition within the length of one segment in *Polyphysia*.

#### *Assumptions in calculations*

A number of assumptions and approximations have been made in estimating the degree of body-wall deformation during the passage of a peristaltic wave. Principally amongst these, as a basis for histological measurement, the assumption was made that the dimensions of segments in the narcotized worm are similar to those of dilated segments in actively burrowing animals. In the latter, however, up to approximately one quarter of the trunk and tail segments at any one time may be involved in peristaltic constriction and have their coelomic volume reduced by approximately 90%. Thus the volume of the narcotized segments will be less and the thickness of the body wall greater than in dilated segments of the active worm. This will result in an over-estimate of the degree of radial increase during the passage of a peristaltic constriction. It will also result in a small overestimate of the error involved in the approximation method. The effect of the approximation involved in ignoring the presence of parapodia will be to underestimate slightly the volume of coelomic fluid displaced since the small, hollow parapodia are retracted during the passage of a peristaltic constriction.

It is concluded that none of the assumptions seriously affects the estimate that the body wall increases in thickness by some three- to fourfold during the passage of a peristaltic constriction.

#### *Adaptations to the soft mud habitat*

In the Clyde estuary *Polyphysia* is taken in the flocculent muds of the deeper waters. It seems possible that the common polychaete burrowing mechanism, by alternate formation of penetration and terminal anchorage points (Trueman, 1968), is less appropriate to dwellers in soft mud. In this method of burrowing, exerted force and reaction are along the long axis of the body and longitudinal slippage is resisted by friction of the body wall and chetae. The polarity of the applied force alternates and its magnitude fluctuates regularly, with periodic maxima. The scraping excavation of *Polyphysia* exerts a smaller but more constant force against the substratum with reaction to the lateral scraping at right angles to the long axis of the body; there is no terminal anchor which might pull out of the soft mud. The trunk and tail do form an 'excavation anchor' equivalent to the penetration anchor of other soft-bodied burrowing forms as discussed above, but because of the utilization of direct peristaltic waves involving localized contraction as much as three-quarters of the trunk and tail segments grip the burrow walls at any one time; the applied force is continuous and unidirectional. The role of the connective tissue in permitting this form of locomotion has been discussed above.

Both of the body-wall muscle layers are thin in *Polyphysia* and it seems probable that the coelomic pressure will prove to be low. Measurements of the coelomic pressure, by continuous recording with a pressure transducer, in another tentacular burrowing animal (*Leptosynapta tenuis*) which exhibits direct peristaltic waves, showed that pressures of only 2–3 cm of water were employed during active burrowing (Hunter & Elder, 1967). Further work will probably reveal a similar pattern in *Polyphysia*; a pattern which contrasts strongly with the higher pressures employed, and the periodic pressure peaks, in burrowers of the terminal anchorage type (Trueman, 1966; Trueman & Ansell, 1969; Seymour, 1971*b*). The drawback to the type of locomotion involving direct peristaltic constriction, noted by Clark (1964) and Mettam (1969), that it must be a low-pressure system since the hydraulic force from contraction in many segments must be resisted by the few involved in the ring of constriction has been turned to advantage by this inhabitant of the soft mud habitat.

#### SUMMARY

1. *Polyphysia* excavates its burrow in soft, sublittoral mud by sinusoidal waves of the septate anterior region of the body and the lateral scraping action of the prostomial horns.

2. Associated with discrete, direct peristaltic constrictions, in which the longitudinal muscles shorten to 40%, and the circulars to 80%, of their distended lengths, hydraulic deployment of coelomic fluid converts the periodic advance of the trunk segments into continuous head progression.

3. Direct peristaltic progression advances the body by one-fifth or less of a wavelength per cycle, which is comparable to the figure for earthworm locomotion.

4. A three-dimensional dermal collagen fibre lattice accommodates extensive folding of the cuticle and epidermis while permitting a three- to fourfold increase in the radial dimension of the body wall during peristaltic constriction. Elastic fibre columns oppose the radial distension and control the cuticular folding.

5. These features are seen as adaptations to burrowing in the soft mud habitat. The high degree of body-wall flexibility permits the transition from contracted to distended configuration within the length of one segment. Some three-quarters of the body surface may be in contact with the burrow wall at any one time. Unlike other soft-bodied burrowing animals the force exerted on the burrow wall is unidirectional and the applied pressure is probably small, relatively constant and spread over a wide area.

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## APPENDIX

*Derivation of the approximation and the error involved*

The terms used are as in Text-fig. 6. On the assumption that the volume of the body-wall tissues of comparable segments remains a constant ( $K$ ) during configurational changes, then

$$\begin{aligned}\pi R^2 L - \pi r^2 L &= K, \\ \pi L (R^2 - r^2) &= K, \\ \pi L (R+r)(R-r) &= K, \\ R-r &= \frac{K}{\pi L (R+r)}.\end{aligned}$$

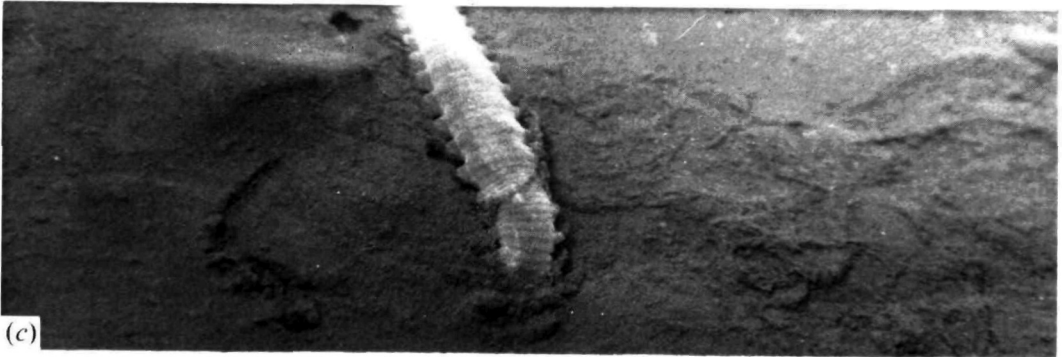
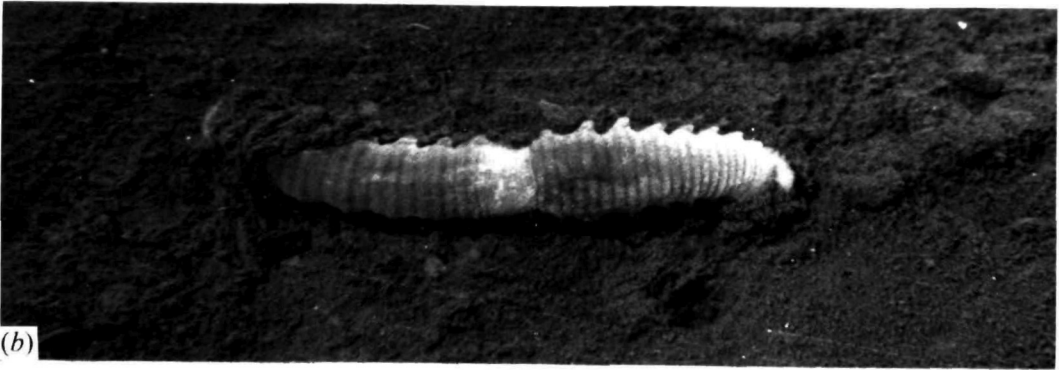
Taking the ratio of the body-wall thickness in the contracted state to that in the dilated state gives,

$$\begin{aligned}\frac{R_2 - r_2}{R_1 - r_1} &= \frac{\pi L_1 (R_1 + r_1)}{K} \frac{K}{\pi L_2 (R_2 + r_2)}, \\ \frac{T_2}{T_1} &= \frac{L_1 (R_1 + r_1)}{L_2 (R_2 + r_2)}.\end{aligned}$$

Provided that the difference between  $R$  and  $r$  is small, we may substitute  $D$  for  $R+r$ , giving,

$$\frac{T_2}{T_1} \approx \frac{D_1 L_1}{D_2 L_2}.$$

The approximation involved in substituting  $D$  for  $R+r$  seems admissible in the dilated segments with a body-wall thickness of 0.2–0.4 mm in a total segmental diameter of some 5–7 mm. It rapidly becomes less so as the segmental diameter decreases and the body-wall thickness increases during the passage of the ring of constriction. Some estimate of the error involved in the approximation can be obtained by substituting data from histological examination. From the two examples given above (p. 12) the ratios of  $T_2/T_1$  were 4 and 3.7 respectively. From Table 2 the mean of  $T_2/T_1$  by the approximation method is 3.17. This latter value is therefore probably underestimated by some 21 and 14% respectively for these two examples.



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(Facing p. 655)

EXPLANATION OF PLATE

(a) A specimen of *Polyphysia* starting to burrow by arching the body off the mud surface, bringing the prostomial horns into contact with the substratum at a steep angle. The head is to the right and a peristaltic constriction is travelling from left to right along the trunk segments. A ring of mucus and mud around the trunk has been passed backwards from the head region by the backward thrust of the parapodia. On the right a previous burrow, now partly filled in, is visible.

(b) A worm attempting to burrow into the substratum, head to the left. The head region is shrouded in a collar of mucus and adhering mud, which probably aids initial penetration. A peristaltic constriction is passing along the trunk from right to left and, as in (a), it can be seen that the parapodia are retracted in the constricted region, and protruded in the other segments.

(c) A worm shortly after initial penetration has been achieved. The head region has not yet submerged and the only purchase is from the parapodial thrust of the head region segments and the frictional force of those segments lying on the surface of the mud (cf. (d)). That region of shortened anterior trunk segments which provides for the advance of the head region by hydraulic extension is seen immediately behind the ring of mucus and mud. On the left, a shallow furrow made by the scraping of the anterior horns in a previous, unsuccessful attempt at initial entry is seen. On the right, extensive deposits of mucus-impregnated mud are visible.

(d) A specimen later in the penetration sequence than that of (c). A few segments of the trunk region have now entered the burrow and a *point d'appui* is achieved by their dilation against the walls (cf. (c)). A peristaltic constriction is passing along the trunk (left to right) and the succeeding constriction is already forming by contraction of the most posterior tail segments. The parapodia are visible as discrete, papillate notopodia and neuropodia. Careful inspection reveals that three segments (three parapodia) are involved in the constriction. Each segment (distended or constricted) has three annulations. See text for further information.