

# FACTORS CONTROLLING THE CHANGE OF SHAPE OF CERTAIN NEMERTEAN AND TURBELLARIAN WORMS

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(With Plate 12)

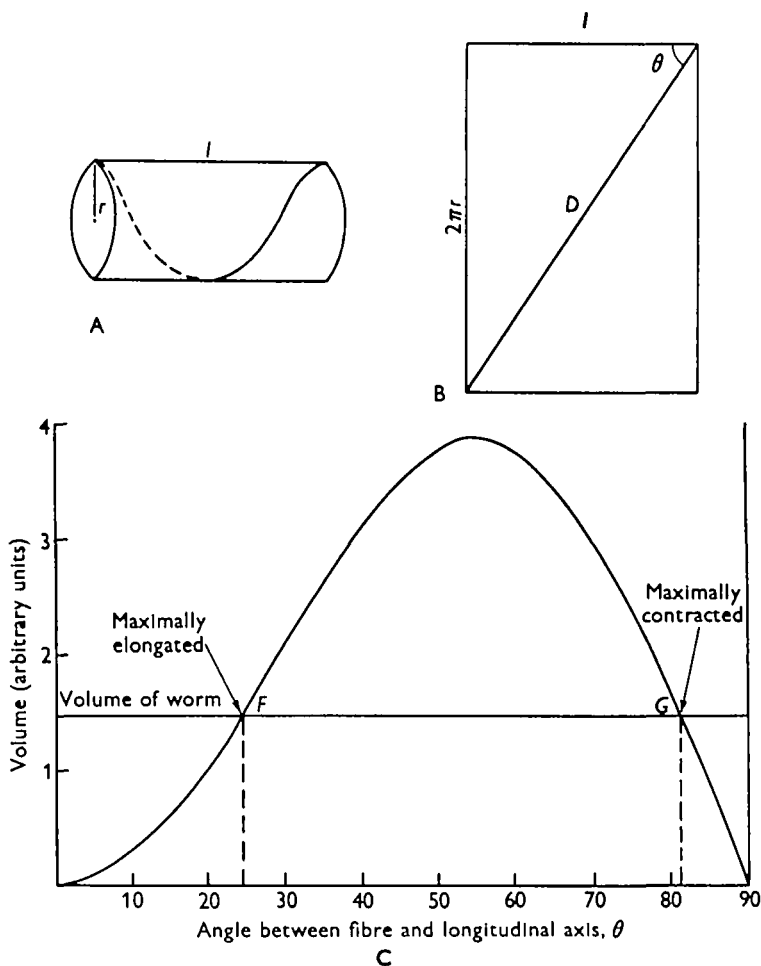
## INTRODUCTION

Two groups of free-living, acoelomate worms, the nemerteans and turbellarians, are noted for their ability to change their shape. The role of circular and longitudinal muscles in producing these changes are well known, but since these worms are not invested by a cuticle, it is not immediately apparent what limits the changes of shape. Obviously the worms are not indefinitely extensible and compressible. Cowey (1952) discovered that the epidermal basement membrane of the nemertean *Amphiporus* is composed of regularly disposed, inextensible fibres arranged in alternate left- and right-handed geodesic helices running around the body of the animal (Text-figs. 1 A; Pl. 12, figs. B, C and D). Although the fibres themselves are inextensible, changes of length of the body, or parts of the body, of the worm are permitted by a change in the angle between intersecting elements in the lattice formed by the fibres, just as in the extension and retraction of lazy tongs or a garden trellis. Cowey demonstrated the way in which these fibres set limits to the change in length of *Amphiporus*. A similar arrangement of fibrillar structures occurs in the cuticle of nematodes and functions in fundamentally the same way, although the nematode system is a highly specialized one (Harris & Crofton, 1957). In this paper we have considered the potentialities of this fibre system and the way it operates in a variety of turbellarians and nemerteans.

In considering the fibre system alone there is a simple relationship between the inclination of the fibres to the longitudinal axis and the length of the system. So for any particular orientation of the fibres the volume depends upon the cross-sectional area. This is greatest when the cross-section is circular, though it may be less if the cross-section is flattened to an ellipse and this can happen without any change in the length of the system, the orientation of the fibres, or the length of the perimeter of the cross-section. As the inclination of the fibres changes, so does the total volume the system can contain. Assuming a circular cross-section throughout, the volume varies as

$$V = \frac{D^3 \sin^3 \theta \cos \theta}{4\pi}, \quad (\text{see Eqn. 2, Appendix})$$

where  $D$  is the length of a single turn of the geodesic fibre bounding the system and  $\theta$  is the angle between the fibre and the longitudinal axis. This relationship is illustrated in Text-fig. 1C and it will be seen that there are two limiting positions. The volume approaches zero as  $\theta$  decreases and the system elongates to become a



Text-fig. 1 A. A unit length of a cylindrical 'worm' bounded by a single turn of the geodesic fibre system. (Fibres running in the opposite sense have been omitted for clarity.) B. The same unit length of worm slit along the top and flattened out. C. The curve represents the theoretical relationship between the volume contained by the fibre system and the inclination of the fibres to the longitudinal axis. The horizontal line represents the actual and constant volume of the nemertean *Amphiporus lactifloreus*. It intersects the curve at  $F$  and  $G$  which are the limiting positions of elongation and contraction, respectively, for that species.

long, thin thread, and the length approaches  $D$ . The other limit, when the volume again approaches zero, is when  $\theta = 90^\circ$ ; the system is then reduced to a thin disk with a circumference equal to  $D$ . At an intermediate point, where  $\tan^2 \theta = 2$ , or  $\theta = 54^\circ 44'$ , the volume contained by the system is at a maximum.

When the antagonistic longitudinal and circular muscles operate on a fluid skeleton it is necessary that the volume should remain constant in order to produce reversible changes of shape (see, for example, Chapman, 1950); and, in fact, in coelomate worms where the coelomic fluid functions as a fluid skeleton, precautions are taken to ensure that none leaks through the nephridia or dorsal pores during the pressure changes that accompany changes in length (Chapman & Newell, 1947; Newell, 1950). When we consider the functioning of the fibre system in a worm it is obvious that if the worm had that volume which is the greatest the fibre system can contain, it would be incapable of any change in length, for to do so would involve a reduction in its volume. This condition almost obtains when a nemertean is full of ripe gonads. However, the volume represented in Text-fig. 1C and Eqn. 2, Appendix, is the maximal and limiting volume for any particular length and orientation of the fibres. The system can always contain less than this volume if the cross-section is elliptical instead of circular. The limits of extension and contraction of the worm are set by the points at which the actual volume of the worm is equal to the greatest volume the system can contain at that particular length and value of  $\theta$ . At these points the worm has a circular cross-section; to extend or contract beyond these points would involve a diminution of volume and that is precluded. Between these points the volume of the worm is less than the limit set by the fibre system and the cross-section is elliptical. The horizontal line in Text-fig. 1C represents the volume of the littoral nemertean *Amphiporus lactifloreus*, and its intersection with the curve at *F* and *G* represent the limits of extension and contraction, respectively, limits which the worm almost reaches in practice and which are determined by the fibre system and the volume of the worm (Cowey, 1952).

In the nematodes the basic properties of the helical fibres in the cuticle are the same as those of the nemertean basement membrane. However, the entire system functions in a highly specialized way in nematodes as Harris & Crofton (1957) have recently demonstrated in their study of *Ascaris*. The chief peculiarities of this nematode (and presumably of other nematodes) are (i) the very high internal hydrostatic pressure, which is opposed by the thick cuticle, and (ii) the existence of only longitudinal muscles in the body wall. As a result of the high internal pressure the cross-section is always circular, although the inclination of the fibres to the longitudinal axis is about  $75^\circ$ . At this point on the curve in Text-fig. 1C a contraction of the longitudinal muscles causing an increase in  $\theta$ , involves a reduction in the volume the fibre-system can contain, or, since the volume of the worm is itself invariable, an increase in turgor pressure. It is this which acts antagonistically to the longitudinal muscles and accounts for the absence of circular muscles. The nematode system can function only over the right-hand half of the curve in Text-fig. 1C. A worm possessing only circular muscles in the body wall could function only over the left-hand half of the curve. Nemerteans and, indeed, all worms other than nematodes and Nematomorpha possess both circular and longitudinal muscles, and the system functions over both right and left halves of the curve within limits set by the volume of the animal and the dimensions of the fibre system.

Helical bounding systems such as occur in the basement membrane of *Amphiporus* and the cuticle of *Ascaris* may be quite widespread, if not general, in soft-bodied, worm-like animals (Picken, Pryor & Swann, 1947). We have, therefore, considered the theoretical potentialities of such a system as they affect the change of length and shape of worms, and have compared the theoretical findings with the actual performance of a number of nemerteans and turbellarians. These worms possess both circular and longitudinal muscles in the body wall and are not constrained by a cuticle. The way in which these muscles can produce changes in body shape within limits set by the fibre system can thus be studied with a minimum of complicating factors.

#### MATERIALS AND METHODS

The following turbellarians and nemerteans have been selected from a wide range of ecological situations to exhibit a variety of body shapes.

##### *Nemerteans*

*Amphiporus lactifloreus* (Johnston), 10 specimens, marine, littoral.

*Lineus gesserensis* (Müller), 10 specimens, marine, littoral.

*L. longissimus* (Gunnerus), 1 specimen, marine, littoral.

*Cerebratulus lacteus* (Leidy), 2 specimens, marine, burrowing and swimming form.

*Malacobdella grossa* (O. F. Müller), 10 specimens, marine, parasitic on the gills of lamellibranchs.

*Geonemertes dendyi* Dakin, 10 specimens, terrestrial.

##### *Turbellarians*

*Dendrocoelum lacteum* Oersted, 10 specimens, fresh-water streams.

*Polycelis niger* Ehrenberg, 10 specimens, fresh-water streams.

*Rhynchodemus bilineatus* (Mecznikow), 2 specimens, terrestrial.

The worms were completely anaesthetized in magnesium chloride sea water, or in 5% pure ethyl alcohol in pond water, and then fixed in Zenker-formol, embedded in celloidin-paraffin and sectioned in the plane of the basement membrane or transversely. They were stained by Wilder's (1935) silver impregnation technique for reticulin fibres.

From the following analysis, it will be seen that the quantities, length and volume, refer to the length and volume of a unit piece of worm which is invested by a single turn of the geodesic helical fibre. Therefore not all the quantities that appear in the equations can be directly measured.

A completely anaesthetized worm takes up the position where  $\theta = 54^\circ 44'$ . This is probably due to a tendency for the semi-fluid constituents of the worm to flatten out as much as possible, and, as we have seen, the greatest flattening that is possible is at the position where there is the greatest discrepancy between the actual volume of the worm and the maximum volume the system can contain. If an anaesthetized worm is passively stretched and then released it returns to this equilibrium, or relaxed, length so that this is a position of great stability which can be

attained simply and reliably and one in which measurements can be made with the greatest accuracy. It is impossible to measure length and volume of a unit section of the worm directly, but they are related to, and can be deduced from, the degree of flattening that occurs in the relaxed position. In fact, the ratio of actual volume to the greatest volume the system can contain is given by

$$\frac{2n_r}{n_r^2 + 1}, \quad (\text{see Eqn. 5, Appendix})$$

where  $n_r$  is the ratio of the length of the major to the minor axis of the elliptical cross-section of the worm in the relaxed position. If  $n_r$  is known, a horizontal line can be drawn on the curve, as in Text-fig. 2C, and its points of intersection with the curve give the theoretical maximum and minimum length of the worm.

The fully extended position can be reached by passively stretching an anaesthetized worm. Once that position is reached considerably greater tension must be applied to tear the tissues. The worm can then be fixed in the fully extended state. The maximally contracted position can be obtained by fixing an unanaesthetized worm directly. Obviously this is a much less accurately determinable position.

From measurements made on the fully extended, fully contracted and relaxed animals, it is possible to calculate all the parameters necessary for a comparison of actual performance with the theoretical predictions.

#### THE STRUCTURE OF THE BASEMENT MEMBRANE

In all nine species of nemerteans and turbellarians studied the structure of the epidermal basement membrane is the same and answers to the description of that of *Amphiporus lactifloreus* given by Cowey (1952). There are alternating layers of reticulin fibres arranged in left- and right-handed geodesic helices. All the worms possess both longitudinal and circular muscles in the body wall, and the fact that some nemerteans have a second layer of longitudinal muscles is irrelevant to the following argument.

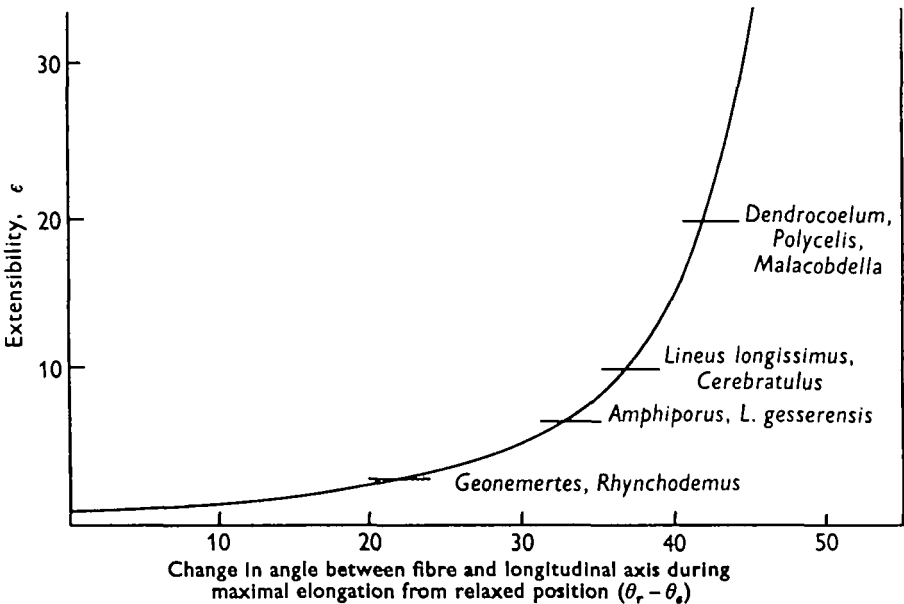
#### THE EXTENSIBILITY OF THE WORMS

The extensibility,  $\epsilon$  (ratio of maximum to minimum lengths), can now be worked out. Text-fig. 2 shows the relationship between the change in the inclination of the fibres on extension from relaxed length to maximum length ( $\theta_r - \theta_c$ ) and the extensibility. The extensibilities which the species under consideration would achieve if the fibre system alone set a limit to their changes in length are marked on the curve. Considerable change in the orientation of the fibres is necessary before large extensibilities are attained, but once a certain point is reached enormous extensibilities are theoretically possible for slight additional changes in the fibre system. The actual extensibilities of the worms can be measured only approximately. The actual and theoretical extensibilities are compared in Table 1.

The performance of the worms with low theoretical extensibilities agrees quite well with the predicted value, those with moderate powers of extension and con-

traction less well, but there is an enormous discrepancy between the theoretical and actual values in those species for which very large extensibilities are predicted.

*Rhynchodemus bilineatus* and *Geonemertes dendyi* have low theoretical extensibilities so that they never depart far from the relaxed position and show a close approximation to a circular cross-section at any length. Their actual extensibility is the same as the theoretical (Text-fig. 3), so that the geodesic fibres are the operative factor in limiting changes of length of these worms.



Text-fig. 2. The theoretical relationship between the extensibility (ratio of fully extended to fully contracted lengths) and the change in the inclination of the fibres from that at the relaxed position as the worm elongates. The theoretical extensibilities of some turbellarians and nemerteans are marked on the curve.

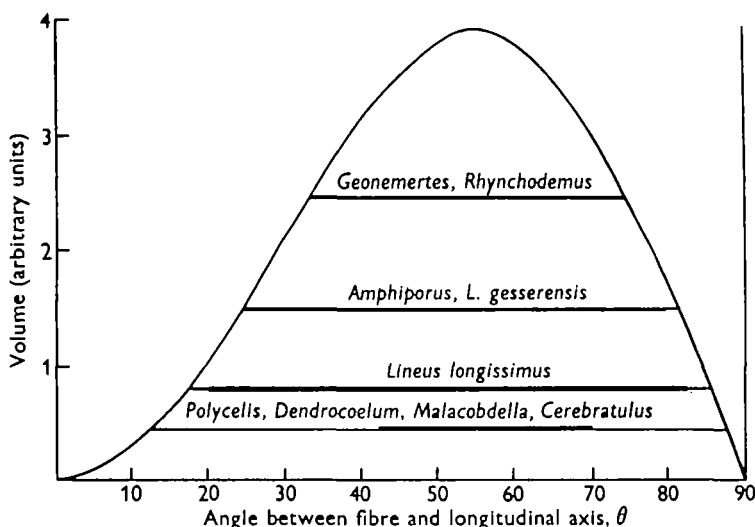
Table 1

Species	Theoretical extensibility	Actual extensibility
<i>Rhynchodemus bilineatus</i>	3	3
<i>Geonemertes dendyi</i>	3-4	3-4
<i>Amphiporus lactifloreus</i>	6-7	5-6
<i>Lineus gesserensis</i>	6-7	5-6
<i>L. longissimus</i>	> 10	< 9
<i>Cerebratulus lacteus</i>	> 10	2-3
<i>Dendrocoelum lacteum</i>	> 20	2-3
<i>Malacobdella grossa</i>	> 20	2-3
<i>Polycelis niger</i>	> 20	2

*Amphiporus lactifloreus*, *Lineus gesserensis* and *L. longissimus* all have an actual extensibility which falls a little short of the theoretical limits of the system. This is indicated by their not quite attaining a circular cross-section at the minimum length

or at both maximum and minimum lengths. The former is the case with *Amphiporus* and *Lineus gesserensis*, the latter with *L. longissimus* (Text-fig. 3). Longitudinal sections of all three species cut from worms that were completely contracted show that the basement membrane is thrown into regular folds (Pl. 12, fig. D), the folds running transversely around the animals. Transverse sections of *L. longissimus* at maximum length also show a regular folding of the basement membrane, but in this case it is a longitudinal folding. Examination of the sections gives the impression that the membrane is folded in order to preserve the area necessary for the support of the epidermal structures resting on it. Whatever the cross-sectional shape of the worm, the surface area is proportional to

$$\sin \theta \cos \theta, \quad (\text{see Eqn. 6, Appendix})$$



Text-fig. 3. The relationship between the volume contained by the fibre system and the inclination of the fibres (as in Text-fig. 1C) on which are superimposed the actual volumes of various nemerteans and turbellarians (fine horizontal lines). The heavy lines show the range over which changes in length take place, indicating where the worms do not reach the limiting positions set by the fibre system (exaggerated for clarity).

and in Text-fig. 4 the relation between the surface area and  $\theta$  is illustrated. The portion of the curve  $XY$  shows how the surface area of *Amphiporus* changes as the worm contracts from maximum to minimum length. The surface area at minimum length is a good deal less than at maximum length and apparently is not sufficient to contain the bases of all the epidermal cells. To some extent this is offset by the folds in the basement membrane which provide the extra area required, but evidently it is insufficient to counteract this effect completely. Thus, in both *Amphiporus* and *Lineus gesserensis*, the maximum length is determined by the fibre system but the minimum length is determined by the minimum surface area which will still accommodate all the epidermal cells. The compression of the epidermis sets a limit to both maximum and minimum lengths of *L. longissimus*, but at the

maximum length the folds are parallel to the longitudinal axis because the circular muscles are contracted and the pressures act transversely in the plane of the basement membrane, i.e. around the worm.

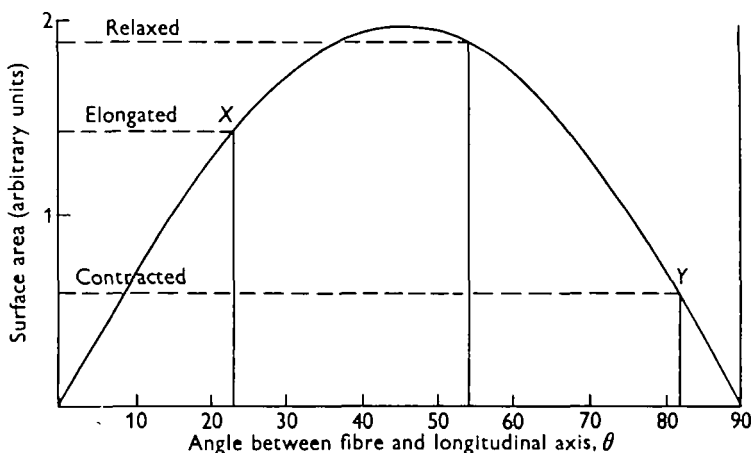
The other four species, *Cerebratulus lacteus*, *Malacobdella grossa*, *Polycelis niger* and *Dendrocoelum lacteum*, all fall very far short of attaining their theoretical extensibilities (Text-fig. 3). The factors responsible for this include:

(1) The longitudinal reticulin fibres in the longitudinal muscle layers which limit the maximum length.

(2) The reticulin fibres in the circular muscle layers (Pl. 12, fig. C), which limit the circumference, and so the minimum length.

(3) The dorso-ventral muscles which preserve the flattened form and so restrict very markedly the changes of length.

(4) The thickness of the body-wall musculature in *Cerebratulus*, a swimming nemertean. In this discussion it has been assumed that the thickness of the muscle layers is negligible. Obviously, if there are large muscle blocks which are not readily deformed, as in *Cerebratulus*, changes in shape are greatly limited.



Text-fig. 4. The theoretical relationship between the surface area of a unit length of worm and the inclination of the fibres. The points *X* and *Y* are the theoretical limiting positions of elongation and contraction, respectively, of *Amphiporus lactifloreus*.

#### CHANGES IN CROSS-SECTIONAL SHAPE

Attention has already been drawn to the fact that ideally the worm is circular in cross-section at the limiting positions of maximum extension and contraction and that it progressively flattens towards the relaxed position.

If  $n$  is the ratio of major to minor axes of the elliptical cross-section and  $\lambda$  the ratio of the length at any position to the theoretically maximum length,

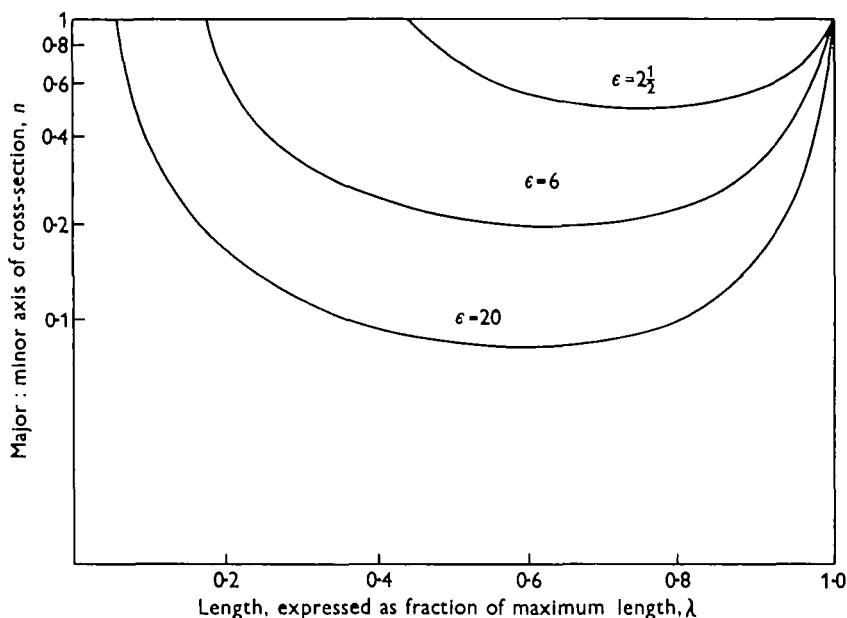
$$n = \frac{\lambda(\sec^2 \theta_e - \lambda^2) - \sqrt{[\lambda^2(\sec^2 \theta_e - \lambda^2)^2 - \tan^4 \theta_e]}}{\tan^2 \theta_e}.$$

(See Eqn. 11, Appendix)



This expression has been evaluated for three values of the parameter  $\theta_e$  (the value of  $\theta$  at the maximally extended position), corresponding to the extensibilities of the three groups of worms in Table 1, and  $n$  is shown plotted against  $\lambda$  in Text-fig. 5. The degree of flattening is, of course, directly related to the extensibilities of the worms.

There are a number of consequences of the change of shape of the body, quite apart from the extensibility, which may be related to the ecology of the three groups of worms.



Text-fig. 5. The flattening of the body as worms pass from theoretical maximum to theoretical minimum length for worms of different extensibilities corresponding to the three groups of species in Table 1.

(1) Those which have slight extensibilities and do not flatten appreciably are terrestrial and move on mucus which they secrete. Conservation of water must therefore present a problem to these animals. Loss by evaporation is reduced to a minimum because the surface area: body volume ratio is minimal when the cross-section is circular. A circular cross-section could be achieved if the worms were fully contracted or fully extended, or if, as in this case, the worms are almost circular in cross-section at the relaxed position and the extensibility is very low. The latter is the more economical and in fact obtains in *Rhynchodemus* and *Geonemertes*.

(2) Those which flatten to a moderate extent and have a considerable extensibility are marine crawling forms and are therefore not concerned with water conservation. Crawling is by means of cilia when the worm is relaxed and the body flattened, and the greatest surface area is presented to the ground.

(3) Those which are markedly flattened but have low extensibilities have ecological or mechanical requirements which demand a permanently flattened form even at the expense of extensibility. *Malacobdella* lives in the mantle cavity of *Cyprina* and other lamellibranchs. It is provided with a sucker in order to maintain its position when the host closes the valves of its shell and shoots a stream of water through its siphons. Its flattened form is obviously necessary for it to live between the gill lamellae or between the gills and the visceral mass of the bivalve. *Cerebratulus* requires a flattened body for effective swimming. The powerful and bulky longitudinal muscles, which are also needed, prevent the worm from realizing the powers of changing its shape which such a body-form otherwise confers upon it. The turbellarians *Polycelis* and *Dendrocoelum* are permanently flattened probably for physical reasons. The mass of an animal generally increases as the cube, the surface area as the square of its linear dimensions. The locomotory efficiency of animals that move by cilia is a function of the surface area, so that at some stage the mass becomes too great to be transported by cilia and a fairly low limit is set to the size the animal can reach. But if the thickness of the animal is the same whatever its size, as is approximately true of the flatworms, mass and surface area both increase as the square of the linear dimensions and no limit is set to the size they can attain. In fact some turbellarians reach comparatively large sizes and still move by ciliary action. A very flat, thin body-form is therefore a mechanical necessity for these worms if they are to move by cilia. A contributory ecological factor which may account for the flattening of some turbellarians, though probably not appreciably for that of *Polycelis* and *Dendrocoelum*, is that they live in fast-flowing streams or in areas of strong tidal currents that might wash them off the stones on which they crawl. A flattened form reduces the likelihood that they will be swept off the substratum.

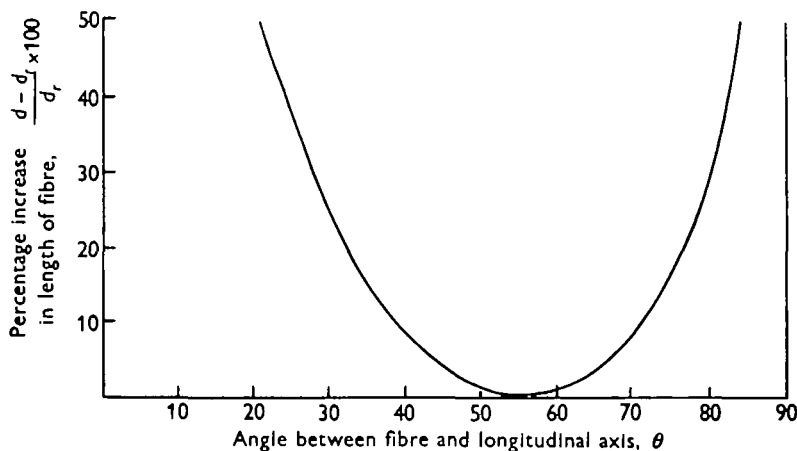
#### ELASTICITY OF THE FIBRES

The reticulin fibres of the basement membrane of *Amphiporus* were found to be inextensible (Cowe, 1952), at least to the extent that they could be snapped on micro-dissecting needles without apparent change in length. The fibres composing the comparable structure in the cuticle of *Ascaris* were assumed to be inextensible by Harris & Crofton (1957). However, it seems possible that some slight elasticity of the fibres might be sufficient to account for the observed extensibilities of the whole worms, particularly of those which do not show marked powers of extensibility.

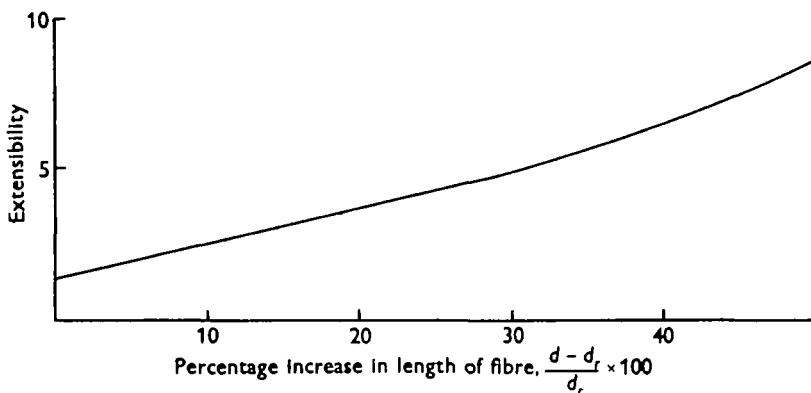
If the cross-section is assumed to remain circular and the fibres to be extensible, they are shortest in the relaxed position where  $\theta = 54^\circ 44'$  and elongation or contraction of the worm involves stretching them. The limits of extension and contraction would be set by the elastic limit of the fibres. If  $d$  is the length of the fibres when they are stretched to the elastic limit and  $d_r$  the resting length of the fibres,

$$\frac{d - d_r}{d_r} = \left( \frac{\cos \theta_r - \cos^3 \theta_r}{\cos \theta - \cos^3 \theta} \right) - 1. \quad (\text{See Eqn. 13, Appendix})$$

The relationship between  $(d-d_r)/d_r$ , which is the fractional increase in the length of the fibres, and  $\theta$  is illustrated in Text-fig. 6. For any value of  $(d-d_r)/d_r$ , there are two values of  $\theta$  which correspond to the positions of maximum and minimum length, and from these we can calculate the extensibilities of the worms for any value of  $(d-d_r)/d_r$ . This is illustrated in Text-fig. 7. To produce an extensibility of  $2\frac{1}{2}$ , the fibres would have to stretch 10% of their resting length, and to produce



Text-fig. 6. Percentage increase in the length of the fibres, assuming them to be elastic and the volume of the system constant, as the inclination of the fibres changes.



Text-fig. 7. The relationship between the extensibility conferred on worms of constant volume bounded by an elastic fibre system and the elasticity of the fibres.

an extensibility of  $3\frac{1}{2}$ , more than 20%. It is obvious that a slight extensibility of the geodesic fibres will not account for even the smallest extensibilities that have been observed in the worms. However, it is interesting to apply the results of this discussion to a consideration of the diagonal muscles which are found developed to a certain extent in nemertean (Bürger, 1895) and are very highly developed in

some turbellarians (Lang, 1884). Synergic contraction of the diagonal musculature will always result in the animal returning to the resting length. This will happen whether the animal is at a length greater or less than the resting length when the contraction of the diagonal muscles takes place. Their greater development in turbellarians is obviously correlated with the flattened form of these worms and prevent too great a departure from the relaxed position where the flattening is maximal.

#### DISCUSSION

A geodesic helical boundary system of fibres such as we have described provides an elastic tissue on which the epidermal cells rest, although it is itself composed of inelastic elements (the reticulin fibres). The system sets an over-all limit to changes in shape, though often other factors supervene and impose closer limits on the flexibility of the worm. Some of these factors, such as the existence of dorso-ventral and diagonal muscles in turbellarians, are clearly adaptive; others such as the compression of the epidermal cells or the existence of a bulky body-wall musculature, are accidental mechanical consequences of the morphology of the worms.

A helical fibre of this sort is known to occur in the basement membrane of only the nemerteans and turbellarians, but a similar system is found in the nematode cuticle and possibly also in the cuticle of annelids (Picken *et al.* 1947; Harris & Crofton, 1957) and may well be found to be a feature of the epidermal basement membrane and the cuticle of all worm-like animals. Clearly, the fundamental dynamic properties of such a fibre system are the same, whether it is internal or external to the epidermis, for in all cases it represents a bounding skeletal system which at once permits a flexibility to the body wall and also sets limits to that flexibility. No worm which possesses a cuticle has anything like the extensibility of some species of nemertean, possibly because the non-cellular matrix within which the cuticular fibre system lies has only very limited elastic properties.

#### SUMMARY

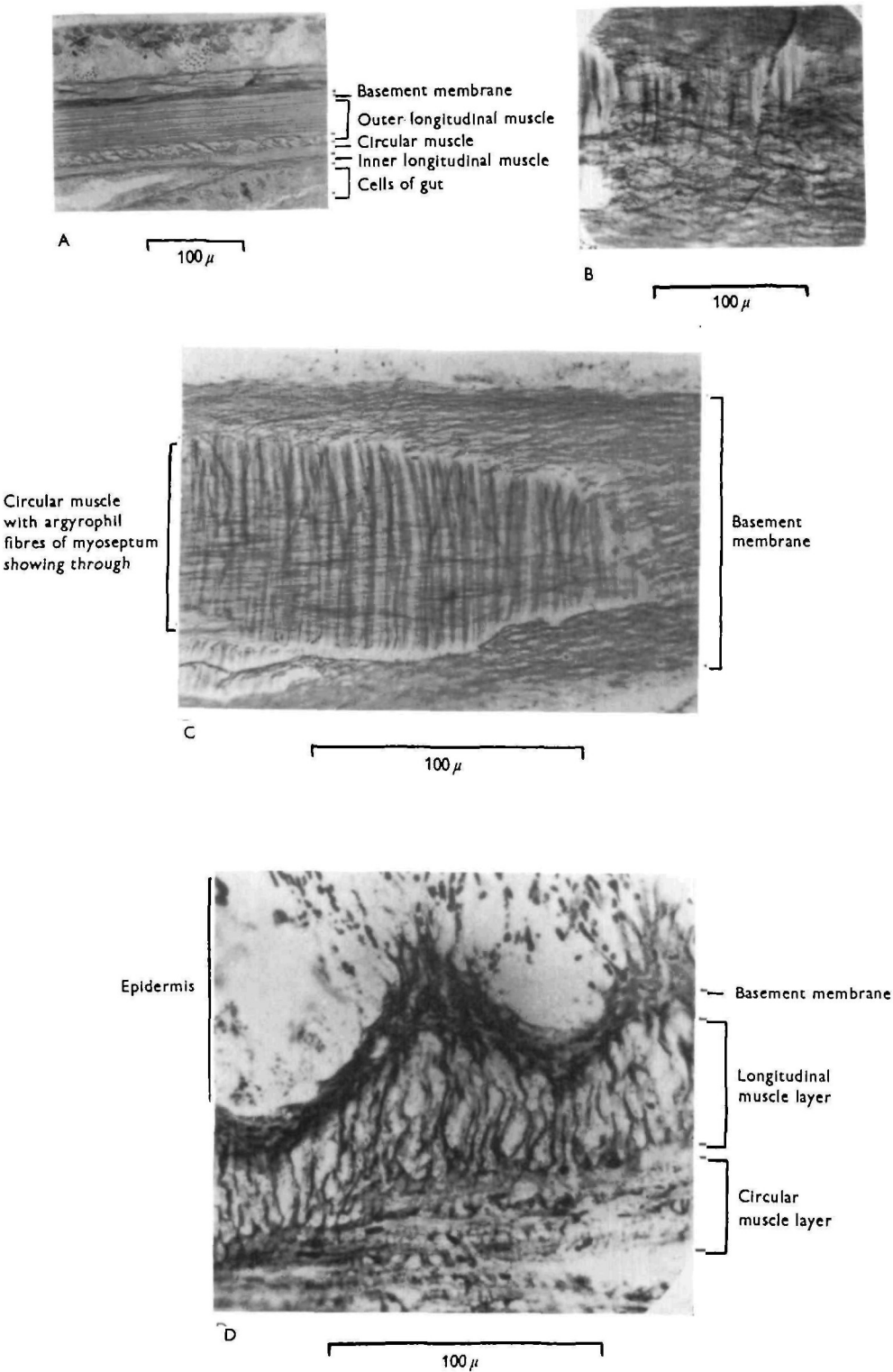
1. Nemerteans and turbellarians have an inextensible fibre system around them in the form of a lattice of left- and right-handed spirals. The effect of this system on the change of shape on these worms has been analysed theoretically and compared with the observed behaviour of nine species of turbellarian and nemertean from widely differing habitats.

2. The following theoretical relationships have been studied:

(a) Variation of the angle between the geodesics and the longitudinal axis of the worm during changes in length, and the role of the fibre system in limiting changes in length of the animal.

(b) The change in cross-sectional shape during changes in length.

(c) The extension of the fibres and the extensibility of the worms, assuming the fibres of the lattice to be elastic.



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3. The species investigated conform with the theoretical predictions to varying degrees and have been grouped accordingly:

(a) *Geonemertes dendyi* and *Rhynchodemus bilineatus* have low extensibilities and fit the prediction well. They are nearly circular in cross-section at all lengths as a result of their low extensibility and this is related to their terrestrial habit and need for water conservation.

(b) *Amphiporus lactifloreus*, *Lineus gesserensis* and *L. longissimus* are moderately flattened in the relaxed position and have extensibilities between 6 and 10. They are marine crawling forms using cilia for locomotion and so must present a fairly large ciliated surface to the substratum. The fibre system does not limit contraction; the compression of the epithelial cells causes the observed extensibilities to fall a little short of the theoretical values.

(c) *Cerebratulus lacteus*, *Malacobdella grossa*, *Polycelis nigra* and *Dendrocoelum lacteum* are very flattened forms and have very high theoretical extensibilities, but very low observed ones. The factors causing this are the thickness of the body-wall musculature (*Cerebratulus*), the limiting effect of longitudinal and circular reticulin fibres in the muscle layers, and the presence of dorso-ventral and diagonal muscles. Their flattened form is correlated with ecological factors (with swimming in *Cerebratulus*, with its parasitic life in the mantle of bivalves in *Malacobdella*) or with physical ones in turbellarians where a permanently flattened form is necessary for these worms to move by ciliary action.

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#### EXPLANATION OF PLATE

- A. Transverse section of the body wall of *Lineus gesserensis*. (Zenker-formol; Heidenhain's Azan.)  
 B. Section in the plane of the basement membrane of *Amphiporus lactifloreus* (Zenker-formol; Wilder's technique.)  
 C. Slightly oblique section through the basement membrane of *Amphiporus lactifloreus* showing also the argyrophilic fibres of the myoseptum. (Zenker-formol; Wilder's technique.)  
 D. Transverse section of *Lineus gesserensis* to show the folding of the basement membrane when the worm is maximally contracted. (Zenker-formol; Wilder's technique.)

## APPENDIX

*Symbols used in the appendix*

- $A$  Surface area of an element invested by one turn of the geodesic.  
 $a$  Semi-major axis of the cross-section.  
 $b$  Semi-minor axis of the cross-section.  
 $a_r$  Value of  $a$  at relaxed length.  
 $b_r$  Value of  $b$  at relaxed length.  
 $D$  Constant length of one turn of the inextensible geodesic fibre.  
 $d$  Length of one turn of the elastic geodesic fibre.  
 $d_r$  Length of  $d$  at relaxed length.  
 $l$  Length of an element investigated by one turn of the geodesic.  
 $l_e$  Value of  $l$  at maximally extended position.  
 $l_c$  Value of  $l$  at maximally contracted position.  
 $n$  Ratio of  $a/b$ .  
 $n_r$  Ratio of  $a_r/b_r$ .  
 $r$  Radius of circular cross-section.  
 $V$  Volume of an element invested by one turn of the geodesic.  
 $\epsilon$  Extensibility, ratio of  $l_e/l_c$ .  
 $\theta$  Angle between the fibres of the lattice and the longitudinal axis.  
 $\theta_c$  Value of  $\theta$  at minimum length.  
 $\theta_e$  Value of  $\theta$  at maximum length.  
 $\theta_r$  Value of  $\theta$  at relaxed length.  
 $\lambda$  Value of ratio  $l/l_e$ .

(1) *Change in length and extensibility*

Consider a length of worm invested by a single turn of the geodesic fibre system (Text-fig. 1 A, B). The fibres are assumed to be inextensible and the cross-section to remain circular

$$l = D \cos \theta, \quad (1)$$

$$r = \frac{D \sin \theta}{2\pi},$$

$$V = \pi r^2 l.$$

Then substituting for  $r$  and  $l$

$$V = \frac{D^3 \sin^2 \theta \cos \theta}{4\pi}. \quad (2)$$

The maximum value of  $V$  is reached when  $dV/d\theta$  is zero, i.e. where  $\tan \theta = \sqrt{2}$  or  $\theta = 54^\circ 44'$ , and this point represents the equilibrium position of the system (Text-fig. 1 C).

The extensibility,  $\epsilon$ , is the ratio of the extended to the contracted lengths

$$\epsilon = \frac{l_e}{l_c} = \frac{D \cos \theta_e}{D \cos \theta_c} = \frac{\cos \theta_e}{\cos \theta_c}. \quad (3)$$

Since the volume of the worm is constant and the same at the two points  $\theta_e$  and  $\theta_o$ , from equation (2) we have

$$\sin^2 \theta_o \cos \theta_o = \sin^2 \theta_e \cos \theta_e. \quad (4)$$

From equations (3) and (4) we may calculate  $\epsilon$  for any value of  $\theta_e$  by substituting the appropriate value of  $\theta_e$  in equation (4), solving the resulting cubic equation in  $\cos \theta_e$  and substituting the result in equation (3). The relationship between  $\theta_e$  and  $\epsilon$  is illustrated in Text-fig. 2.

The values of  $\theta_e$  and  $\theta_o$  cannot be measured readily because of the folding of the basement membrane which occurs in some species when the worms are fully extended or contracted, but the values can be deduced if the ratio of major to minor axes of the cross-section at the relaxed position is known.

The perimeter of the elliptical cross-section (Text-fig. 8 A, B) is approximately\*

$$2\pi \sqrt{[\frac{1}{2}(a_r^2 + b_r^2)]} = 2\pi \sqrt{\left[\frac{1}{2}a_r^2 \left(\frac{n_r^2 + 1}{n_r^2}\right)\right]},$$

and the volume of an element of length  $l$  is

$$\pi a_r b_r l = \frac{\pi a_r^3 l}{n_r}.$$

The greatest volume the system can contain at the relaxed position is that when the cross-section is circular, with radius  $r$ . The actual volume of an element of the worm need not be so great, in which case the cross-section is flattened to an ellipse with the same perimeter as the circle. Thus:

$$2\pi r = 2\pi \sqrt{\left[\frac{1}{2}a_r^2 \left(\frac{n_r^2 + 1}{n_r^2}\right)\right]}.$$

The greatest volume the system can contain is

$$\pi r^2 l = \pi \frac{1}{2} a_r^2 \left(\frac{n_r^2 + 1}{n_r^2}\right) l,$$

substituting for  $r$  from the previous equation. So that the ratio of the actual volume of the element at relaxed length to the greatest volume the system can contain is

$$\frac{\pi(a_r^3/n_r) l}{\pi \frac{1}{2} a_r^2 [(n_r^2 + 1)/n_r^2] l} = \frac{2n_r}{n_r^2 + 1}. \quad (5)$$

The theoretical extensibility of the worm can be read off the graph in Text-fig. 1 C after a horizontal line has been drawn representing the actual volume of the element, or it can be calculated by manipulating equations (2) and (3).

\* This expression is accurate for nearly circular figures, but overestimates the value of the perimeter if the ellipse is markedly flattened. If  $a=10b$ , the error is nearly 10%.



(2) *Changes in surface area*

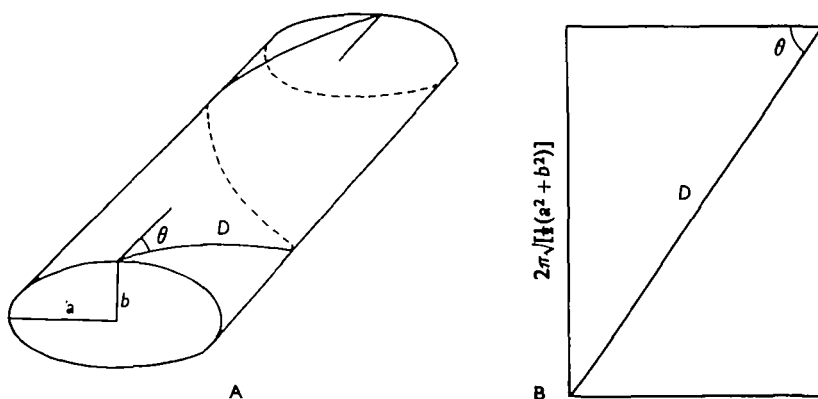
The length of an element is  $D \cos \theta$  and the circumference, whatever the cross-sectional shape, is  $D \sin \theta$  (see Text-fig. 1 B), so that the surface area

$$A = D^2 \sin \theta \cos \theta,$$

and since  $D$ , the length of the fibre, is constant

$$A \propto \sin \theta \cos \theta. \quad (6)$$

The relationship between  $A$  and  $\theta$  is illustrated in Text-fig. 4, where  $A$  is plotted in arbitrary units.



Text-fig. 8A. A unit length of a cylindrical 'worm' with an elliptical cross-section bounded by a single turn of the geodesic fibre system. B. The same unit length slit along the top and flattened out.

(3) *Change in cross-sectional shape*

The element is circular in cross-section at the limits of extension and contraction set by the geodesic fibres and elliptical at intermediate points. If this ellipse has semi-major and minor axes of  $a$  and  $b$  respectively, and the ratio of major to minor axes is  $n$  (see Text-fig. 8):

$$V = \pi a b l, \quad (7)$$

$$d^2 = l^2 + 2\pi^2(a^2 + b^2), \quad (8)$$

$$d = l_e \sec^2 \theta_e. \quad (9)$$

Equation (7) becomes

$$V = \pi n b^2 l,$$

and eliminating  $d$ ,  $a$  and  $b$  from equation (8) we have

$$l_e \sec^2 \theta_e = l^2 + 2\pi \frac{V}{\pi n l} (1 + n^2),$$

or

$$V = (l_e^2 \sec^2 \theta_e - l^2) \frac{n l}{2\pi(1 + n^2)}.$$

Now the volume of the element is constant so that

$$dV = \frac{n}{2\pi(1+n^2)} (l_e^2 \sec^2 \theta_e - 3l^2) dl + \frac{l}{2\pi} (l_e^2 \sec^2 \theta_e - l^2) \frac{(1-n^2)}{(1+n^2)^2} dn = 0,$$

i.e. 
$$\frac{n}{2\pi(1+n^2)} (l_e^2 \sec^2 \theta_e - 3l^2) dl = \frac{l}{2\pi} (l_e^2 \sec^2 \theta_e - l^2) \frac{n^2 - 1}{(1+n^2)^2} dn.$$

This may be arranged in an integrable form:

$$\frac{l_e^2 \sec^2 \theta_e - 3l^2}{l(l_e^2 \sec^2 \theta_e - l^2)} dl = \frac{n^2 - 1}{n(n^2 + 1)} dn. \quad (10)$$

The constant of integration can be found by considering the maximally extended position. There  $l = l_e$  and  $n = 1$ , since the cross-section is circular.

The complete integration of equation (10) is

$$\frac{n^2 + 1}{n} = 2\lambda \frac{(\sec^2 \theta_e - \lambda^2)}{\tan^2 \theta_e},$$

where  $\lambda = l_e/l$ . This is a simple quadratic equation in  $n$ , the roots of which are

$$n = \frac{\lambda(\sec^2 \theta_e - \lambda^2) \pm \sqrt{[\lambda^2(\sec^2 \theta_e - \lambda^2)^2 - \tan^4 \theta_e]}}{\tan^2 \theta_e}.$$

The two roots are reciprocals of each other and correspond to the conditions that  $a/b = n$  or  $b/a = n$ , so that the only one which need be considered is

$$n = \frac{\lambda(\sec^2 \theta_e - \lambda^2) - \sqrt{[\lambda^2(\sec^2 \theta_e - \lambda^2)^2 - \tan^4 \theta_e]}}{\tan^2 \theta_e}. \quad (11)$$

The relationship between  $n$  and  $\lambda$  has been computed for three values of  $\theta_e$  and is illustrated in Text-fig. 5.

#### (4) *The elasticity of the fibres*

The extensibility of a geodesic system in which the volume remains constant and the cross-section circular, but in which the fibres are elastic can be calculated as follows.

From Text-fig. 1:

$$V = \pi r^2 l,$$

$$d^2 = l^2 + 4\pi^2 r^2.$$

Therefore

$$d^2 = l^2 + \frac{4\pi V}{l};$$

or

$$V = \frac{d^2 l - l^3}{4\pi}. \quad (12)$$

Since  $d = l \cos \theta$ , equation (12) can be rearranged and written

$$d = \left( \frac{4\pi V}{\cos \theta - \cos^3 \theta} \right)^{\frac{1}{2}}.$$

This has a minimum value when  $\theta = 54^\circ 44'$  as in the case considered in section 1 of the Appendix.

If  $d_r$  is the length of  $d$  at this minimum position, the fractional increase in the length of the fibre at any value of  $\theta$  is

$$\frac{d-d_r}{d_r} = \left( \frac{\cos \theta_r - \cos^3 \theta_r}{\cos \theta - \cos^3 \theta} \right)^{\frac{1}{2}} - 1, \quad (13)$$

where  $\theta_r$  is the value of  $\theta$  at the relaxed length, ie.  $\theta = 54^\circ 44'$ . The relationship between  $(d-d_r)/d_r$  and  $\theta$  is illustrated in Text-fig. 6.

For any value of  $(d-d_r)/d_r$ , equation (13) is satisfied by the value of  $\theta$  corresponding to maximum elongation and contraction of the worm. The extensibility

$$\epsilon = \frac{l_e}{l_o} = \frac{\cos \theta_e}{\cos \theta_o},$$

so that the extensibility can be determined for any value of the elasticity of the fibres. The relationship is illustrated in Text-fig. 7.