OF THE MOVEMENT OF WORMS

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(Received 10 June 1949)

(With Three Text-figures)

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I. INTRODUCTION

There is little published work dealing with the movement of worm-like animals, apart from descriptive papers such as that of Foxon (1936), and analyses of the application of muscular contraction to the substratum such as are found in the papers of Gray (1939) and Gray & Lissmann (1938a, b). The possession of the right volume of coelomic fluid was shown by Chapman & Newell (1947) to be important in the burrowing of the lugworm, and the function of the body fluid in the extrusion of the proboscis of *Nephtys* and in the movements of *Calliactis* has been demonstrated (Chapman, 1949 and 1950). There appears, however, to be no satisfactory account of the interaction of the antagonistic muscles which is made possible by the presence of the body fluid, although von Buddenbrock (1937) mentions the antagonism between the longitudinal and circular muscles and describes their nervous coordination.

In the present paper an attempt is made to examine theoretically the working of antagonistic longitudinal and circular muscles in cylindrical fluid-filled animals. In the movement of these creatures there are features upon which it is necessary to lay stress, and although they may not all be self-evident they may, for convenience, be stated concisely until a more rigorous proof can be given.

(a) The longitudinal and circular muscles are antagonists which depend for their antagonism upon the presence within the animal of a fluid-filled cavity of fixed volume. (The fluid-filled cavity varies in size in different animals and although, in many, the volume of coelomic fluid is small, nevertheless that which is contained within the body wall may be regarded as fluid and incompressible for the purposes under review.)

(b) The maximum thrust which the musculature of an animal can exert is measured by the internal hydrostatic pressure and the area of application. The maximum
pressure can be increased above the internal hydrostatic pressure by the application of the principle of the wedge.

(c) The maximum thrust which the animal can exert is commensurate with the friction forces available to resist it.

(d) The absolute change in length of the animal which can be brought about by a given percentage contraction of the circular muscles depends on the shape of the animal, i.e. upon the relation of length to diameter.

It is necessary, then, to put forward some justification for the previous statements, and to examine their bearing on the shapes, sizes and muscular construction of soft-bodied invertebrates.

II. THE ANTAGONISM OF CIRCULAR AND LONGITUDINAL MUSCLES

It has been understood since the time of Leonardo da Vinci that a muscle 'uses its power along the line of its length'. In general terms this power is exerted during contraction, and a muscle is unable to exert its power again until it is restored to its resting length by an external agent. Spontaneous elongation of the muscles of the starfish podium has been reported by Paine (1929), but Smith (1946) has clearly refuted the suggestion and has collected considerable experimental and histological evidence to show that it does not occur, the elongation of the isolated tube foot being due to the unfolding of the crumpled collagen fibres which can exert sufficient force slowly to stretch the muscle.

To restore its 'useful' (relaxed) state a muscle may have in opposition to it either the force of another muscle, an elastic force or possibly a ciliary pressure. It may be noted that the force developed by the restoration system need not be as great as that developed by the effector. If the muscle works against an elastic restoring agent the work which it can perform externally is diminished by the work which is required to deform the elastic body.

The deformation of an elastic substance and the use of ciliary pressure cannot be regarded as important methods of restoration in the animal kingdom as a whole, although elasticity may play a part in the functioning of the muscular system of nematodes and ciliary pressure in that of coelenterates. Whilst it is true that ciliary pressures are of the order of mm. of water only (Pantin, private communication), it is also true that very small forces suffice during life to extend the body wall of certain actinians (see, for example, Jordan, 1935).

If a muscle works against an antagonistic muscle the work which it can perform externally is diminished only by the work necessary passively to extend the antagonist through the transmission system by which its force is applied. In many of the lower invertebrates this takes the form of a hydrostatic skeleton consisting of a fixed volume of liquid or tissue which is in a practically fluid state during life. The liquid may be the contents of the enteron, the coelom or the haemocoel, but one of its functions in all instances is that of a pressure-transmission system which causes the effects of contraction of any one muscle automatically to be felt by all the remaining muscles in the body wall. The contraction of a muscle in the body wall running parallel to the surface would cause a diminution in the volume enclosed by the body wall if
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the fluid were compressible. Since, however, it is incompressible the contraction of any one muscle must bring about an increased internal pressure and an extension of the remaining muscles.

Any fluid-muscle system which consists of a fluid surrounded by a muscular wall has inherently in its construction its muscular restoring agent, provided that muscle fibres of the wall run in longitudinal and circular directions, or that the skeletal materials of the wall contain an element of elasticity in their physical properties. This can be seen by considering a hypothetical animal whose body wall consists of circular fibres only and lacks any skeletal elasticity. Contraction of the muscles at one end could bring about a thinning of that end, and either an elongation or a thickening at the other (see Fig. 1). If this thickening were to take place, all that would be necessary to restore the original condition would be a contraction of the dilated end. But, on the other hand, if an elongation were to occur, there would be no way of getting back to the original condition since contraction of the muscles in the elongated region would serve only to relax the muscles in the original contracting end, and so to thicken it without shortening the body as a whole (see Fig. 1). It is interesting to note here that, where only a single muscular coat occurs in a hollow organ such as a starfish podium, there is a strong inelastic sheath of collagen fibres which prevents increase in diameter of the foot on contraction of its muscles. When this occurs the contained fluid is driven into the ampulla, which together with the tube foot, acts as a closed system.

In most soft-bodied invertebrates the musculature of which the body wall is composed is arranged according to a uniform plan in which the outer layer consists of fibres running in a circular manner, whilst the inner layer of fibres runs along the

Fig. 1. Diagram to illustrate the action of a hypothetical animal with circular muscles only. In A all the muscles are relaxed. In B the muscles of the right-hand end have contracted but the length of this end has remained the same. If this takes place it is impossible for the original length of the right-hand muscles to be restored by the contraction of the left-hand muscles. In C an alternative arrangement is shown. The muscles of the right-hand end have contracted, but the muscles of the left-hand end have relaxed. There has been no change in length. By the contraction of the left-hand muscles the right-hand muscles could be restored to their original length.
length of the animal. This arrangement enables the muscles to act antagonistically to one another without the necessity for the body wall to possess any skeletal elastic component, provided that the nervous system arranges for the muscles to be suitably stimulated. If the action of an animal in which there are circular and longitudinal muscles be compared with that of the hypothetical organism consisting of circular muscles only, it can be seen that the contraction of the circular muscles at one end can bring about four different muscular configurations which are

![Diagram](image)

**Fig. 2.** Diagram to illustrate four possible results of the contraction of circular muscles at one end of a cylindrical animal. In A the muscles are all relaxed. In B the circular muscles of the right-hand end have contracted and this end has elongated. The left-hand end has remained unaltered. In C the length of the right-hand end has remained the same but the diameter of the left-hand end has increased. In D the length of the right-hand end has also remained the same. The length of the left-hand end has increased but not its diameter. In E the length of both ends has increased but their diameters have remained the same as in B and D.

illustrated in Fig. 2. Restoration of the original body shape from any of these states can be brought about by the contraction of appropriate other parts of the musculature as can be seen on inspection of the figure.

That the ordering of the muscle fibres in a longitudinal and circular manner is the only arrangement which makes possible the movements of soft-bodied invertebrates can be seen by considering the results of the arrangement of the fibres at an angle of 45° to the long axis in such a way that they are arranged in two spirals of opposite sense. The effect of the contraction of one spiral on the dimensions of the body
would be the same as that of the other so that neither could be said to be in opposition to the other nor do they constitute a mutually restorative system. On the other hand, the arrangement of inextensible skeletal fibres in this manner allows change of dimensions of the animal at fixed volume without stretching of the skeletal material.

The antagonism of relaxed muscles to those which are contracting depends on the presence of a body fluid which in its turn necessitates a non-leaking body wall. In those animals which have been examined this has been found to occur. In *Arenicola* the nephridiopores are sphinctered apertures capable of resisting a pressure greatly in excess of that normally produced by contraction of the body-wall muscles. Loss of body fluid causes loss of burrowing efficiency, which is prevented on mutilation by the marked constriction of the body wall on to the gut (Chapman & Newell, 1947). In *Calliaactis* practically no water leaves the stomodaeum or the cinclides on normal contraction (Chapman, 1950). In *Lumbricus* free flow of fluid about the body is prevented, and escape of fluid on mutilation is hindered, by the presence of muscular septa; neither do the dorsal pores nor the nephridiopores leak during life (Newell, private communication).

### III. HYDROSTATIC PRESSURE AND MUSCULAR TENSION

The relation between the pressure in a hollow cylinder and the stresses in its walls can be seen by considering the forces exerted on a longitudinal section passing through the axis and also the forces on a cross-section.

If 't' is the thickness of the wall, 'l' the length, 'r' the radius and 'f_c' and 'f_l' the circumferential and longitudinal stresses respectively, the total push due to the pressure on one half of the longitudinal section equals \( p \cdot 2rl \). This must be balanced by the circumferential stress in the walls, viz. \( f_c \cdot 2tl \). Therefore

\[
p = \frac{f_c \cdot 2tl}{2rl} = \frac{f_c}{r}.
\]

Similarly, for the cross-section the total pressure on the ends must be balanced by the longitudinal stresses in the walls, viz. \( p \cdot \pi r^2 = 2\pi r f_l \). Therefore

\[
p = \frac{2\pi r f_l}{\pi r^2} = \frac{f_l \cdot 2r}{r^2}.
\]

Considering now the tensions in the longitudinal and circular muscles of a worm, and the pressures which they exert on the contained fluid, \( T_o \) can be written instead of the expression \( f \cdot l \) for the circumferential stress as being the total tension in the whole circular muscle layer so that

\[
p \cdot 2r = 2T_o,
\]

Therefore

\[
p = \frac{2T_o}{2rl} = \frac{T_o}{rl}.
\]

Similarly, the total tension in the whole longitudinal muscle layer, \( T_l \), can be written for the expression \( 2\pi r f_l \) so that the equation becomes

\[
p \cdot \pi r^2 = T_l.
\]

Therefore

\[
p = \frac{T_l}{\pi r^2}.
\]
From the expressions relating pressure with longitudinal and circumferential stresses it can be seen that

\[
\frac{T_c}{r_l} = p = \frac{T_l}{\pi r^2}, \quad \frac{T_c}{r_l} = \frac{T_l}{\pi r^2}, \quad \frac{T_c}{T_l} = \frac{\pi r^2}{\pi r} = \frac{\pi r}{l}.
\]

It follows from this expression that if the ratio of the tensions in the longitudinal and circular muscles is equal to \(\pi r/l\), then the pressures being exerted on the contained fluid by the two muscle layers are equal. Whilst, therefore, there is no doubt that this equation may hold good at any instant, it is of interest to inquire if the quantities of longitudinal and circular muscle present in a typical 'worm' are such that the equation holds good when both layers are contracting maximally. This can be discovered by inspection, if it is assumed that the tension which a muscle can exert is proportional to its cross-sectional area. If \(A_l\) and \(A_c\) are the total cross-sectional areas of the longitudinal and circular muscles respectively, then

\[
A_l = \frac{\pi r}{l}.
\]

Average measurements made from camera lucida drawings of sections of earthworms of different sizes are set out in Table 1.

### Table 1. Dimensions of body-wall muscles of Lumbricus

<table>
<thead>
<tr>
<th>Dimensions in mm. and sq.mm.</th>
<th>Large worm</th>
<th>Medium worm</th>
<th>Small worm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Approximate length before fixation</td>
<td>150</td>
<td>110</td>
<td>60</td>
</tr>
<tr>
<td>Radius</td>
<td>2.7</td>
<td>1.8</td>
<td>1.0</td>
</tr>
<tr>
<td>Radial thickness of circular muscles</td>
<td>0.1</td>
<td>0.05</td>
<td>0.04</td>
</tr>
<tr>
<td>Total cross-sectional area of circular muscles</td>
<td>15.0</td>
<td>5.5</td>
<td>2.4</td>
</tr>
<tr>
<td>Radial thickness of longitudinal muscles</td>
<td>0.3</td>
<td>0.3</td>
<td>0.2</td>
</tr>
<tr>
<td>Total cross-sectional area of longitudinal muscles</td>
<td>5.9</td>
<td>3.0</td>
<td>1.2</td>
</tr>
<tr>
<td>(\frac{A_l}{A_c}) (approx.)</td>
<td>0.4</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>(\frac{\pi r}{l})</td>
<td>0.05</td>
<td>0.05</td>
<td>0.05</td>
</tr>
</tbody>
</table>

It can be seen from the table that in the earthworm \(A_l/A_c\) is not equal to \(\pi r/l\), implying either that the tension exerted by the muscles is not proportional to their cross-sectional area or, which is much more likely, that at their maximal contraction the circular and longitudinal muscles are not balanced. From the values of \(\pi r/l\) calculated from the values of \(r\) and \(l\) it would appear that, for equal pressure to be exerted by circular and longitudinal layers, \(T_c\) should be approximately \(20 \times T_l\) (or \(A_c\) should be approximately equal to \(20 \times A_l\)) whereas, in fact, \(A_c\) is only approximately \(2 \times A_l\). If, then, both sets of muscles in the worm were to contract maximally, the pressure exerted by the longitudinal layers (\(T_l/\pi r^2\)) would be approximately ten times that exerted by the circulars (\(T_c/rl\)).

Since contraction of the circular muscles gives rise to a forward thrust they might have been expected to be the stronger, for they would seem to be the more important both for progression and for burrowing through the soil. However, since the animal probably burrows largely through existing crevices, the longitudinal muscles may be of greater importance since they serve to increase the diameter of the body and
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hence to thrust aside the soil particles. (This argument presupposes, of course, that the body is totally enclosed by the soil, because otherwise the longitudinal muscles can generate only as much pressure as the circular muscles are capable of withstanding.)

The maximum pressures in both *Arenicola* and *Lumbricus* occur during phases of contraction of the anterior circular muscles when the animals are unconfined, but in *Arenicola*, enclosed in a glass tube, values of between 80 and 90 cm. of sea water have been recorded as compared with the highest values of 50–60 cm. of sea water previously registered (Chapman & Newell, 1947). This pressure is not as great as the theoretical maximum but it shows, nevertheless, that greater pressures can be exerted by the longitudinal than by the circular muscles.

It is clear that the hydrostatic pressure in the body fluid is a measure of the pressure which can be applied to the substratum, so that the measurement of hydrostatic pressure is a convenient way of measuring the ‘strength’ of soft-bodied invertebrates, although the total pull which can be exerted by an animal during the contraction of its longitudinal muscles cannot be measured by the measurement of hydrostatic pressure since the transmission of the muscular tension does not require the intervention of any fluid. In this connexion it is interesting to note that the figure given by Gray & Lissmann (1938a) for the maximum pull which an earthworm can exert (70 g.) is in excess of the thrust which it normally exerts on extension (2–8 g.). This figure of 2–8 g. is in good agreement with the hydrostatic pressure as measured by Newell. His values have a maximum of about 30 cm. of water, i.e. 30 g./sq.cm. For a worm of diameter 0.6 cm., of cross-sectional area 0.28 sq.cm., the total thrust would therefore be about 8.5 g.

In order to compare the pressure exerted by the circular muscles with the hydrostatic pressure it is necessary to assume, as has been done before, that the tension which a muscle can exert is proportional to its cross-sectional area. If this is done, and the pull exerted by the longitudinal muscles is used as a standard, it is possible to compute the pressure which ought to be exerted by the contraction of the circular muscles. If the pull due to the longitudinal muscles of an earthworm of about 0.3 cm. radius is 70 g., the cross-sectional area of its longitudinal muscles being 0.06 sq.cm., then the tension in the circular muscles, of cross-sectional area 0.15 sq.cm., should be \( \frac{70 \times 0.15}{0.06} \) g. The pressure exerted on the contained fluid \( (T_c/rl) \) should therefore be \( \frac{70 \times 0.15}{0.06 \times 0.3 \times 15} \) g./sq.cm. This value, of 38 g./sq.cm., is again in quite good agreement with the measured value of 30 cm. of water.

It is interesting to notice here that the pressure exerted by the circular muscles is not dependent upon their simultaneous contraction along the total length of the animal if the creature is capable of being divided into water-tight compartments. If, for example, a third of the length is in contraction, then the cross-sectional area of the circular muscles in this portion will be a third of the total circular muscles in the body, but so will the value of ‘l’ in the equation

\[
\text{pressure} = \frac{T_c}{l}
\]
If, on the other hand, the body cavity is open and the fluid in the region undergoing contraction is in communication with the remainder, then the development of pressure in the body cavity is dependent upon the development of tension in the muscles as a whole. Examples of the open and septate coelom are seen in the lugworm and the earthworm respectively.

IV. THE APPLICATION OF THE INTERNAL PRESSURE TO THE SUBSTRATUM

Whether the thrust is applied by the extrusion of the proboscis as in *Nephthys* and *Nereis*, or by the extension of the anterior end as in *Lumbricus*, the effective application of the thrust resulting from the contraction of the body-wall muscles depends upon the ability of the animal to withstand the reaction to the thrust.

Although it may perhaps unduly extend the meaning of the term friction to include the resistance provided by parapodia and setae, nevertheless the forces exerted by these portions of the animal must be included with the friction of the body. Frictional forces have been measured for the earthworm by Gray & Lissmann (1938a), but no measurements of the frictional forces of the animals in their natural environment appear to have been made. Friction between an earthworm and the walls of its burrow may be considerable, since animals can easily be broken when attempts are made to pull them out. Presumably, therefore, if the longitudinal muscles of *Lumbricus* are capable of exerting a tension of 70 g., the frictional resistance which must be overcome in pulling a worm from its burrow can be at least 70 g.

It is also worth comment that the contraction of the longitudinal muscles serves to increase the diameter of the body and therefore may increase the pressure applied at right angles to the surface of the body of the worm.

If the frictional force which must be overcome for movement to occur be 'f', then the coefficient of friction is \( f/n \), where 'n' is the normal reaction between the applied surfaces. In Gray & Lissmann's example of an earthworm moving over a glass plate the frictional resistance was 2–8 g., say 5 g., and the weight of the worm was, say, 5 g. The coefficient of friction is therefore 1. If the coefficient of friction is the same for a worm being pulled from its burrow and if \( f = 70 \) g., then, since \( 70/n = 1, n = 70 \), or the total reaction between the worm and its burrow is 70 g. Taking the superficial area of the worm to be 25 sq.cm. the pressure of the worm on its burrow is \( 70/25 \) g./sq.cm. This figure, of less than 3 g./sq.cm., is obviously well within the limits of the pressure occurring in the body fluid. Even if it were to be multiplied by a factor of 10, as would be necessary if only one-tenth of the superficial area of the worm were in contact with the wall of the burrow, it would imply a pressure of 30 g./sq.cm., which it is still well within the animal's power to generate.

It would appear to be fallacious to assume, as has in fact been done, that the coefficient of friction between the earthworm and a smooth plate is the same as that between a worm and its burrow, although the presence of mucus in both instances might well have the effect of lessening any differences. Some rough measurements with a dynamometer, made by dragging eight fresh *Arenicola* along the surface of drained sand, showed that each animal required a force of 10 g. weight to move it
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against the force of friction. The freshly dug worms which were used in this experiment weighed about 10 g. each so that the coefficient of friction between drained sand and the animal was about 1, which does not differ from the value deduced from Gray & Lissmann's observations on the earthworm. Forces involving the displacement of particles of muddy sand are not reliable quantities to measure, and not too much significance can be attached to these results.

To sum up, the figure of 30 g./sq.cm. of water necessary for an earthworm to resist a pull of 70 g. when one-tenth of its length is in its burrow is well within the maximum pressure which the worm is capable of exerting.

Newell (private communication) has pointed out that an earthworm can increase the pressure which it applies to the substratum by reducing the area in contact with the soil. If the anterior end of the animal is regarded as a truncated cone and if the internal pressure be applied to the larger end of the cone, the pressure exerted on the soil by the small end will be in the inverse ratio of the areas of the two ends. In this way, working at an internal pressure of 30 g./sq.cm., and with the area of application of the force one-twentieth that of the cross-sectional area of the worm, a force of 600 g./sq.cm. or 8 lb./sq.in. can be applied. If the total cross-sectional area of the worm is 0.25 sq.cm., then the diameter of the smaller area of application of the force would be between 1 and 2 mm. This figure certainly appears to be of the right order. It will be realized that this is a considerable pressure when compared with that of 2.5 lb./sq.in. exerted on the ground by a man standing on both feet; and it is highly likely that the tissue of the animal would be deformed by such pressure so that the area of contact would be immediately increased. It is worth noting, however, that the anterior end of an earthworm is a nearly solid muscular region which can be made rigid by contraction. It will also be seen that, since the forward thrust is expressed as a pressure, i.e. force per unit area, it implies that no increase is necessary in the frictional forces (between the animal and the ground) which resist the forward thrust.

V. CHANGES OF MUSCLE LENGTH AND BODY SHAPE

In their simplest form, taking no account of the changes in shape of the muscles themselves, the variation in length and circumference of a cylindrical animal can be regarded as those changes which take place in a cylinder of variable dimensions and fixed volume, \( V \).

\[
V = r^2l = \text{a constant.}
\]

Therefore

\[
l = \frac{V}{r^2},
\]

from which it can be shown that

\[
\frac{dl}{l} = -\frac{2dr}{r} \quad \text{(Blaney, private communication).}
\]

That is, a percentage change in length is accompanied by half that percentage change in circumference. For example, the dimensional changes in a cylinder of fixed
volume of 15,700 cubic units are given in Table 2, a radius of 5 units and a length of 200 units being proportions not unlike those of a 'worm'.

Table 2. Variations in the length, circumference and radius of a cylinder of fixed volume

(Volume \( V \) = 15,700 cubic units, \( r \) = radius, \( c \) = circumference, \( l \) = length.)

<table>
<thead>
<tr>
<th>( r )</th>
<th>( c )</th>
<th>( l )</th>
<th>( V )</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>12.5</td>
<td>1260.0</td>
<td>15,700</td>
</tr>
<tr>
<td>3</td>
<td>18.9</td>
<td>555.6</td>
<td>15,700</td>
</tr>
<tr>
<td>4</td>
<td>25.1</td>
<td>312.4</td>
<td>15,700</td>
</tr>
<tr>
<td>5</td>
<td>31.4</td>
<td>200.0</td>
<td>15,700</td>
</tr>
<tr>
<td>6</td>
<td>37.7</td>
<td>138.9</td>
<td>15,700</td>
</tr>
<tr>
<td>7</td>
<td>43.9</td>
<td>102.1</td>
<td>15,700</td>
</tr>
<tr>
<td>8</td>
<td>50.3</td>
<td>78.0</td>
<td>15,700</td>
</tr>
</tbody>
</table>

The graph which can be drawn from the relation between '\( l \)' and '\( c \)' is shown in Fig. 3, and shows clearly that for a given percentage change in length of the circular muscles the longitudinals change in length by twice that percentage. Alternatively, for a given absolute change in length of the circular muscles the change in length of the longitudinals produced by it may be great or small according to whether \( l/r \) is at its greatest or smallest. An implication of this is that, since the smallest change in length of the animal for a fixed change in length of the circulars occurs when the animal is at its 'fattest', it would be expected that burrowing animals would carry out their burrowing when thick and not when thin. Conversely, when
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an animal is crawling it will, for each fixed contraction of the circular muscles, progress farthest if it is thin. If, for example, the working range of an earthworm were 25% of its resting length, then, although this means a 50% change in length for the longitudinals, it involves only a normal working range of 25% for the circulars. Whether this difference in requirements is based on any difference in the physiology of the muscles is unknown.

VI. SUMMARY

Four aspects of the functioning of a fluid-filled cylindrical animal have been examined, viz.: (1) the role of the body fluid as a skeleton for the interaction of the longitudinal and circular muscles of which the animal must be composed; (2) the measurement of the maximum thrust which the animal can exert by measurement of its internal hydrostatic pressure; (3) the application of the force to the substratum and the part played by friction; (4) the relation between the changes in dimensions of the animal and the working length of the muscles.

Under (1) the necessity for a longitudinal and circular construction has been shown and the necessity for a closed system emphasized.

Under (2) the pressure exerted on the body fluid by the contraction of the longitudinal and circular muscles is discussed, and from their cross-sectional areas it is shown to be probable that when contracting maximally in Lumbricus they are not balanced, but that the longitudinals are about ten times as strong as the circulars.

Under (3) it is shown that the strength of an animal as measured by its internal hydrostatic pressure is sufficient to account for its customary activities. Use which may be made of the longitudinals during burrowing is pointed out.

Under (4) it is shown to be mechanically sound for burrowing animals of cylindrical form to be ‘fat’, but that a ‘thin’ animal is more efficient at progression.

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