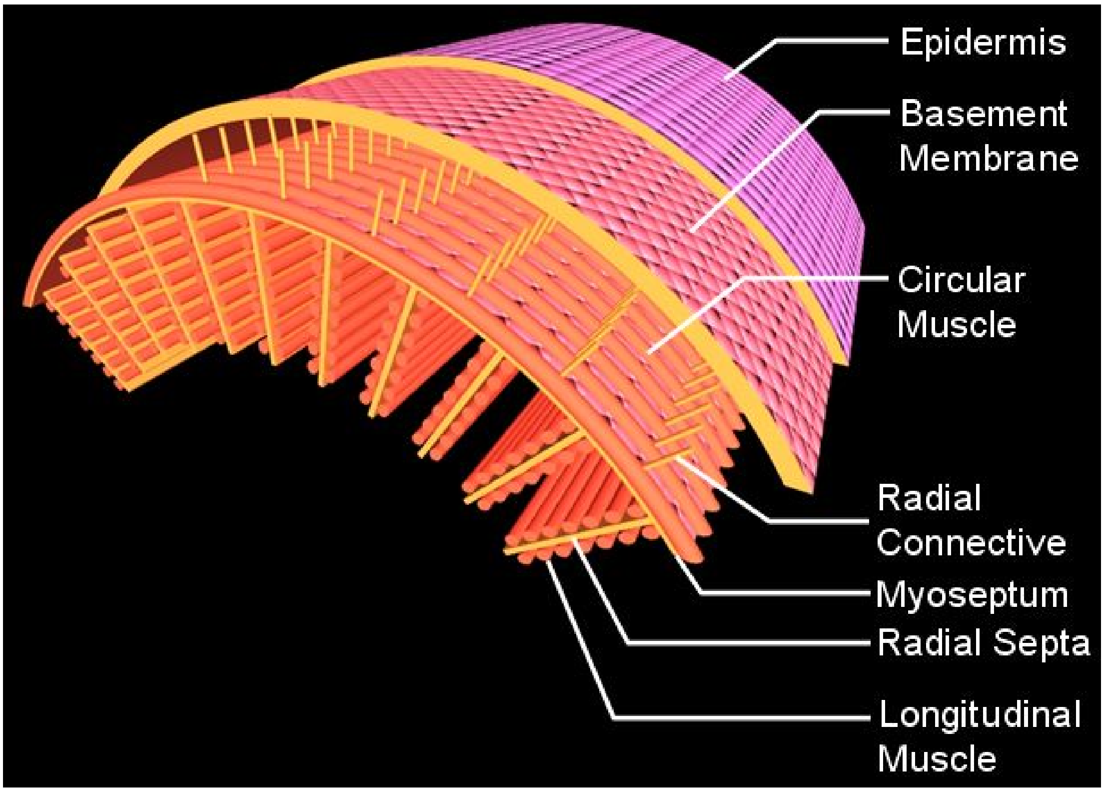
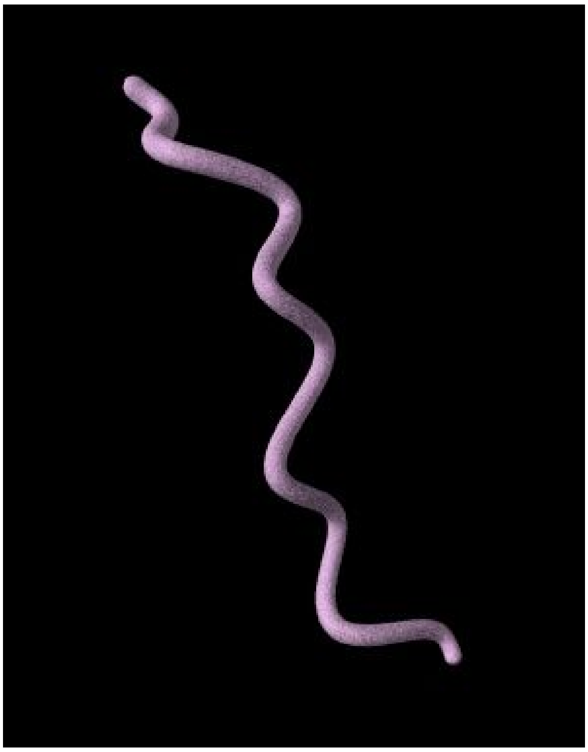
A model of locomotion in Nemerteans

Nemerteans (ribbon worms) are capable of considerable changes in shape. *Lineus longissimus* is one of the longest animals on Earth, often reaching 30 m and lengths of 50 – 60 m having been reported. These worms are typically able to vary their body length by a factor of 10 through muscular contraction. Contraction of circular muscles (running around the circumference of the worm) makes the worm thinner and more elongated, whereas contraction of longitudinal muscles (running along the main axis of the worm) makes the animal shorter and wider.



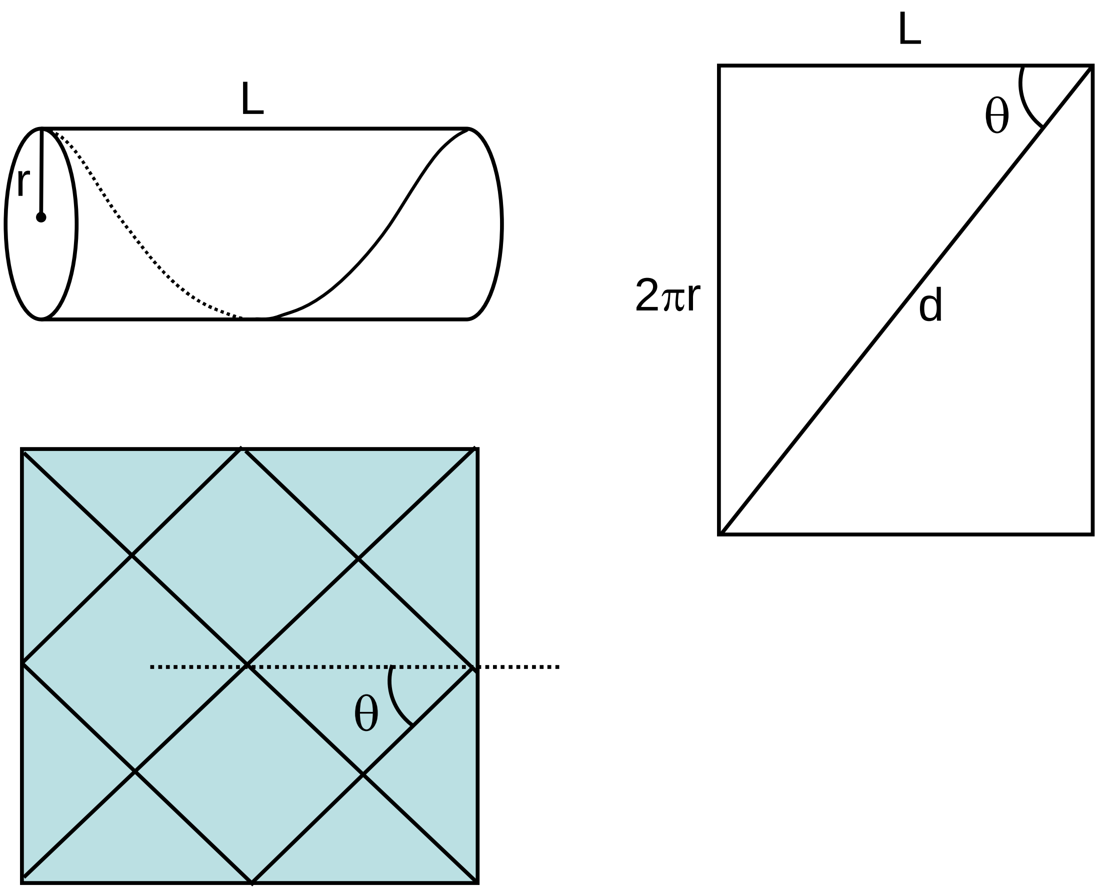
Above: a sector of the body wall of a nemertine worm. There is no cuticle secreted by the epidermis, a single-layered covering of living cells, which secretes mucus, however. Beneath the epidermis is the basement membrane which is thick and consists of alternate layers of criss-crossing protein fibres. These fibres traces spirals around the long axis of the worm. Connective tissue fibres (radial connectives) connect the basement membrane to the myoseptum, which is a basement-membrane like sheet underneath the circular muscle fibres. Beneath the myospetum are radial sheets of connective tissue supporting rows of longitudinal muscle fibres.

When crawling across a solid surface these worms will move in a manner similar to earthworms: by peristaltic waves of muscle contraction alternately shortening and elongating sections of the worm (though these worms are not segmented as are earthworms). When swimming these worms undulate in sinusoidal waves (rather like swimming eels). When part immersed in water and part on land, the part immersed will undulate whilst the part on land will undergo peristaltic crawling.



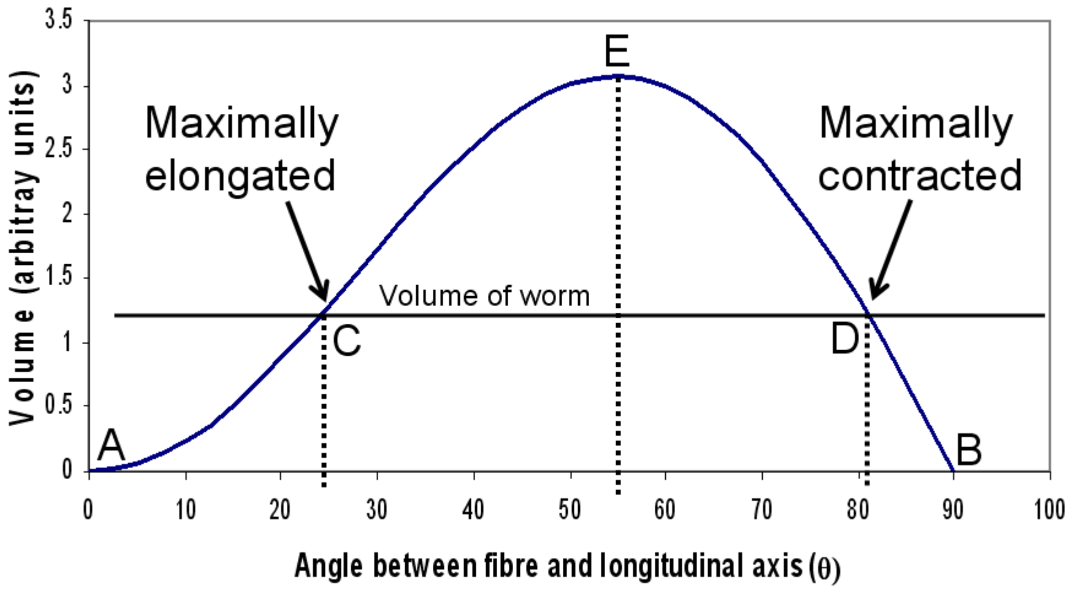
Above: a model of a nemertine swimming.

We are going to model extension and contraction in these worms as determined by contractions of the circular and longitudinal muscles resulting in changes in the angle at which the spiral fibres of the basement cross. We shall model one unit length of worm as shown below:



At top left we have one unit length of worm, modeled as a circular cylinder of radius r and length L with one basement membrane fiber, of length d, shown spiraling around it. At the top right this cylinder has been cut along its length and unraveled into a sheet with sides $2\pi r$ (the circumference of the circle) and length L. At the bottom part of the basement membrane is shown in face view, showing that the angle between crossing fibers is 2θ, such that θ can vary from 0^o when the worm is maximally extended or elongated into a thread and all fibers are parallel to the long axis and 90^o when the worm is maximally contracted and all fibers are perpendicular to the long axis of the worm (that is circumferential) and the worm is contracted into a disc.

In theory both the maximally contracted disc and maximally elongated thread would have zero volume and somewhere in between the volume would peak at a maximum, as shown in the graph below. Point A corresponds to the theoretical maximum elongation point, at which the worm would have zero volume and point B to the theoretical point of maximum contraction where again the volume would be zero. Since the worm is mostly water and solution bathes its tissues, this can not in fact happen as water is barely compressible and closely approximates an incompressible fluid. The horizontal line shows the volume of a real worm (strictly the volume of one unit length of worm) which must remain fixed throughout.



Above: changes in the volume of a unit length of model worm as the angle between the basement membrane fibers, theta (θ), changes from zero to 90 degrees.

The point E on the graph indicates the point at which volume is maximal, with theta around 55^o. A real worm will have a fixed volume: the one indicated here can not decrease its volume below this limit due to the incompressibility of water and so its maximum elongation occurs when theta is about 25^o and its maximum contraction around theta equal to 80^o. The muscles are unable to change the angle of the fibers beyond these limits.

In between the points of maximum elongation and maximum contraction, the worm has less volume than the fiber system can accommodate and so it adopts an elliptical cross-section. (An ellipse has a smaller surface area than a circle of the same circumference or perimeter and so an elliptical cylinder encloses a smaller volume than a circular one of the same length). At the limits of contraction and extension, the worm is predicted to have a circular cross-section.

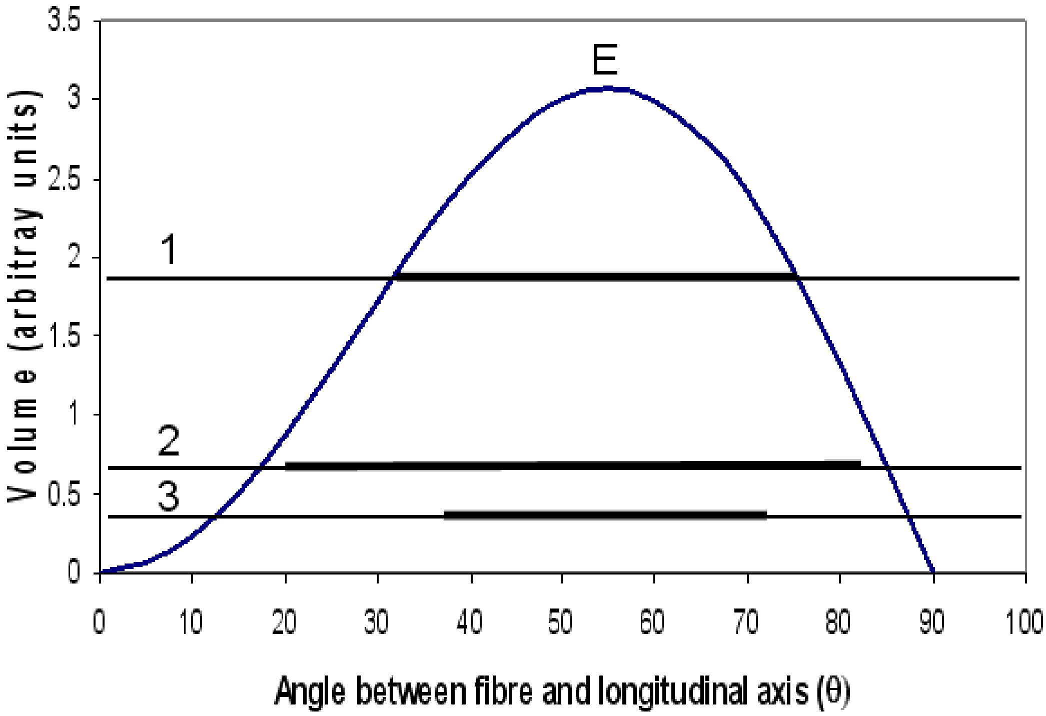
The derivation of the equation for the volume is given below, where we have assumed that the basement membrane fibers are inextensible (that is d = constant which we have set equal to 1).

$$
\begin{aligned}
&d = \text{constant} = 1\\
&\mathrm{L} = \mathrm{L}(\theta)\\
&\mathrm{r} = \mathrm{r}(\theta)\\
&volume = V = \pi r^2 L\\
&\cos\theta = \frac{L(\theta)}{d} = L\\
&\sin\theta = \frac{2\pi r(\theta)}{d} = 2\pi r \Rightarrow r = \frac{\sin\theta}{2\pi}\\
&therefore\\
&V = \frac{\sin^2\theta\cos\theta}{4\pi}
\end{aligned}
$$

A model is of little use if it is does not match reality. Observing the extensibility of actual worms with a given volume per section of their length, it is apparent that the model works better for some worms than others. It also works when applied to turbullerian flatworms (which belong to a different phylum: Platyhelminthes). Some examples are illustrated in the graph below.

Type 1 worms have limited extensibility as predicted by the model: their fibers are restricted in the angles they can adopt due to the incompressibility of the fluids inside the worm. The terrestrial nemertine *Geonemertes dendyi* and the terrestrial flatworm *Rhynchodemus bilineatus* belong to this type. There is little difference between the actual volume of the worm and the theoretical mximum, so these worms are almost circular in cross-section. One reason put forward to account for this is that these worms need to minimise their surface area to volume ratio to reduce water loss by evaporation (a circular cylinder has a smaller surface area than an ellipsoidal cylinder of the same volume). It could also be an adaptation to persitaltic crawling. Worms which are full of eggs become very rigid and are barely able to change length; these will lie near the top of the curve (close to E on the graph above).

Worms of type 2 have great extensibility, as predicted to high accuracy by the model. This category includes the enormously long and marine bootlace worm, *Lineus longissimus*. There is a large difference between the actual volume of each section of the worm and the theoretical maximum the fiber system can accommodate and so these worms are generally elliptical in cross-section and hence flattened. Many marine nemertines and flatworms benefit from having a flattened shape because it increases the surface area of the skin for gas exchange and also increases the surface area of the side of the animal in contact with the substrate over which many of these worms can creep by the beating of tiny hair-like cilia, aided by mucus secretion. *Lineus longissimus* can not quite reach the theoretical limits, since its cross-section never becomes quite circular.



Above: extensibility of different types of ribbon worm and flatworm. Type 1 includes the terrestrial *Geonemertes* and *Rhynchodemus*. Type 2 includes the marine nemertine *Lineus longissimus*. Type 3 includes the nemertines *Malacobdella grossa* and *Cerebratulus lacteus* and the flatworms *Dendrocoelom lacteum* and *Polycelis nigra*.

In these worms the limit of contractility and extensibility is due to the epidermis, which has some rigidity and gets thrown into circular folds when the animal is highly contracted and longitudinal folds when it extends and becomes thinner.

Type 3 are worms which theoretically would have massive extensibility, but deviate from the model in that they never contract or extend to their theoretical limits as they are mechanically unable to. These worms remain elliptical in cross-section and flattened, as predicted. They have inextensible connective tissue fibers running longitudinally and circumferentially, limiting their maximum elonation and contraction respectively. in addition, dorsoventral muscles 9spanning from the front or belly of the worm to the back) contract to maintain the elliptical cross-section, which therefore also limits the extensibility and contractibility. This enables these worms to crawl more efficiently by ciliary action.

The limit of extensibility for nemertines is about 10: they can contract to no more than 10% of their maximally extended length. However, it should be noted that some nemertines can contract further by coiling (as in *Lineus socialis*).

Bibliography

The original source of this model:

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