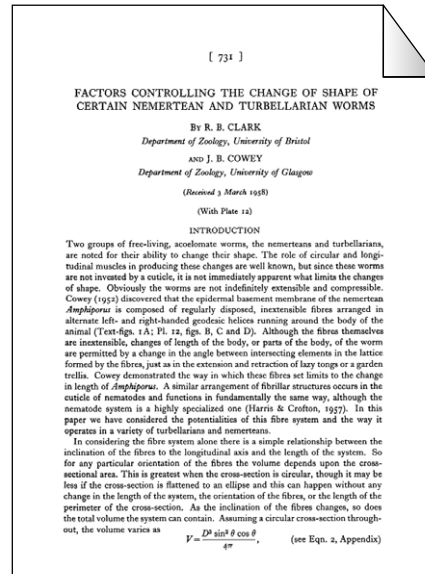


FOUNDATIONS OF ANIMAL HYDRAULICS: GEODESIC FIBRES CONTROL THE SHAPE OF SOFT BODIED ANIMALS



Robert Shadwick discusses R. B. Clark and J. B. Cowey's 1958 paper entitled 'Factors controlling the change of shape of certain nemertean and turbellarian worms'. A copy of the paper can be obtained from <http://jeb.biologists.org/cgi/reprint/35/4/731>.

In 1958 R. B. Clark and J. B. Cowey published a paper in which they presented a simple geometric model, based on the idea of a fibre-reinforced cylinder, to explain the mechanism underlying shape changes in ribbon worms and flatworms (Clark and Cowey, 1958). While their results may have been of interest to only a few biologists at that time, the essential idea of this paper, that a structure composed of inextensible fibres could accommodate large extensibility, has endured and its application has become widespread, first in numerous biomechanical case studies and, more recently, in modern biomimetics and mechanical engineering. The basic model that was developed is now entrenched as a design principle in biomechanics. The paper continues to be cited, and its summary concept (as seen in Fig. 1) has been reproduced in numerous texts or reviews over the past several decades (e.g. Alexander, 1968; Alexander, 1979; Alexander, 1988; Chapman, 1975; Clark, 1964; Gray, 1968; Vogel, 1988; Vogel, 2003; Wainwright et al., 1976; Wainwright, 1988).

What set the stage for this work? The 1940s and early 1950s produced many descriptive and experimental studies that investigated how soft-bodied animals

move. The idea that hydrostatic pressure plays a role in invertebrate support and locomotor systems had been explored by other researchers (e.g. Batham and Pantin, 1950; Chapman, 1950; Chapman and Newell, 1947; Chapman and Newell, 1956; Harris and Crofton, 1957; Newell, 1950; Wells, 1944); phenomenological explanations were established and the concept of a 'hydrostatic skeleton' came into use. This term defines a system in which muscles shorten to act against a contained volume of fluid, rather than rigid skeletal elements, to maintain shape and effect movement. These earlier papers described the basic workings of hydrostatic skeletons of cnidarians, annelids and nematodes.

The initial focus of the Clark and Cowey research was to find a functional explanation for the high extensibility of some nemerteans (such as the extremely long bootlace worm, *Lineus longisimus*). To a certain extent the role of circular and longitudinal muscles in producing dimensional changes in some invertebrates was understood, but the mechanism responsible for limiting shape changes was not. For example, it was not clear exactly how length changes were related to diameter changes produced by circular muscle contractions, or how a worm-like animal could move if it had only one set of muscles (as in the case of nematodes). So Cowey and Clark set out to match morphology with mechanics, an approach that had been well established at the *Journal of Experimental Biology* under the influence of Sir James Gray. The idea that the geometry of the reinforcing fibres in the body wall was the key to the solution was first explored in a study of structure and extensibility of a common British nemertean, *Amphiporus lactifloreus*, and published in a 1952 paper in which Cowey affirms the partnership by acknowledging the assistance of R. B. Clark 'in mathematical matters' (Cowey, 1952). They showed that the epidermal basement membrane of *Amphiporus* was invested with silver-staining 'reticulin' (primarily collagen) fibres that were nearly inextensible and laid down in crossed arrays in a latticework that could change shape, 'just as in the extension and retraction of lazy-tongs'. They then suggested that the orientation and inextensibility of the fibres set the physical limits on length changes that can occur, and showed how these limits can be extreme, with changes of more than 5 fold being observed in *Amphiporus*. This subject was explored further in the 1958 paper, which presented additional experimental data and a more detailed exposition of their geometric model.

The essence of this model is presented in Fig. 1, which shows the familiar representation of a worm as a fluid-filled tube stiffened by helical wrappings of inextensible fibres. The length of a segment bounded by one full turn of the fibre is controlled by the fibre angle θ , defined as the inclination of the fibres to the longitudinal axis. With extension, the segment's diameter and fibre angle both decrease; conversely, with segment shortening the fibre angle and diameter increase. If the segment maintains a circular cross-section, its volume, V , will vary, according to the curve in Fig. 1C. V decreases towards zero as θ goes to 0° (a long, thin thread) or 90° (a flat disc), and it peaks at an intermediate angle of 54.74° . But an extensible worm, in most cases, does not change volume, so it cannot follow the curve. However, according to Clark and Cowey, 'The system can always contain less than this volume if the cross-section is elliptical instead of circular,' allowing a worm to adopt a flattened, elliptical cross-section as it changes length along a horizontal line of constant volume, as shown in Fig. 1C. The extremes of shortening and lengthening occur where this line intersects the V vs θ curve and

only here will the worm be circular. The greatest degree of flattening occurs when $\theta=54.74^\circ$, also the angle where circumferential and longitudinal stresses in a pressurized cylinder balance (Wainwright et al., 1976). This is probably the reason why Clark and Cowey observed that a worm fully relaxed by anaesthesia adopts a length where $\theta \approx 55^\circ$. The vertical position of the extensibility line is determined by the degree of ellipticity, or flattening, that the segment adopts when relaxed (i.e. the ratio of major to minor axes, n). In theory, a flatter worm should have a higher range of extensibility, because of its lower position on the plot in Fig. 1C, i.e. there is a greater range of lengths possible between the extremes bounded by the V curve.

The elegantly simple experimental component of the paper tested this hypothesis. In nine species of nemertean and turbellarian worms, Clark and Cowey determined the range of possible lengths the worms could achieve, with the maximum based on passive stretching of an anaesthetized worm, while the fully contracted length was achieved by dropping an unanaesthetized worm in formaldehyde. The degree of flattening, n , was measured

at the relaxed length and from this the volume relative to the maximum possible if the worm was circular was calculated as $2n/(n^2+1)$. This volume established the position of the horizontal extensibility lines for each species shown in Fig. 2, and allowed predictions of the maximum and minimum lengths to be compared with the measured values. The worms with moderate or low extensibility showed remarkable agreement with the theory, leading to the conclusion that, 'the geodesic fibres are the operative factor in limiting length changes.' Interestingly, the flattest species which had the greatest theoretical extensibilities had the least observed ones. This was explained as being the result of additional connective tissue elements and muscles in these species that impose restrictions to deformability, although the fibre system was still regarded as setting an overall limit to their changes in shape. It is also likely that the method used underestimated minimum length because it involved full contraction of circular and longitudinal muscles together, rather than contraction of just the latter.

An interesting outcome of Clark and Cowey's study is the idea that the body wall provides a passive elastic antagonist to muscle contraction, even though there are no elastic (i.e. stretchy) elements. As they stated, the geodesic fibre structure 'provides an elastic tissue ... although it is itself composed of inelastic elements.' Furthermore, since the fibres are loaded in tension this sets up the possibility of elastic energy storage to aid in the recoil and extension of the relaxing muscle, giving us an explanation for the nematodes. In these worms, a stiff helical fibre-reinforced cuticle with $\theta=75^\circ$ is the only antagonist to the longitudinal muscles; no circular muscles exist. Because these worms maintain a high internal pressure they are cylindrical and thus occupy a position on the right-hand side of the volume curve in Fig. 1, where circular muscles are unnecessary. It is now recognized that energy-saving mechanisms based on tensile fibre lattices are potentially at work in many skeletal systems, such as fish skin, cetacean subdermal tissues or squid mantle wall (see Wainwright, 1988; Pabst, 1996; Gosline and Shadwick, 1983).

My first introduction to the helical winding principle of Clark and Cowey was from *Animal Mechanics* (Alexander, 1968), which I used as a text in an undergraduate biophysics course in 1974. This was one of several key examples in Alexander's book that made the idea of using mechanics to understand animal function very appealing. In a subsequent graduate course using *Mechanical Design in Organisms*

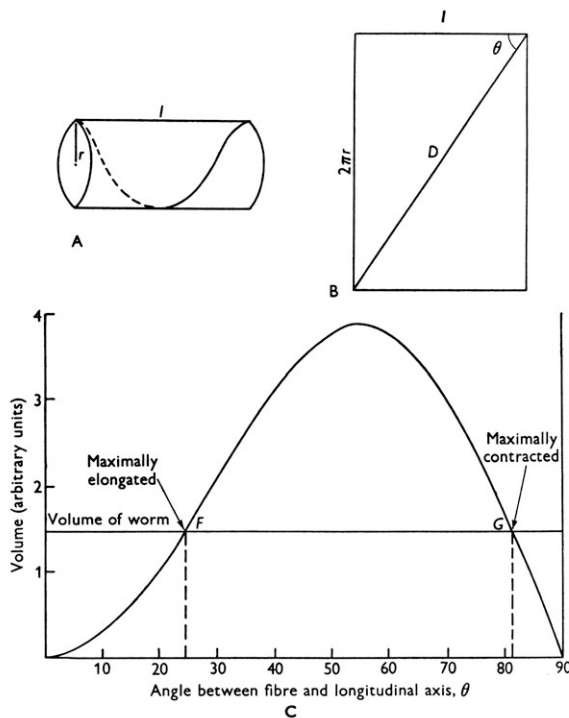


Fig. 1. (A) A unit length segment of a model worm, represented as a cylinder (radius r , length l) wrapped by one full turn of an inextensible fibre having length D ; fibres with the opposite sense are omitted. The fibres follow the course of geodesics (i.e. the shortest line between two points on a curved surface). (B) The unit length in A cut along the top and laid open. (C) A curve representing the volume contained by the cylindrical fibre system at different fibre angles θ , showing the maximum occurring at 54.74° . Segments at low θ are long and thin; at high θ they are short and fat. The horizontal line represents the constant volume of the nemertean *Amphiporus lactifloreus*. It intersects the curve at F and G, which represent the maximum and minimum lengths, respectively. Figure reproduced from Clark and Cowey (Clark and Cowey, 1958).

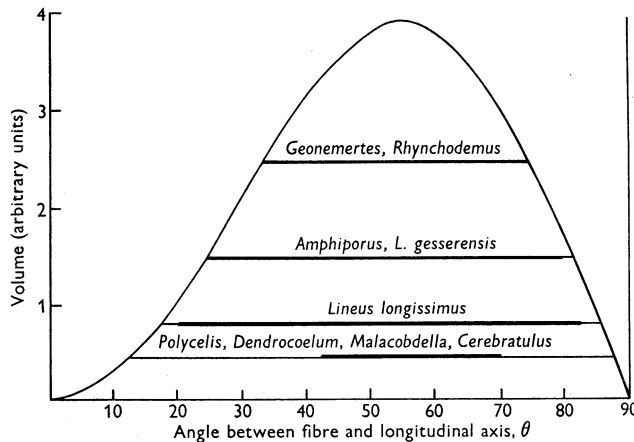


Fig. 2. The relationship between volume and fibre angle θ as in Fig. 1C, on which are superimposed the actual volumes of various nemerteans and turbellarians (fine horizontal lines). The heavy line segments show the range over which changes in length take place, comparing the experimental with theoretical extensibilities. Figure reproduced from Clark and Cowey (Clark and Cowey, 1958).

(Wainwright et al., 1976), the Clark and Cowey model was espoused as one of the key design principles of structural systems in biology. Perhaps the greatest advocate of the usefulness of analysing hydrostatic skeletons according to this model has been Steve Wainwright, who wrote a book on the subject [*Axis and Circumference* (Wainwright, 1988)] and encouraged many students to do research in this area. A sampling of these efforts reveals studies on such topics as elephant trunks, lizard tongues, cephalopod arms, notochord development, fish skin, echinoderm tube feet, and cetacean dermal and subdermal structures (Hebrank, 1980; Kier and Smith, 1985; Kier and Stella, 2007; Koehl et al., 2000; Long et al., 1996; McCurley and Kier, 1995; Pabst, 1996; Wainwright et al., 1978).

In discussing the significance of their work, Clark and Cowey state that, 'helical bounding systems ... may be quite widespread, if not general, in soft-bodied, worm-like animals,' suggesting that their findings could have broad application in biology. Indeed this has proven to be the case; time has shown that helical fibre winding is ubiquitous in nature, including plants, animals (see Vogel, 1988; Vogel, 2003; Wainwright, 1988) and even bacteria (Wolgemuth et al., 2003). Engineers, too, have taken inspiration from the worms. Efforts to create compliant actuators for robotics have adopted the geodesic fibre-reinforcing model, based on that described by Clark and Cowey. For example, a crossed helical fibre-reinforced flexible tube

will change shape when pressurized, according to the rules laid out in Fig. 1. If the resting θ is $<55^\circ$ then increasing pressure will tend to increase volume and θ , driving the shape up the left-hand side of the volume curve. This results in shortening and provides the basis for an artificial muscle and its control (e.g. Liu and Rahn, 2003). Similarly, polymer hydrogels encased in helical fibre lattices, again mimicking the worm model, are effective high-force actuators that can be controlled by gel swelling changes in the presence of water (e.g. Santulli et al., 2005). What started simply as a search for an explanation of the 'curiously high extensibility of 'certain nemertean worms' has provided good service to biomechanicists interested in support and locomotion over the past five decades, and has now entered the realm of biomimetics and robotics. Certainly, such endurance and breadth of application of the original work in this 1958 JEB paper is the hallmark of a true 'classic'.

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