

Tongues, tentacles and trunks: the biomechanics of movement in muscular-hydrostats

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Muscular-hydrostats, muscular organs which lack typical systems of skeletal support, include the tongues of mammals and lizards, the arms and tentacles of cephalopod molluscs and the trunks of elephants. In this paper the means by which such organs produce elongation, shortening, bending and torsion are discussed. The most important biomechanical feature of muscular-hydrostats is that their volume is constant, so that any decrease in one dimension will cause a compensatory increase in at least one other dimension. Elongation of a muscular-hydrostat is produced by contraction of transverse, circular or radial muscles which decrease the cross-section. Shortening is produced by contraction of longitudinal muscles. The relation between length and width of a constant volume structure allows amplification of muscle force or displacement in muscular-hydrostats and other hydrostatic systems. Bending requires simultaneous contraction of longitudinal and antagonistic circular, transverse or radial muscles. In bending, one muscle mass acts as an effector of movement while the alternate muscle mass provides support for that movement. Torsion is produced by contraction of muscles which wrap the muscular-hydrostat in a helical fashion.

KEY WORDS:—Tongues – tentacles – cephalopods – biomechanics – muscular-hydrostats.

CONTENTS

Introduction	308
Morphology of muscular-hydrostats	308
Constant volume of muscular-hydrostats	309
Elongation	312
Shortening	316
Bending	318
Stiffening	319
Torsion	320
Summary	322
Acknowledgements	322
References.	323

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INTRODUCTION

A number of organs in animals, including the tongues of many terrestrial vertebrates, the appendages of cephalopod molluscs and the trunks of elephants are composed almost entirely of muscle. These muscular organs, although lacking an obvious system of skeletal support, are capable of diverse, complex and highly controlled movements. The means by which an organ composed entirely of muscle produces movement is of interest because locomotion, maintenance of posture and other muscular activities are generally considered to depend on the interaction of muscle with a system of skeletal support. A skeletal support system transmits the force produced by muscle contraction, allows muscles to be returned to their resting length by action of antagonistic muscles, provides the support necessary to resist the compressive and bending forces exerted by muscles, and finally, amplifies the resultant force, speed or displacement of muscular activity.

Skeletal support systems in animals are divided into two general types. The first is characterized by hardened skeletal elements such as the internal skeleton of vertebrates, external skeleton of arthropods, and the test of many echinoderms. The second type of skeletal support is characterized by hydrostatic skeletons, typically a connective tissue fibre-reinforced container surrounding a fluid-filled cavity, as seen in polyps and the diverse vermiform animals. The means by which both hydrostatic and hardened skeletons function in support of muscular activities has been extensively studied (Alexander, 1968; Chapman, 1958, 1975; Clark, 1964, 1981; Clark & Cowey, 1958; Schmidt-Nielsen, 1979; Wainwright, 1970, 1982; Wainwright *et al.*, 1976).

In this paper we will discuss the means by which muscular organs such as tongues, tentacles and trunks, which lack a distinct skeletal system, produce their varied and complex movements. We refer to these structures as 'muscular-hydrostats' to emphasize the importance of the musculature in both support and movement, while noting their resemblance to hydrostatic skeletons. Below, we examine the major morphological features which characterize muscular-hydrostatic organs and discuss the general mechanical principles involved in elongation, shortening, bending and torsion.

MORPHOLOGY OF MUSCULAR-HYDROSTATS

We discuss three distinct groups of muscular-hydrostatic organs: the tongues of lizards and mammals, the arms and tentacles of cephalopod molluscs and the trunks of elephants. The morphology of many of the organs we discuss has been previously described and the similarities in arrangement of musculature between a number of these organs has been noted. Cuvier (1817) compared the arms of octopus to the tongue of mammals and Owen (1843) noted the similarity in 'mechanical arrangement' of muscle in the tentacles of the chambered nautilus and the proboscis of the elephant. More recently, Tittel (1961, 1964), Saban (1971) and Gutmann (1981) noted the similarity in morphology between a number of muscular-hydrostats including the arm of the octopus, the mammalian tongue and the elephant trunk. Boas & Paulli (1908, 1925) described in detail the arrangement of musculature in the trunk of the elephant. Many papers discuss the arrangement of the intrinsic muscles of cephalopod appendages (i.e. Colasanti, 1876; Guérin, 1908; Owen, 1832) and the tongue in

lizards (i.e. Gandolfi, 1908; Richter, 1933; Sewertzoff, 1929; Sondhi, 1958) and mammals (i.e. Abd-el-Malek, 1938; Bennett & Hutchison, 1946; Dabelow, 1951; Doran, 1975; Doran & Baggett, 1970; Doran & Allbrook, 1973; Griffiths, 1968, 1978; Hellstrand, 1981; Livingston, 1956). However, only a few of the above papers attempt a mechanical analysis of movement.

A muscular-hydrostat is characterized by a closely packed three-dimensional array of musculature. Individual muscle fibres may be oriented in three general directions, (1) perpendicular to the long axis, (2) parallel to the long axis and (3) helical or oblique around the long axis of the organ.

Muscle fibres perpendicular to the long axis can be arranged in a transverse, radial or circular pattern. Transversely-arranged muscle fibres are found in the arms and tentacles of squid (Fig. 1A), octopus (Fig. 4A) and in most mammalian tongues (Figs 1B, 2B). Typically, the transverse muscle fibres are arranged in an orthogonal array so that alternating layers of fibres run horizontally and vertically across the organ (Fig. 2). Radially-arranged muscle fibres are found in the tentacles of the chambered nautilus (Fig. 3A) and in the elephant proboscis (Fig. 3B). The radial muscle fibres lie perpendicular to the long axis, originate in the centre of the organ and radiate out to the periphery. Circular muscle arrangements are found in a number of mammalian and lizard tongues (Fig. 4B) and in the squid tentacle (Fig. 1A). In some circular muscles (see the lizard tongue, (Fig. 4B) individual muscle fibres do not extend around the entire circumference but instead are short and run tangentially within the circular muscle mass.

Muscle fibres parallel to the long axis are arranged in longitudinal bundles. In muscular-hydrostats capable of elaborate bending movements, such as mammalian tongues (Figs 1B, 2B), octopus arms (Fig. 4A) nautilus tentacles (Fig. 3A) and elephant proboscides (Fig. 3B), the longitudinal muscle bundles are arranged in the periphery around the central core of musculature. The longitudinal muscles of some protrusible lizard tongues are located centrally (Fig. 4B).

Muscle fibres arranged helically or obliquely around the long axis of a muscular-hydrostat are also common and are generally present in two layers of opposite handedness, wrapping the central core of musculature (Figs 1B, 3, 4A).

The radial and transverse musculature of these organs often has its origin on a centrally-located connective tissue sheath. In the cephalopod appendages the connective tissue sheath surrounds the axial nerve cord, while in the elephant proboscis the connective tissue surrounds the nasal passages. In mammal tongues the horizontal transverse musculature originates on a longitudinally-arranged verticle connective tissue septum (Fig. 1B). The peripheral insertion of the radial and transverse muscle fibres typically occurs on a connective tissue sheath which surrounds the musculature (Dabelow, 1951; Doran, 1975).

Although there may be nerve cords, blood vessels or fat pads within these muscular-hydrostats, the characteristic feature is that the organ is composed almost entirely of muscle. There is no evidence of a distinct fluid-filled or hydrostatic cavity.

CONSTANT VOLUME OF MUSCULAR-HYDROSTATS

The most important biomechanical feature of a muscular-hydrostat is that it is a structure of constant volume. There is no evidence of major flow of fluid into

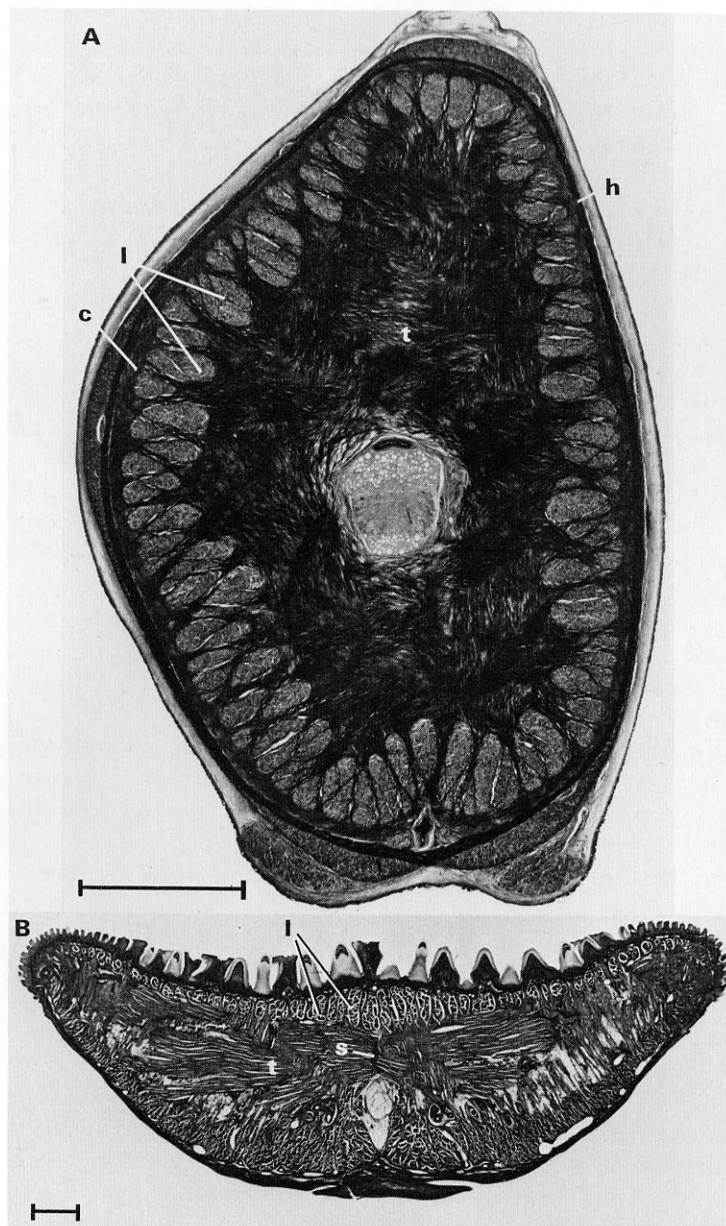


Figure 1. A, Light micrograph of a transverse section of a tentacular stalk of the squid, *Loligo pealei*. Muscle fibres of the transverse muscle mass (t) surround the centrally-located axial nerve cord. In the periphery, bundles of longitudinal muscle fibres (l) interdigitate with the transverse muscle mass. Muscle fibres of the transverse mass extend into and become part of a circular muscle layer (c). Wrapping the circular muscle layer is a pair of helically-arranged muscle fibres (h), one layer in a right-hand and the other in a left-hand helix. Direct microscopy of a paraffin section stained with Mallory's Triple Stain. Scale bar = 1 mm. B, Transmitted light photograph of a transverse section of the tongue of the cat, *Felis domestica*, showing the intrinsic tongue musculature. A mass of transverse muscle fibres (t) is located centrally in the tongue. The horizontally-arranged muscle fibres of the transverse muscle mass originate on a vertical connective tissue septum (s). Light structure below the septum is a fat deposit. In the periphery, bundles of longitudinal muscle fibres (l) interdigitate with muscle fibres of the transverse muscle mass. Photograph of a frozen section stained with Masson's Trichrome Stain. Scale bar = 1 mm.

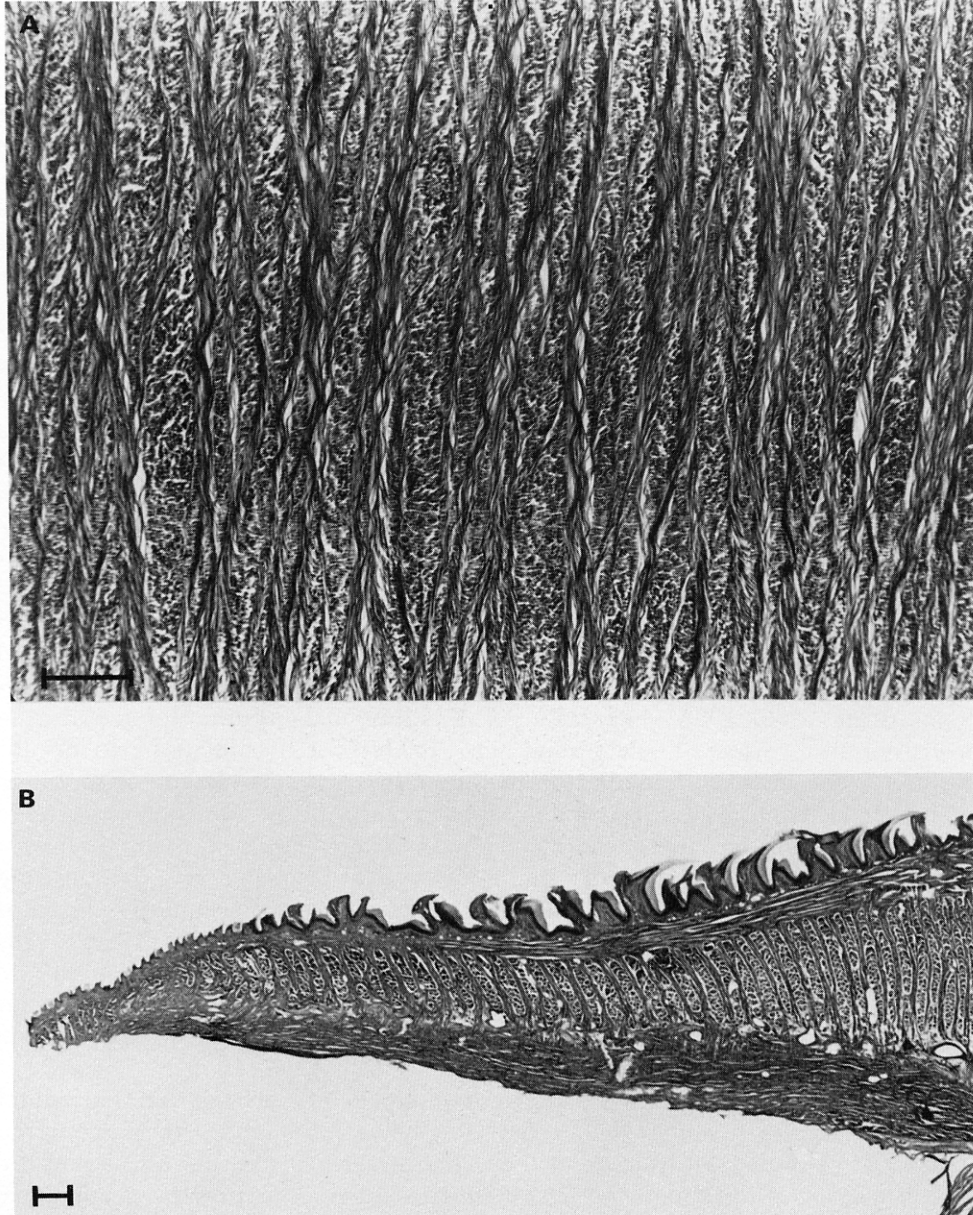


Figure 2. A, Light micrograph of a parasagittal section of the transverse muscle mass of the tentacular stalk of the squid, *Loligo pealei*. Note that the transverse muscle mass is made up of alternating layers of vertically arranged muscle fibres (cut in longitudinal section) and horizontally arranged muscle fibres (cut in cross section). Direct microscopy of paraffin section stained with Mallory's Triple Stain. Scale bar = 100 μ m. B, Transmitted light photograph of a parasagittal section of the tongue of the cat, *Felis domestica*. The transverse muscle mass of the tongue is made up of alternating layers of vertically arranged and horizontally arranged muscle fibres. Longitudinal muscle fibres can be seen dorsally and ventrally. Photograph of frozen section stained with Masson's Trichrome. Scale bar = 1 mm.

or out of the structures we discuss. Muscle tissue is composed primarily of an aqueous liquid which is practically incompressible at physiological pressures. Further, contraction of muscle does not significantly change its volume. Experiments on frog sartorius muscle have shown the volume to decrease during contraction by only 0.002% (Abbott & Baskin, 1962), an amount too small to be important within the context of this analysis. In a muscular-hydrostat or other structure of constant volume, any change in one dimension will cause a compensatory change in at least one other dimension. This principle serves as the basis for the following analysis of structure and movement in muscular-hydrostats.

ELONGATION

A cylindrical structure of constant volume will be elongated by contraction of musculature that decreases the cross-sectional area. Cross-sectional area will be decreased by activity of musculature which lies perpendicular to the long axis of the muscular-hydrostat, i.e. transverse, circular or radial arrangements. It appears that a number of muscular-hydrostats utilize elongation as a mechanism to produce protrusion. Kier (1982) found that the very rapid protrusion of the squid tentacle during prey capture was produced by elongation. Direct measurement of elongation of the tongue in a number of animals was obtained using cineradiographic films (Smith, 1984). Small lead markers were placed within the body of the tongue and the animals were filmed during normal behavior. Measurements of the change in distance between markers demonstrate a 70–100% expansion of the long axis of the tongue during protrusion in a variety of behavioural acts (Table 1). Experimental evidence for the role of the intrinsic musculature in tongue protrusion in lizards is provided by Smith (1980, 1984). Electromyographic recordings of the intrinsic tongue musculature in the tegu lizard, *Tupinambis nigropunctatus*, which has a morphology similar to that of the monitor lizard in Fig. 4B, demonstrate electrical activity of the circular muscle during tongue protrusion and electrical activity of the longitudinal muscles during retraction. Griffiths (1968, 1978) discussed similar mechanisms for protrusion in the echidna. Bennett & Hutchinson (1946) and Abd-el-Malek (1938) have provided evidence that elongation due to activity of intrinsic muscles is responsible for tongue protrusion in a number of mammals.

In the case of animals with alternating layers of vertical and horizontal transverse muscles, a similar mechanism may be used to change the shape of the organ. For example, contraction of the vertical and longitudinal muscles in the tongue will cause the tongue to flatten and broaden. This may be particularly important in movements and shape changes of the mammalian tongue.

Mechanical amplification of muscle displacement or force is typically thought to be possible only for support systems which utilize hardened skeletal elements to provide leverage (Osborne, 1967). We suggest, however, that mechanical amplification analogous to leverage is possible for muscular-hydrostats and other hydrostatic skeletons. The relation between the length and diameter of a cylinder of constant volume is plotted in Fig. 5. In a constant volume cylinder with a high initial length/width ratio (Fig. 5C, D) a small decrease in diameter will produce a large increase in length. A brief review of lever systems in general

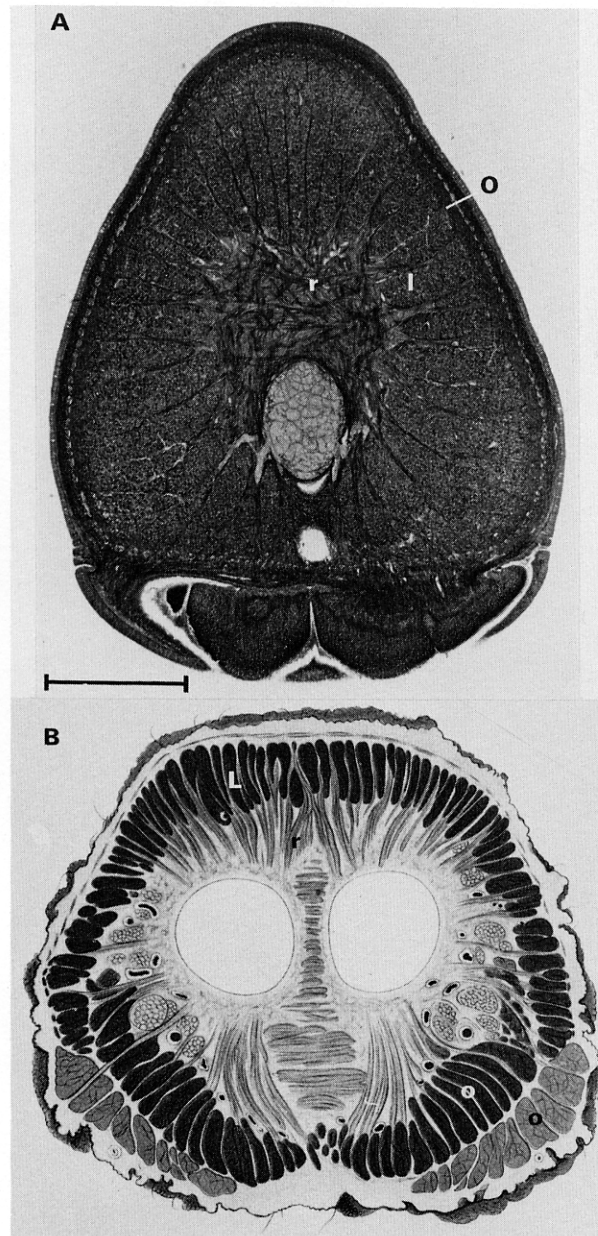


Figure 3. A, Light micrograph of a transverse section of the tentacle (digital cirrus) of the chambered nautilus, *Nautilus pompilius*. Radially arranged muscle fibres (r) extend from a central mass to the periphery where they interdigitate with bundles of longitudinal muscle (l). Wrapping the inner core of muscle on each side of the tentacle is a layer of obliquely arranged muscle (o). The oblique muscle layers on each side are opposite in handedness. Direct microscopy of a paraffin section stained with Masson's Trichrome. Scale bar = 1 mm. B, Photograph of plate 14 (2) from Boas & Paulli (1908) of a transverse section of the proboscis of the elephant. The rectus muscle is radially arranged (r) and extends peripherally to interdigitate between fascicles of longitudinal muscle (l), the maxillolabialis, and two obliquely arranged muscle groups (o), the *pars rimana* (superficial) and the *pars supralabialis* (deep). The two oblique muscle groups are opposite in handedness. Scale not indicated on original. Permission to reproduce the plate has been granted by courtesy of the Library of the Museum of Comparative Zoology, Harvard University.



Figure 4. A, Light micrograph of a transverse section of the arm of the octopus, *Octopus bimaculoides*. A central mass of transverse muscle (t) surrounds the axial nerve cord and extends peripherally to interdigitate with bundles of longitudinal muscle fibres (l). Oblique muscle layers (o), of both left and right handedness, are located peripherally wrapping the inner core of musculature. Direct microscopy of paraffin section stained with Masson's Trichrome. Scale bar = 1 mm. B, Light micrograph of a transverse section of the tongue of the monitor lizard *Varanus exanthematicus*. Two large longitudinal muscle masses (l) are wrapped by circumferential muscle layers (c). Muscle fibres of the circumferential muscle layer typically do not extend around the entire circumference and instead run in short, tangential trajectories. Direct microscopy of paraffin section stained with Masson's Trichrome. Scale bar = 1 mm.

Table 1. Percent expansion within the tongue during protrusion in four animals

Species	N	Expansion
<i>Tupinambis nigropunctatus</i> (tegu lizard)	8	106%
<i>Varanus exanthematicus</i> (monitor lizard)	5	70%
<i>Dasypus novemcinctus</i> (nine-banded armadillo)	6	97%
<i>Didelphis virginianus</i> (opossum)	3	72%

The lizards have circular arrangements of tongue muscles; the mammals have transverse tongue musculature. In each animal lead markers were placed within the body of the tongue and cineradiographic film was taken of lapping in *Tupinambis* and *Dasypus*, food transport in *Didelphis* and sensory tongue protrusion in *Varanus*. Minimum and maximum distance between the markers was measured for each cycle and the difference (amount of expansion) expressed as a percentage of the minimum distance. N is number of cycles. For further details on technique see Smith (1984). Data on *Didelphis* courtesy of A. W. Crompton.

will help to illustrate the importance of this relation. In Fig. 6 it can be seen that lever systems may be designed to increase mechanical advantage, so that the resultant force is greater than the applied force (Fig. 6A). Alternatively, the lever may increase displacement so that the resultant displacement or velocity is greater than the applied displacement or velocity (Fig. 6B). In the former case the mechanical advantage is greater than one, but the velocity advantage is less than one. In the latter case the mechanical advantage is less than one, but the velocity advantage is greater than one (Smith & Savage, 1956). In organs with high initial length/width ratios the velocity advantage of the transverse, circular or radial muscles which create the increase in length is greater than one, analogous to case B in Fig. 6. Thus, as a result of the geometrical relations of a constant volume cylinder, the resultant displacement and speed created by these muscles is amplified in a manner similar to leverage. The resultant force for elongation in organs with high length/width ratios is reduced.

Protrusible tongues in lizards and mammals typically show greater resting length/width ratios than non-protrusible tongues. Doran & Baggett (1970) and Doran (1975) classify mammalian tongues as intra-oral and extra-oral. Intra-oral tongues (Type 1) are used to move food in the mouth during mastication. They are typically protruded less than 50% of resting length. Extra-oral tongues (Type 2) are protruded by more than 100% of resting length and function in food gathering. Intra-oral tongues have a low length/width ratio while the protrusible extra-oral tongues show a high resting length/width ratio. Examples of the extra-oral type include tongues of the spiny anteater, *Tachyglossus*, the honey possum, *Tarsipes*, and the pangolin, *Manis*. A similar relation between protrusibility and high length/width ratios also holds for lizard tongues. The resting length/width ratio of the protrusible tongue of the tegu lizard, *Tupinambis*

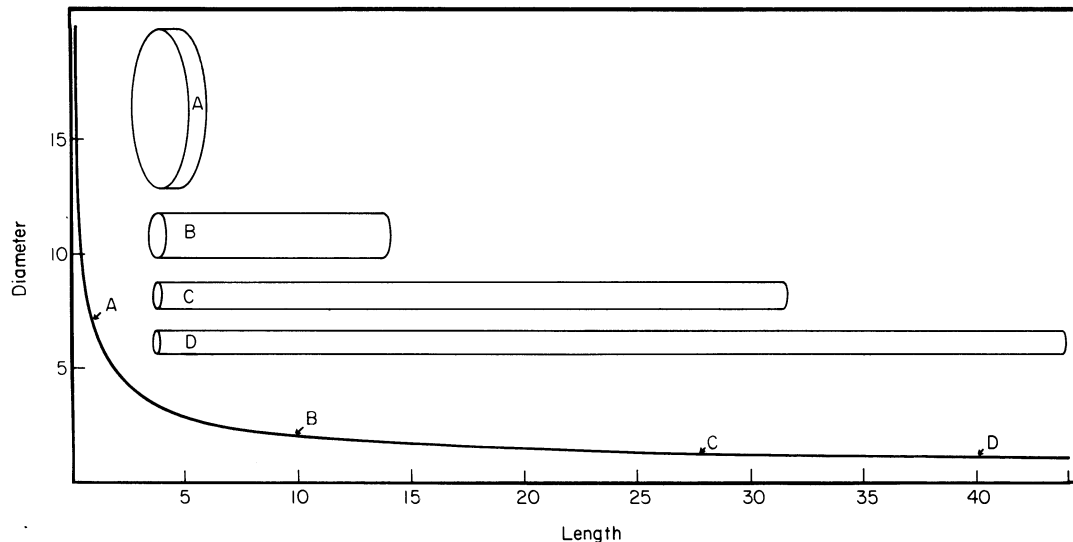


Figure 5. Plot of relation between length and diameter of a cylinder of constant volume. The positions on the graph of shapes A through D (drawn to scale) are indicated. A small decrease in diameter from shape B to D causes a large increase in length.

nigropunctatus, is three times that of the non-protrusible tongue of the lizard, *Ctenosaura similis* (Smith, 1984). The extensible tentacles of squid and the extensible cirri of *Nautilus* have a high length-to-width ratio in the retracted state, approximately 20 : 1 in the former and 25 : 1 in the latter (Kier, 1982, 1983).

Thus the simple geometrical relation between length and width in a constant volume cylinder provides the muscular-hydrostat with a system of mechanical amplification analogous to a lever system. It is important to note that this relation is of significance not only in this analysis of muscular-hydrostats, but in the study of all organs or bodies with hydrostatic support systems.

SHORTENING

From the standpoint of the longitudinally-arranged muscles which retract a muscular-hydrostat, a high length to width ratio results in a mechanical advantage greater than one and a velocity advantage less than one. For a given decrease in length created by these muscles, the resultant increase in diameter is less. The longitudinal muscles of an extensible structure with a high length/width ratio therefore operate over a much greater range of extension and contraction than the antagonistic radial, circular or transverse musculature. The longitudinal muscles of the extensible squid tentacle and extensible cirrus of *Nautilus* are made up of obliquely-striated muscle fibres. Obliquely-striated muscle fibres are characterized by their great range of elongation and flattened length-tension relationship (Hidaka *et al.*, 1969; Miller, 1975). For example, the obliquely-striated muscles of leeches can reversibly elongate by up to 300% of their fully contracted state. Lanzavecchia & Arcidiacono (1981) suggest that this is due to a change in stagger of thick filaments in addition to thin filaments 'changing partners' at extreme elongation.

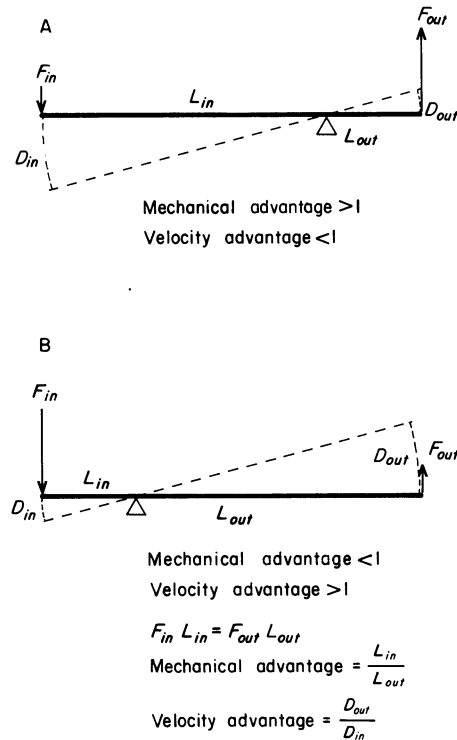


Figure 6. Diagram illustrating mechanical advantage and velocity advantage of lever systems. If a force, F_{in} , is applied to a lever, a resultant force, F_{out} , is applied by the lever. The relative magnitudes of F_{in} and F_{out} depend on the distances L_{in} and L_{out} from the fulcrum to the point of application of the forces. The mechanical advantage is defined as the ratio L_{in}/L_{out} . If D_{in} is the distance travelled by the point of application of F_{in} , then D_{out} is the distance travelled by the point of application of F_{out} . The velocity advantage is defined here as the ratio D_{out}/D_{in} .

Usually, the longitudinal muscles that retract the protrusible lizard and mammal tongue are cross-striated muscle. This muscle type has a much smaller range of elongation than obliquely-striated muscle. Gans & Bock (1965: 123) report that "the vast majority of entire muscles cannot shorten by more than 30%...", although Rice (1973: 238) claims that individual sarcomeres "can be reversibly contracted to about 40% of their fully extended length". If the longitudinal retractor muscles are longer than the tongue itself, however, their elongation will be reduced. (A longitudinal retractor muscle twice as long as the tongue will experience a 50% elongation for a 100% extension of the tongue.) This is indeed the case in many protrusible lizard and mammal tongues. In the monitor lizard, *Varanus* (see Fig. 4B), the *M. hyoglossus* which are the longitudinal muscles responsible for retraction of the tongue, originate on the ceratobranchial processes of the hyoid apparatus and project anteriorly for approximately one-third of the total hyoglossal muscle length before entering the tongue. The *M. sternoglossus*, the retractor muscle of the extensible tongue of the pangolin, *Manis*, originates at the base of the sternum on the xiphoid cartilages and passes through the thorax and neck to reach the oral cavity (Doran & Allbrook, 1973; Livingston, 1956).

The retractor muscles of the tongue of the chameleon (*Chameleo*) are a special

type of supercontracting cross-striated muscle. This muscle fibre type has perforated Z-discs, which allow the thick filaments to slide through the adjacent sarcomeres rather than abutting the Z-discs. As a result, chameleon tongue retractors can contract repeatedly to 16% of their fully extended length (Rice, 1973).

BENDING

Bending of a soft body or organ can be produced by contraction of longitudinal muscle on one side of the body or organ. This unilateral longitudinal muscle contraction will cause bending only if the longitudinal compressional force, tending to shorten the entire organ or body, is resisted. Without resistance to longitudinal compression, unilateral longitudinal muscle activity will cause shortening without bending.

Any shortening of a cylinder of constant volume must result in an increase in diameter. Shortening due to a longitudinal compressional force can therefore be prevented by resisting increase in diameter. Figure 7A illustrates bending of a cylinder of constant volume produced by a unilateral decrease in length in combination with maintenance of constant diameter. In a muscular-hydrostat, unilateral decrease in length may be created by contraction of longitudinal muscle on one side of structure while constant diameter may be maintained by contractile activity of transverse, radial or circular musculature. Without simultaneous activity of the musculature maintaining constant diameter, unilateral longitudinal muscle contraction would cause little or no bending (Fig. 7B).

Bending of a constant volume cylinder may also be produced by a decrease in diameter in consort with maintenance of unilateral constant length (Fig. 8A). In a muscular-hydrostat, decrease in diameter may be produced by transverse, radial or circular muscle contraction and unilateral constant length can be maintained by contractile activity of longitudinal muscle on one side of the cylinder. Without simultaneous longitudinal muscle activity, contraction of

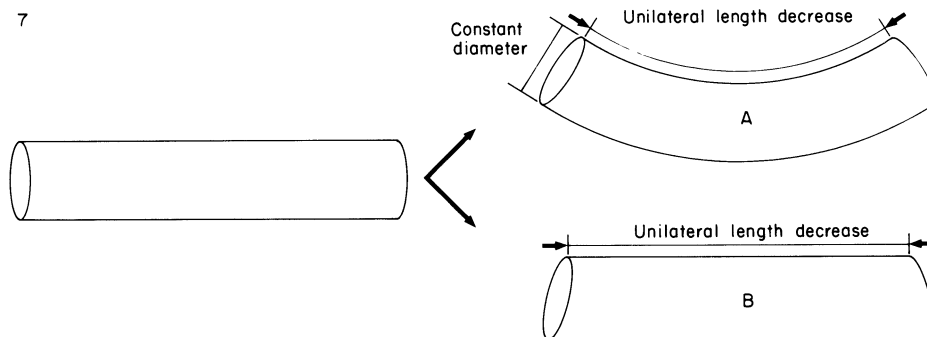


Figure 7. Diagram illustrating the requirements for bending in a muscular-hydrostat. Unilateral length decrease is caused by contraction of longitudinal muscle on one side of the structure. In case A, constant diameter is maintained thereby providing resistance to longitudinal compression and causing the structure to bend. Constant diameter can be maintained by contractile activity of transverse, radial or circular muscle. In case B, constant diameter is not maintained and without resistance to longitudinal compression the structure is shortened but not bent.

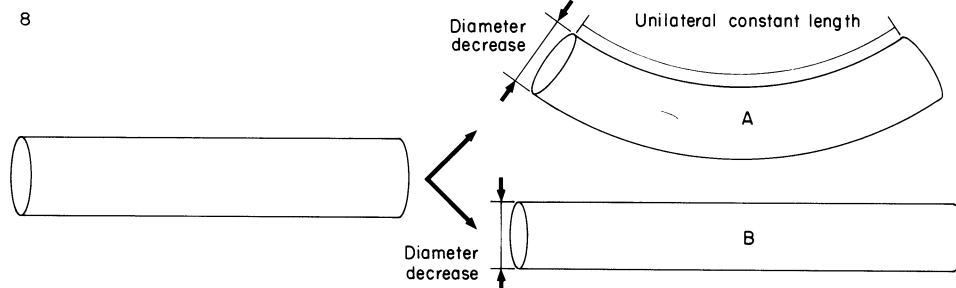


Figure 8. Diagram illustrating the requirements for bending in a muscular-hydrostat. Diameter decrease is caused by contraction of transverse, radial or circular muscle. In case A, unilateral constant length is maintained by contractile activity of longitudinal muscle on one side of the structure and thereby causes bending. In case B, unilateral constant length is not maintained and diameter decrease simply causes elongation.

transverse, radial or circular muscle would cause elongation without bending (Fig. 8B). Bending therefore requires simultaneous activity of longitudinal muscle and its antagonist: transverse, radial or circular muscle.

The octopus arm (Fig. 4A), the *Nautilus* tentacle (Fig. 3A), the elephant trunk (Fig. 3B) and many mammalian tongues (Fig. 1B) are capable of bending movements in many planes and illustrate the anatomical requirements for bending in a muscular-hydrostat. The longitudinal muscle masses must be situated peripherally in the structure. The further the longitudinal muscles are situated from the neutral axis, the greater is the moment arm for bending the structure. In order for bending to occur in any plane, the structure must have many longitudinal muscle bundles arrayed around the circumference of the structure as seen in the above examples.

Localized bending of a muscular-hydrostat requires localized control of both the longitudinal muscle and the antagonists and necessitates a highly partitioned neuromuscular system. By changing the pattern and coordination of the longitudinal and the antagonistic muscle activity, the specific point or direction of bending may be varied. The system is thus more flexible than many other musculoskeletal systems and may make possible, for example, the rapid and complex movements involved in human speech (Bowman, 1971; Lowe, 1981).

The same arrangement of musculature used for bending can also be used for extension and retraction by simply altering the sequence of contractile activity. With appropriate nervous control, bending in many planes, extension and retraction can all be produced by the same muscular arrangement. The ability both to change length and to produce bending movements is shared by the elephant trunk (Boas & Paulli, 1908, 1925), many lizard and mammalian tongues (Smith, 1984), the octopus arm and *Nautilus* tentacle (Kier, 1983). Presumably the musculature that extends these structures can also act in consort with the longitudinal musculature to produce bending movements.

STIFFENING

A structure of constant volume will be stiffened if dimensional changes are resisted by either muscle activity or connective tissue. For example, a structure wrapped with connective tissue which prevents dimensional change will stiffen

in response to muscle contraction. Such a stiffened structure may become a supporting element in movement as Gans & Gorniak (1982) have suggested for tongue protrusion in toads. We suggest that multi-axial muscular activity is an important stiffening mechanism in many muscular-hydrostats. It may be more significant in stiffening mammalian tongues than lytta, cavernous spaces, or sublingua (Doran, 1975).

TORSION

Torsion, the twisting of a muscular-hydrostat along its long axis, is produced by a helical or oblique arrangement of musculature. The direction of torsion depends on the handedness of the helical or oblique musculature. Contraction of a right-hand helix causes counter-clockwise torsion of the tip relative to the base when viewed from base to tip. Contraction of a left-hand helix causes clockwise torsion. Separately innervated right- and left-hand helically-arranged muscle may create torsion in either direction and simultaneous contractile activity of both right- and left-hand helical musculature results in an increase in resistance to torsional forces. The oblique or helical muscle arrays in the muscular-hydrostats we have studied are located typically in the periphery of the structure, wrapping the inner core of musculature. The peripheral location provides a larger moment through which the torque is applied than a more central location.

Helically-arranged muscle fibres may also contribute to changes in length of a muscular-hydrostat. Their effect depends on fibre angle, the angle that the helical muscle fibres make with the long axis of the structure. To investigate the function of helically-arranged muscle fibres, a model of a constant volume system with helically-arranged fibres of variable length was developed (Kier, 1983). The model is a modification of those proposed by Harris & Crofton (1957), Clark & Cowey (1958) and Clark (1964), for investigating the role that a crossed helical connective tissue fibre system plays in controlling shape changes in nemertean, nematode and turbellarian worms.

A cylinder of constant volume wrapped by a single turn of helical fibre is shown in Fig. 9A. If the cylinder is slit longitudinally and spread out flat, it appears as in Fig. 9B. The fibre angle, θ , is the angle that the helical fibre (length D) makes with the longitudinal axis of the cylinder. The length, radius and volume are, respectively:

$$L = D \cos \theta \quad (1)$$

$$r = D \sin \theta / 2\pi \quad (2)$$

$$V = \pi r^2 L \quad (3)$$

Substituting for r and L in equation (3) gives,

$$V = D^3 \sin^2 \theta \cos \theta / 4\pi \quad (4)$$

The cylinder is constant in volume and we wish to solve for the helical fibre length:

$$D = \sqrt[3]{4\pi V / \sin^2 \theta \cos \theta} \quad (5)$$

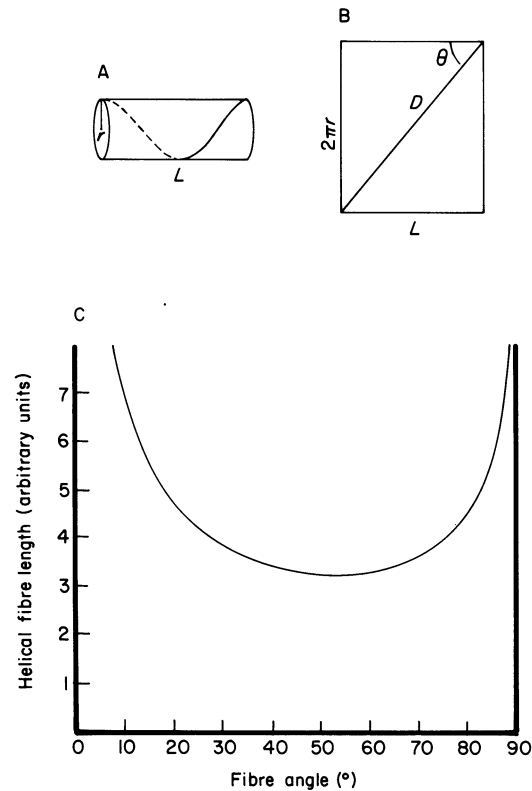


Figure 9. Diagram illustrating the effect of fibre angle on the length of a helical fibre wrapping a constant volume cylinder. See explanation in text.

Helical fibre length can then be plotted against fibre angle, θ , Fig. 9C. The length of the helical fibre is at a minimum when the fibre angle equals $54^{\circ}44'$ and approaches maxima when the fibre angle approaches 0° and 90° . This means that helically-arranged muscle fibres with a fibre angle greater than $54^{\circ}44'$ will, upon contraction, create force for both torsion and elongation. Helically-arranged muscle fibres with a fibre angle less than $54^{\circ}44'$ will create force for both torsion and shortening.

Torsional movements have been observed in the arms and tentacles of squid (Kier, 1982), the arms of octopuses (Kier, 1983), the cirri of *Nautilus* (Kier, 1983) and the trunks of elephants (Boas & Pauli, 1908). Each of these appendages is equipped with both a left-hand and right-hand array of either helical or oblique muscles. With the exception of the squid arm, the muscular-hydrostats listed above have been observed to change in length. The fibre angle of the oblique or helical muscle layers must increase during shortening and decrease during lengthening. For example, the fibre angle measured in the helical muscle layers of the squid tentacle (Kier, 1982) ranged from approximately 67° in a retracted tentacle to approximately 36° in a fully extended tentacle. This range of fibre angles indicates that in addition to creating a torsional force, the helical fibres of the squid tentacle may produce force for elongation in a retracted tentacle and force for retraction in an

elongated tentacle. The range of fibre angles during extension and retraction in the other extensible structures has not been measured. The fibre angle of the oblique muscle layers of the inextensible squid arm is approximately 72° (Kier, 1982). In addition to creating a torsional force, the oblique muscle layers will therefore create a force for elongation that may aid the transverse musculature in resisting longitudinal compression.

SUMMARY

Muscular-hydrostats differ from more common musculoskeletal systems because muscles alternately stiffen and support a structure, or produce movement. The musculature therefore acts both as the effector of movement and as the support for movement.

Elongation results from contraction of transverse, radial or circular muscle. If the structures possess a high length/width ratio, mechanical amplification of the displacement and speed of the transverse, radial or circular muscles results. Mechanical amplification of radial, transverse or circular muscle contraction is possible not only for vertebrate tongues, cephalopod appendages and elephant trunks but for any elongate cylindrical constant volume body or organ. Examples might include vermiform invertebrates such as annelids, nemerteans, echiurans, priapulids, phoronids and holothuroids, and protrusible organs such as proboscides and tentacles.

Shortening results from contraction of longitudinal musculature. If the range of elongation and shortening is great, the longitudinal musculature must be capable of a large working range. Alternatively, the length of the longitudinal musculature may be greater than the length of the protrusible organ and will experience a smaller percentage elongation.

Bending results from simultaneous longitudinal and transverse, radial or circular muscle contraction. A peripheral location of longitudinal muscles provides a greater moment for bending a muscular-hydrostat (or other hydrostatic body or organ) than a central location. Localized bending requires localized control of both the longitudinal muscles and their antagonists (transverse, radial or circular) and therefore requires musculature that is subdivided both morphologically and neurally.

Torsion results from contraction of helically or obliquely-arranged muscle. In order for torsion to occur in both directions, separately innervated right- and left-hand helical or oblique muscle layers must be present. The helical or oblique layers may also effect changes in length depending on the fibre angle. Contraction of a helical muscle layer with a fibre angle greater than $54^\circ 44'$ causes elongation whereas contraction of a helical muscle layer with a fibre angle less than $54^\circ 44'$ will cause shortening. Finally, a peripheral location of helical muscle provides a greater moment through which torque is applied than a central location.

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