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Trunks, Tongues, and Tentacles: Moving with Skeletons of Muscle

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The ability of the elephant's trunk to bend, lift, twist, and elongate is striking (Fig. 1). The movements of the trunk are not only varied but extremely strong: an elephant can lift a tree with its trunk. The tongues of mammals and reptiles exhibit a similarly surprising range of movements, including bending, extending, retracting, and twisting. One need only consider the part played by the human tongue in speech to appreciate the rapid, complex, and varied motions of which it is capable. Phenomena of the same kind are found among the cephalopods. The squid catches its prey with a rapid motion that requires its two tentacles to elongate by 70% or more in less than three hundredths of a second. After the prey is captured, the squid's eight arms reposition it for eating using complex bending movements. The octopus has eight arms capable of an almost infinite range of movements—bending, twisting, elongating, and shortening. It uses its arms to move, to anchor itself, to capture prey, and to explore its environment.

These organs belong to a group of structures with unique biomechanical properties. Notable for their functional diversity and complexity of movement, they are distinctive because they are composed almost entirely of muscle; they lack any obvious system of skeletal support. The musculature itself both creates movement and provides skeletal support

for that movement. It can provide this support because it is composed primarily of an incompressible liquid and is thus constant in volume. In recognition of this mechanism we have called such organs muscular hydrostats (Kier and Smith 1985). In this paper we will describe the morphological and functional characteristics

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of this remarkable group of structures and suggest ways in which an understanding of muscular hydrostats provides new insights into the diversity of animal form.

A skeletal system may consist of hardened internal elements such as the bony skeleton found in vertebrates or hardened external elements such as the exoskeletons of crabs, insects, or other arthropods (Alexander 1968; Hildebrand 1988; Wainwright et al. 1976). Alternatively, the skeletal support system may be a container reinforced with connective tissue surrounding a cavity filled with liquid. Such hydrostatic skeletons are observed in soft-bodied organisms such as polyps and in the

diverse wormlike invertebrate animals (Chapman 1950, 1958, 1975; Clark 1964, 1981; Wainwright 1970, 1988).

One of the primary roles of a skeletal support system is the transmission of the force produced by muscle contraction. This is important for a number of reasons. Since muscles do not possess an intrinsic capacity for forceful elongation once shortened, they must be elongated by the contraction of opposing muscles called antagonistic muscles. The skeletal support system provides the means by which the antagonistic muscle re-extends a shortened muscle to its resting length. Skeletal support systems are also crucial in resisting the compressive forces produced by muscle contraction. Without a system to resist compression, the contraction of a muscle on one side of an organ would merely cause the organ to shorten without bending around any specific axis. Furthermore, without a skeletal support system a bent structure cannot be straightened. In addition, hardened skeletal support systems channel muscle forces to specific bending points, or joints. Joints may also be modified so that leverage—the amplification of force, speed, or displacement—is possible.

These functions are exemplified in the movements of the human arm. Two groups of muscles—the biceps and the triceps—respectively flex and extend the forearm. The humerus, or long bone of the arm, resists the longitudinal compression that occurs when one of these muscle groups contracts. Without such resistance the arm would merely shorten when either the biceps or the triceps contracted. The arrangement of the surfaces of the joint between the humerus and the smaller bones of the forearm channels movements into

Figure 1. The elephant's trunk is only one of a number of organs capable of remarkably diverse and complex movements in the absence of conventional skeletal support. Made up almost entirely of muscle, such organs are able to support the varied movements they produce because they are structures of constant volume composed of incompressible liquid. This mechanism offers advantages over both hardened skeletons, which restrict movement to joints, and hydrostatic skeletons, which provide support through large, liquid-filled cavities and thus allow only unlocalized movements. The tongues shown at the top belong to a nectar-feeding bat and a Tokay gecko; the squid at the right has rapidly extended its tentacles to catch a small fish, while the octopus below explores its surroundings.

the bending of the elbow joint and the rotation of the forearm. The difference in the forearms of various mammals is related to differences in the proximity of the muscle insertion to the joint. The farther the muscle insertion from the fulcrum, the greater the leverage of the forearm. A larger ratio between distance from fulcrum and forearm length is generally seen in animals that require particularly forceful movements of the forearms, such as burrowers. A smaller ratio provides for greater speed and displacement and is generally seen in running animals such as the horse (Hildebrand 1987, 1988).

Structure of muscular hydrostats

Trunks, tongues, and tentacles have many characteristics in common, the most important being the fact that they are composed almost entirely of muscle. They have no hardened internal or external skeletal elements, nor is there evidence of the distinct liquid-filled cavities characteristic of hydrostatic skeletons. In muscular hydrostats the individual muscle fibers are generally arranged in bundles that form a complex pattern. This apparent complexity, however, can be reduced to a few simple categories of muscle arrangement. In most cases the muscle fibers are arranged in one of three general patterns: perpendicular to the long axis of the organ, parallel to the long axis, or wrapped helically, or obliquely, around the long axis (Fig. 2).

Muscle fibers perpendicular to the long axis are often arranged in a transverse pattern made up of alternating layers of horizontal and vertical fibers in the core of the organ (Fig. 3). This pattern is particularly characteristic of the mammalian tongue but a similar arrangement is also found in squid arms and tentacles and in octopus arms. Other perpendicular muscles originate in connective tissues in the center of the organ and radiate out to the periphery. Examples of this radial arrangement are found in the tentacles of the chambered nautilus (Kier 1987) and in the elephant's trunk. A third type of perpendicular muscle, in which the fibers have a circular configuration, is found in most lizard tongues, some mammalian tongues, and the tentacles of the squid.

Muscle fibers parallel to the long axis form what are called the longitudinal muscles. In structures capable of complex bending, such as mammalian tongues, elephant trunks, and octopus arms, these bundles are arranged in the periphery of the structure. In tongues particularly adapted for protrusion—those of snakes, many lizards, and mammalian anteaters—the major longitudinal bundles are located in the center of the organ (Doran and Allbrook 1973; Griffiths 1968).

Muscle fibers wrapped helically around the long axis are typically arranged in two peripheral layers wound around the central core of the organ in opposite directions. Such an arrangement is found, for example, in squid tentacles (Kier 1982). In some cases, such as octopus arms or the tongues of monitor lizards, the helical layers consist of a composite of muscle and connective tissue fibers (Kier 1988; Smith 1986). Sheets of oblique muscle fibers arranged along one or two sides of the structure form a portion of the helix; connective tissue fibers join the ends of the muscle fibers to complete the helix.

The mechanics of movement

The most important biomechanical feature of a muscular hydrostat is its constant volume. Muscle is composed primarily of an aqueous liquid that is essentially incompressible at physiological pressures. In a muscular hydrostat or any other structure of constant volume, a decrease in one dimension will cause a compensatory increase in at least one other dimension. This principle serves as the basis for the following analysis of movement in muscular hydrostats.

Several of the organs described above work by elongating and shortening. Because these structures are constant in volume, elongation can be produced simply by a reduction in the diameter or cross-sectional area of the organ. Since muscle fibers arranged perpendicular to the long axis reduce the diameter of the organ when contracted, they produce elongation. By contrast, the contraction of muscle fibers arranged parallel to the
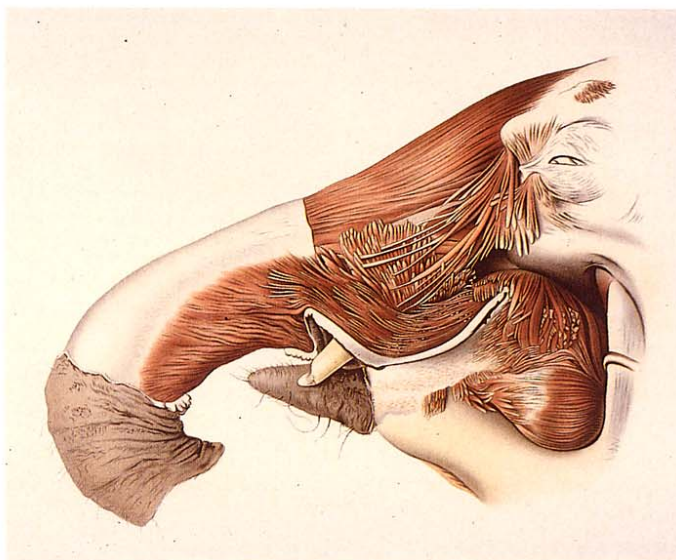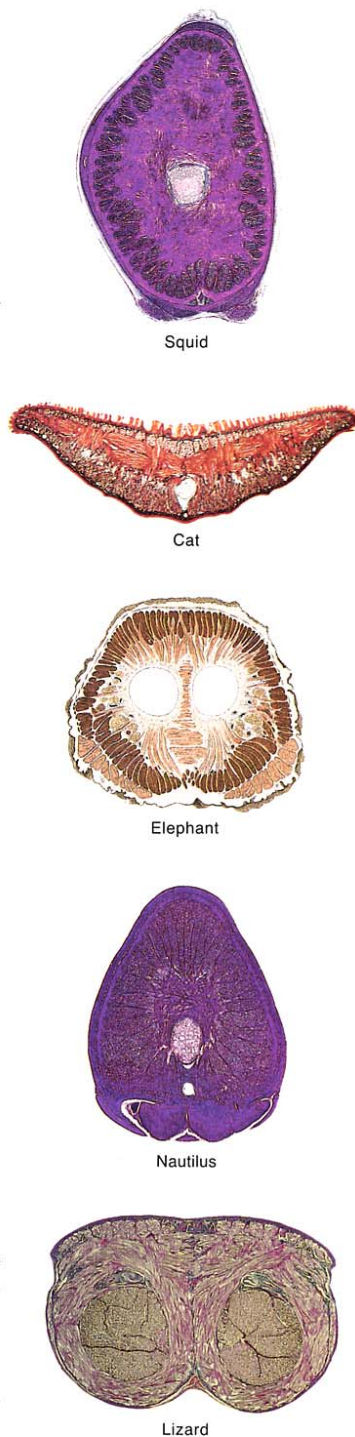

Figure 2. An anatomical drawing of an elephant's trunk indicates the three major types of muscles that work together to produce the wide range of movements typical of muscular hydrostats. Visible along the top of the trunk is a portion of the longitudinal muscles, which parallel the long axis of the organ. The core of the trunk is occupied by the perpendicular muscles, not shown in this drawing. The slanting fibers on the underside of the trunk are part of the helical muscles, which produce twisting. (From Boas and Paulli 1908, by permission of the Library of the Museum of Comparative Zoology, Harvard University.)

Figure 3. Three different arrangements of perpendicular muscles are found among muscular hydrostats. In the squid tentacle and the cat tongue the muscle fibers are arranged in a transverse pattern, with alternating sheets of vertical and horizontal fibers; bundles of longitudinal muscles are visible around the periphery of each organ. By contrast, in the elephant's trunk and the tentacle of the nautilus the perpendicular muscles are arranged radially, extending from the center to interweave with bundles of longitudinal muscles around the periphery. A third pattern is found in the lizard tongue, where perpendicular fibers arranged in a circular fashion surround two central bundles of longitudinal muscles. (Cross section of the elephant's trunk from Boas and Paulli 1908, by permission of the Library of the Museum of Comparative Zoology, Harvard University; all other photos by the authors.)

Squid

Cat

Elephant

Nautilus

Lizard

long axis—the longitudinal muscles—produces shortening of the structure and re-extension of the muscles responsible for elongation. This basic mechanism of protrusion and retraction has been confirmed by x-ray movies in which the tongue movements of a variety of mammals and reptiles were measured directly through small metal markers implanted in the tongues. The movies show that the tongue extends lengthwise during protrusion and shortens during retraction (Hiiemae and Crompton 1985; Kier and Smith 1985; Smith 1984, 1986).

The tentacles of squid are marvelous examples of muscular hydrostats specialized for rapid elongation. As mentioned above, the elongation of the squid tentacle by 70% or more in catching prey occurs in less than three hundredths of a second. Two factors appear to be important in producing such a remarkably rapid extension. The first is the specialization of the cells of the perpendicular muscles that occupy more than 80% of the cross-sectional area of the tentacle. These transverse and circular muscle fibers exhibit a cross-striated pattern typical of fast-contracting muscle cells. Cross-striated muscles are rare in cephalopods, and the transverse and circular muscles of the squid tentacle differ from other muscles of both squid and cephalopods in general (Kier 1985).

The second factor is a mechanism, first pointed out by Chapman (1950), by which the perpendicular muscles amplify speed and displace-

ment. In most systems of leverage—for example, that of vertebrate skeletons—the amplification of speed and displacement is produced by means of a rigid lever and fulcrum. In the squid and other muscular hydrostats, however, it is achieved through the relation between the length and diameter of an elongate cylinder of constant volume. This relation is plotted in Figure 4 for four cylinders of equal volume but varying dimensions. Note that for an initially elongate cylinder, a relatively small decrease in diameter creates a very large increase in length. Since the ratio of length to width in a resting squid tentacle is approximately 20:1, we can calculate that for an extension of 70% the perpendicular muscles will need to shorten by only 20%. Thus the speed and displacement produced by the contraction of these muscles are greatly amplified.

The amplification of displacement produced by the perpendicular muscles requires that the longitudinal muscles that retract these organs be capable of a much greater range of lengthening and shortening than the perpendicular muscles. In squid tentacles, the longitudinal muscles are composed of typical cephalopod muscle cells, obliquely striated and capable of producing force over a wide range of lengths. In at least two lizard genera, *Varanus* and *Tupinambis*, the tongue is expanded by more than 100% in length when it is protruded. This means that the longitudinal muscles that retract the tongue would also be extended by 100%. The longitudinal muscles in these animals appear to be composed of typical vertebrate cross-striated cells, which would be severely damaged if extended to such a degree. However, in these lizards the longitudinal muscle bundles are almost twice as long as the tongue itself; thus if the tongue extends by 100%, the muscle will be stretched by only 50% of its resting length.

This model of leverage in muscular hydrostats allows us to understand, for example, the diversity of form found in snake and lizard tongues. Snakes use their tongues entirely for sensory behaviors, whereas lizards may also use their tongues to capture food and transport it through the mouth (Smith 1984, 1986). In sensory behaviors, snakes and lizards extend their
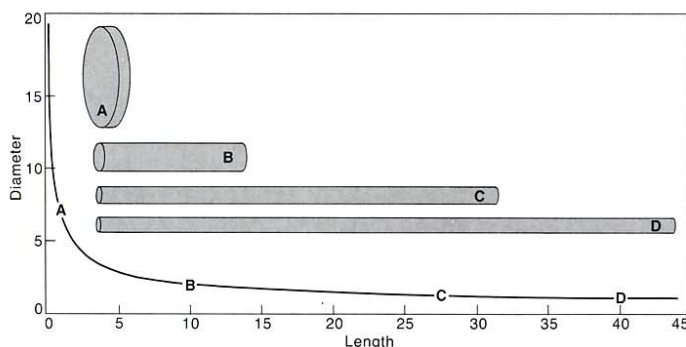
Figure 4. The dramatic ability of the perpendicular muscles to amplify speed and displacement by contraction is illustrated in a graph plotting the relation between length and diameter in cylinders of varying dimensions but constant volume. For a cylinder in which the ratio of length to diameter is high, a relatively small decrease in diameter creates a very large increase in length.

tongues, sweep them up and down through the air or on the ground, and retract them into their mouths (Figs. 5 and 6). It is thought that through this process the tongue picks up chemical particles that are then deposited near the entrance of a special sense organ in the roof of the mouth. The ability to respond to such chemosensory cues varies among these reptiles, as does their ability to protrude their tongues. Our model predicts that those reptiles that rely the most on chemosensory cues and are capable of the greatest degree of tongue protrusion will possess tongues with the largest ratio of length to width. This prediction has been confirmed by measurements of such ratios in a variety of lizards (Smith 1986).

It should be noted that not all animals use the mechanics of tongue movement discussed here. In lizards of the iguanid and agamid families there is little evidence that muscular-hydrostatic lengthening contributes to tongue protrusion (Smith 1984, 1988). These lizards do not use their tongues for sensory behaviors and do not extend them over long distances. The most spectacular tongue extenders among reptiles are chameleons, which project their tongues with great force over long distances to catch prey (Gans 1967). Chameleons project their tongues ballistically by generating force on a stable bony structure. Plethodontid salamanders, which also use their tongues to catch prey, also use ballistic projection, although the specifics of the mechanism are quite different (Lombard

and Wake 1977). In our model of leverage in elongate muscular hydrostats the advantage is associated with displacement rather than force. Thus animals that primarily require forceful projection might be expected to use other mechanisms.

More complex movements

Elongation is a fairly simple movement with relatively straightforward requirements. The action of muscles in bending is more complex: muscular activity must both shorten the organ unilaterally and provide skeletal support. Some of the requirements of the motion of bending were briefly sketched above. Without some means of resisting longitudinal compression, unilateral shortening will not produce bending. Moreover, contraction of antagonistic muscles will not straighten an organ but only shorten it further.

In muscular hydrostats the resistance to longitudinal compression is produced by the same mechanism that produces elongation: the activity of muscles perpendicular to the long axis. In the motion of bending, however, the muscles do not necessarily elongate the structure but rather act to prevent shortening by maintaining a constant diameter (Fig. 8). If a constant diameter is not maintained the structure will be shortened but not bent.

A fairly simple example will help explain how the longitudinal muscles on one side of the organ work with

the perpendicular muscles—in this case the transverse muscle fibers that form the core of the tongue—to create bending. When a cat licks its lips, it first extends its tongue. The tongue is bent upward and then curled laterally to sweep one side or the other of the upper jaw as it is withdrawn (see cover and Fig. 1). In muscular hydrostats the following sequence of muscular events can be hypothesized. The contraction of the central core of transverse muscles causes the tongue to protrude. The activity of the dorsal longitudinal muscles produces bending with continuing activity of the transverse muscles. If there were not simultaneous activity, the tongue would be retracted when the dorsal longitudinal muscles contracted. The tongue is twisted sideways by the activity of the transverse muscles acting together with the longitudinal muscles on the side of the tongue toward which the bending occurs. Finally the tongue is swept backward and retracted by the continued activity of the longitudinal muscles and the cessation of activity in the transverse muscles.
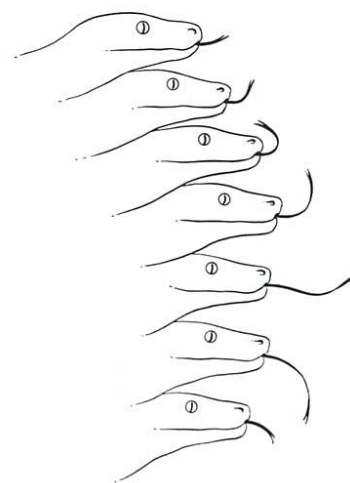

Figure 5. The components of tongue flicking, an important sensory behavior in snakes, are shown in this diagram of a characteristic sequence in which the snake protrudes its tongue, sweeps it up and down, and retracts it. The differing arrangement of muscles in the back and front of the tongue, seen in cross section in Figure 7, suggests that the back is specialized for protruding, the front for bending. (Drawing by B. Smith, after Gove 1979.)

This model of tongue movement differs from others in hypothesizing a constant interaction of all tongue muscles in all movements. It has usually been assumed that the tongue as a whole is moved by the activity of the extrinsic muscles that suspend it from the jaw and hyoid bone, and that the intrinsic muscles merely change the shape of the tongue. In our account, however, protrusion occurs both by movement in space and by expansion of the tongue in the long axis. Thus tongue movements involve extensive interaction between the intrinsic and extrinsic muscles, and the musculature of the tongue is seen as a whole: all muscle groups are important in all types of movements.

This general account of muscle interaction allows us to predict specific arrangements of muscle bundles in muscular hydrostats adapted for specific kinds of bending. The maximum versatility of movement will be produced by a system in which the central core consists of transverse muscle fibers—vertical and horizontal fibers arranged in alternating sheets, as described above—rather than radial or circular ones. This arrangement, with proper neural control, allows the vertical and horizontal fibers to function independently, making possible a wide range of movements and changes in shape. For example, flattening of the tongue will be produced by the vertical fibers of the transverse muscles acting together with the longitudinal muscles, rolling of the tongue by the activity of the dorsal horizontal fibers and the longitudinal muscles. Such a subdivision of function would not be possible with radial or circular fibers. This potential versatility may explain why a core of transverse perpendicular muscle is the predominant pattern in muscular hydrostats and characterizes the tongues of virtually all mammals.

In muscular hydrostats such as mammalian tongues, elephant trunks, and octopus arms, bundles of longitudinal muscle are located around the periphery of the structure. This location provides greater leverage for bending than a more central location near the axis of the organ. With a whole array of bundles around the periphery, movement in virtually any direction is possible. It is easy to see how such an arrangement

Figure 6. The tongue of a northern copperhead bends upward in the complex flicking motion by which compounds containing sensory cues are gathered and transported to a sense organ in the roof of the mouth. The extreme flexibility of the snake tongue is the result of complicated interaction between muscles in the back and front of the tongue. Recent work has shown that the tips of the tongue are not inserted into the sense organ, as once thought, but merely brushed across the floor of the mouth (Burghardt 1980). The function of the forked tips is not known. (Animals Animals/Joe McDonald.)

allows muscular hydrostats an extraordinary diversity of movement. Given sufficient subdivision of musculature and neural control, a virtually limitless system of points, directions, and degrees of movement is possible.

The tongues of advanced snakes provide an interesting example of subdivision for specific functions within a muscular hydrostat. One of the most characteristic behaviors of snakes is the rapid flicking of the tongue discussed above, which involves protrusion followed by repeated up and down movements of the tip. An examination of the anatomy of the tongue in advanced snakes suggests that the front and back of the tongue are specialized for bending and protrusion respectively (Fig. 7). In the posterior region of the tongue four simple sheets of muscle surround a pair of longitudinal muscles located in the center. One sheet is positioned between the paired muscles, two are placed on either side of the pair, and one is located above. Thus each longitudinal bundle is surrounded by a triangle of muscle fibers. The combined activity of these sheets will decrease the diameter of the tongue, which will cause it to protrude; activity of the
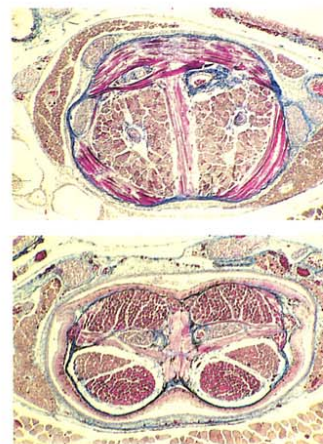

Figure 7. Cross sections of the tongue of the garter snake, *Thamnophis*, show differences in muscle structure that are related to function. In the back of the tongue (top), two large bundles of longitudinal muscles are surrounded by four sheets of transverse muscle. The contraction of the transverse muscles will reduce the diameter of the tongue, causing it to protrude. In the front of the tongue (bottom), however, the bundles of longitudinal muscles are located around the periphery and the transverse muscles are central, an arrangement that provides for bending. (Photos by the authors.)
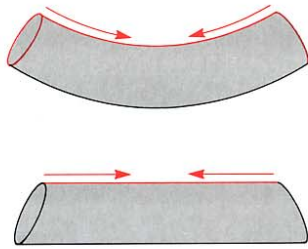
Figure 8. In order to bend, a muscular hydrostat must simultaneously decrease its length on one side and maintain a constant diameter, as shown in the upper cylinder, where color indicates axes of muscular contraction. A constant diameter is maintained by the perpendicular muscles, which provide resistance to longitudinal compression. Without such resistance to a change in diameter the organ will be shortened but not bent, as illustrated in the lower cylinder. (After Kier and Smith 1985.)

longitudinal bundles will retract the tongue.

The tip of the colubrid tongue displays a notably different arrangement of muscles and appears to be specialized for bending. Here the longitudinal muscles are peripheral; the perpendicular muscles are arranged in the form of a cross that occupies the center of the tongue. These muscles will resist longitudinal compression by resisting increases in diameter and may also contribute to protrusion. The longitudinal muscles are split into two approximately equal-sized groups, one at the top and one at the bottom, which can produce the observed up and down flicking movement. Note that in the front of the tongue the longitudinal muscles are located peripherally and will thus produce bending, whereas

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in the back they are central and thus close to the axis of bending. Unless small portions of the longitudinal bundles located away from the axis are active, contraction of the longitudinal muscles in the back of the tongue will produce little bending.

Much of the complexity of movement seen, for example, in the elephant's trunk arises from the addition of twisting around the long axis to the motions just discussed. This twisting, or torsion, involves the selective contraction of muscle layers arranged in a helical pattern. The contraction of helical fibers causes the free end of the organ to twist relative to its base. The direction of the torsion depends on the direction in which the helical fiber is wound (Fig. 9). In order to produce twisting in both directions, two helical muscle layers must be present, one winding to the right and one to the left. This is exactly what we find in muscular hydrostats capable of twisting in either direction: elephant trunks, octopus arms, the arms and tentacles of squid, the tentacles of the chambered nautilus, and some lizard tongues.

In addition to creating torsion in either direction, the helical muscle layers are also capable of resisting torsional forces. Furthermore, depending on the angle between the helical fiber and the longitudinal axis, helical fibers will either shorten or elongate the structure. Fibers with an angle of less than about 55° to the long axis will both shorten the structure and produce torsion, whereas those with an angle greater than this will contribute to elongation (Kier and Smith 1985). In the elephant's trunk the "longitudinal" fibers on the bottom and sides are actually low-angle helical fibers (Boas and Paulli 1908, 1925). Observations suggest that most sideways bending of an elephant's trunk actually involves a combination of ventral bending and lateral twisting, as would be expected from the arrangement of the muscle bundles.

Mechanical considerations dictate that the helical muscle layers should also be located peripherally, away from the central axis of the organ. Such an arrangement maximizes the torsional force exerted by the structure during twisting. Examination of the structure of various muscular hydrostats capable of twisting shows that the two helical muscle
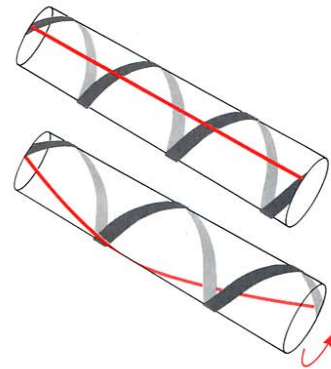

Figure 9. The mechanics of torsion are demonstrated in a diagram of the twisting of an elongated cylinder around its axis. Here the contraction of a single strand of helical muscle winding to the left results in a twisting of the structure, visible in the distortion of the colored line. Most muscular hydrostats have both right-handed and left-handed helical muscles, allowing them to twist in either direction. (After Kier 1982.)

layers almost invariably occupy a peripheral location, wrapping an inner core of perpendicular and longitudinal muscle.

Unique capabilities

Although Cuvier compared the arms of the octopus to the mammalian tongue as early as 1817 and Owen noted mechanical similarities between the tentacles of the chambered nautilus and the elephant's trunk in 1843, a coherent view of the biomechanics of organs composed entirely of muscle has been slow to emerge. Aspects of the mechanical features of hydrostatic and muscular-hydrostatic organs have been treated over the years. The functional morphology and phylogeny of many hydrostatic skeletons have been discussed previously (Chapman 1950, 1958, 1975; Clark 1964, 1981; Wainwright 1970, 1988). Tittel has analyzed the structure of octopus arms (1964), and the interaction of muscle groups in the tongue has been explored (Abd-El-Malek 1938; Bennett and Hutchinson 1946; Doran 1975).

The model we have described, however, represents the first attempt to arrive at an integrated account of how these muscular structures work. As such it provides a general framework within which to evaluate the

mechanical significance not only of muscular hydrostats but of all soft-bodied organisms and organs with hydrostatic skeletons. It has already proved useful in the comparative analysis of elongate structures such as lizard tongues (Smith 1984, 1986). It should also provide insight into the mechanisms of less elongate hydrostatic skeletons, such as the individual segments of burrowing worms, that may amplify force rather than displacement and speed.

Although we initially studied muscular hydrostats to discover how they function without an obvious system of skeletal support, we have found that they have unique capabilities. Hardened skeletal systems restrict movement to joints. The movements of hydrostatic skeletons with large liquid-filled cavities are not localized because the tension produced by a muscle is transmitted as an increase in pressure throughout the skeleton. A muscular hydrostat, however, is not restricted to movements at joints, and the highly subdivided muscular and neural systems produce movements that are both localized and remarkably complex and diverse.

Structures with muscular-hydrostatic properties are probably widespread, at least within the invertebrates. Much of the muscular system of the cephalopods is characterized by these properties. For example, the fins of the cuttlefish, *Sepia officinalis*, are composed entirely of muscle fibers arranged in three planes perpendicular to each other. There are no hardened skeletal elements like those seen in the fins of bony fishes. The fins, which are used in swimming, are bent up and down in undulating waves that travel forward and backward along the length of the fin. Although the fins are flattened plates, the support for bending is provided by the interaction of muscle contractions in a manner similar to that outlined above (Kier, in press). Muscular hydrostats are far more common in molluscs than is generally realized (Kier 1988), and many of the bodies and organs of wormlike invertebrates may also use muscular-hydrostatic principles. The recognition and study of additional muscular hydrostats promise to extend even farther our growing sense of the versatility and resourcefulness of animal form.

References

Abd-El-Malek, S. 1938. A contribution to the study of the movements of the tongue in animals, with special reference to the cat. *J. Anat.* 73:15–30.

Alexander, R. M. 1968. *Animal Mechanics.* Univ. of Washington Press.

Bennett, G. A., and R. C. Hutchison. 1946. Experimental studies on the movements of the mammalian tongue. II. The protrusive mechanism of the tongue (dog). *Anat. Rec.* 94:59–72.

Boas, J. E. V., and S. Paulli. 1908. *The Elephant's Head: Studies in the Comparative Anatomy of the Head of the Indian Elephant and Other Mammals.* Part I:1–79. Gustav Fisher.

———. 1925. *The Elephant's Head: Studies in the Comparative Anatomy of the Head of the Indian Elephant and Other Mammals.* Part II:80–129. Gustav Fisher.

Burghardt, G. M. 1980. Behaviorial and stimulus correlates of vomeronasal functioning in reptiles: Feeding, grouping, sex and tongue use. In *Chemical Signals: Vertebrates and Aquatic Invertebrates,* ed. D. Müller-Schwarze and R. M. Silverstein. Plenum.

Chapman, G. 1950. Of the movement of worms. *J. Exp. Biol.* 27:29–39.

———. 1958. The hydrostatic skeleton in the invertebrates. *Biol. Rev.* 33:338–71.

———. 1975. Versatility of hydraulic systems. *J. Exp. Zool.* 194:249–70.

Clark, R. B. 1964. *Dynamics in Metazoan Evolution: The Origin of the Coelom and Segments.* Oxford Univ. Press.

———. 1981. Locomotion and the phylogeny of the Metazoa. *Bolletino di Zoologia* 48:11–28.

Cuvier, G. 1817. Mémoires pour servir à l'histoire et à l'anatomie des mollusques. *Memoire sur les cephalopodes et sur leur anatomie.* Paris: Deterville.

Doran, G. A. 1975. Review of the evolution and phylogeny of mammalian tongues. *Acta Anatomica.* 91:118–29.

Doran, G. A., and D. B. Allbrook. 1973. The tongue and associated structures in two species of African pangolins, *Manis gigantia* and *Manis tricupis. J. Mammal.* 54:887–99.

Gans, C. 1967. The chameleon. *Nat. Hist.* 76:52–59.

Gove, D. 1979. A comparative study of snake and lizard tongue-flicking, with an evolutionary hypothesis. *Z. Tierpsychol.* 51:58–76.

Griffiths, M. 1968. *Echidnas.* Pergamon.

Hiiemae, K. M., and A. W. Crompton. 1985. Mastication, food transport and swallowing. In *Functional Vertebrate Morphology,* ed. M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake, pp. 262–90. Belknap Press.

Hildebrand, M. 1987. The mechanics of the horse leg. *Am. Sci.* 75:594–601.

———. 1988. *Analysis of Vertebrate Structure.* 3rd ed. Wiley.

Kier, W. M. 1982. The functional morphology of the musculature of squid (Loliginidae) arms and tentacles. *J. Morph.* 172:179–92.

———. 1985. The musculature of squid arms and tentacles: Ultrastructural evidence for functional differences. *J. Morph.* 185:223–39.

———. 1987. The functional morphology of the tentacle musculature of *Nautilus pompilius.* In *Nautilus: The Biology and Paleobiology of a Living Fossil,* ed. W. B. Saunders and N. H. Landman, pp. 257–69. Plenum.

———. 1988. The arrangement and function of molluscan muscle. In *The Mollusca, Molluscan Form and Function,* ed. E. R. Trueman and M. R. Clarke, pp. 211–52. Academic Press.

———. In press. The fin musculature of cuttlefish and squid (Mollusca, Cephalopoda): Morphology and mechanics. *J. Zool. Lond.*

Kier, W. M., and K. K. Smith. 1985. Tongues, tentacles, and trunks: The biomechanics of movement in muscular-hydrostats. *Zool. J. Linn. Soc.* 83:307–24.

Lombard, R. E., and D. B. Wake. 1977. Tongue evolution in the lungless salamanders, Family Plethodontidae. II. Function and evolutionary diversity. *J. Morph.* 153:39–80.

Owen, R. 1843. On the structure and homologies of the cephalic tentacles in the pearly nautilus. *Annals and Mag. of Nat. Hist.* 12:305–11.

Smith, K. K. 1984. The use of the tongue and hyoid apparatus during feeding in lizards. *Ctenosaura similis* and *Tupinambis nigropunctatus. J. Zool. London* 202:115–42.

———. 1986. Morphology and function of the tongue and hyoid apparatus in *Varanus* (Varanidae, Lacertilia). *J. Morph.* 187:261–87.

———. 1988. Form and function of the tongue in agamid lizards with comments on its phylogenetic significance. *J. Morph.* 196:157–71.

Tittel, K. 1964. Saugnapf-, epi- und hypofasciale Armmuskulatur der Kephalopoden-ein Beitrag zur funktionellen Anatomie freibeweglicher Skelettmuskelkörper. *Gegen. morph. Jahrb.* 106:90–115.

Wainwright, S. A. 1970. Design in hydraulic organisms. *Naturwiss.* 57:321–26.

———. 1988. *Axis and Circumference: The Cylindrical Shape of Plants and Animals.* Harvard Univ. Press.

Wainwright, S. A., W. D. Biggs, J. D. Curry, and J. M. Gosline. 1976. *Mechanical Design in Organisms.* Wiley.