COMMENTARY

The diversity of hydrostatic skeletons

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Summary

A remarkably diverse group of organisms rely on a hydrostatic skeleton for support, movement, muscular antagonism and the amplification of the force and displacement of muscle contraction. In hydrostatic skeletons, force is transmitted not through rigid skeletal elements but instead by internal pressure. Functioning of these systems depends on the fact that they are essentially constant in volume as they consist of relatively incompressible fluids and tissue. Contraction of muscle and the resulting decrease in one of the dimensions thus results in an increase in another dimension. By actively (with muscle) or passively (with connective tissue) controlling the various dimensions, a wide array of deformations, movements and changes in stiffness can be created. An amazing range of animals and animal structures rely on this form of skeletal support, including anemones and other polyps, the extremely diverse wormlike invertebrates, the tube feet of echinoderms, mammalian and turtle penises, the feet of burrowing bivalves and snails, and the legs of spiders. In addition, there are structures such as the arms and tentacles of cephalopods, the tongue of mammals and the trunk of the elephant that also rely on hydrostatic skeletal support but lack the fluid-filled cavities that characterize this skeletal type. Although we normally consider arthropods to rely on a rigid exoskeleton, a hydrostatic skeleton provides skeletal support immediately following molting and also during the larval stage for many insects. Thus, the majority of animals on earth rely on hydrostatic skeletons.

Key words: hydrostatic skeleton, muscle, connective tissue, support, antagonism.

Introduction

Animal skeletons serve a variety of functions in support and movement. For example, the skeleton transmits the force generated by muscle contraction, providing support for maintenance of posture and for movement and locomotion. Also, because muscle as a tissue cannot actively elongate, skeletons provide for muscular antagonism, transmitting the force of contraction of a muscle or group of muscles to re-elongate their antagonists. In addition, the skeleton often serves to amplify the displacement, the velocity or the force of muscle contraction. A wide range of animals and animal structures lack the rigid skeletal elements that characterize the skeletons of familiar animals such as the vertebrates and the arthropods. Instead, these animals rely on a 'hydrostatic skeleton' (Chapman, 1958; Clark, 1964) in which the force of muscle contraction is transmitted by internal pressure. In this Commentary, I will summarize the arrangement of the muscle fibers and their role in support and movement in hydrostatic skeletons. I will also describe the connective tissue fibers of hydrostatic skeletons that play a crucial role in controlling and limiting shape change. I will then describe the principles of support and movement and will illustrate these principles with an overview of the remarkable diversity of animals and animal structures that rely on hydrostatic skeletal support.

Structure and function of hydrostatic skeletons
Arrangement of musculature

Many of the animals and animal structures that rely on hydrostatic skeletons are approximately cylindrical in shape (Wainwright, 1988). The musculature is typically arranged so that both the diameter and the length of the cylinder can be actively controlled (Fig. 1). Three different muscle arrangements are observed that can control the diameter. All are arranged perpendicular to the longitudinal axis: (1) circular musculature, with a layer of fibers wrapping the cylinder circumferentially; (2) radial musculature, with fibers or fiber bundles originating near the central axis of the cylinder and extending towards the surface; and (3) transverse musculature, with fibers extending across the diameter of the cylinder as parallel sheets, typically in two orientations that are perpendicular to each other. Control of the length is achieved by longitudinal muscle fibers, which are oriented parallel to the longitudinal axis and can be arranged as a continuous sheet or as isolated bundles. Helical muscle fibers are sometimes also present; their function is discussed below in the section on muscular hydrostats.

Principles of support and movement

The fundamental principles of support and movement in hydrostatic skeletons are straightforward. In addition to the musculature described above, conventional hydrostatic skeletons typically include a volume of enclosed fluid. The fluid is usually a liquid (essentially water) and thus has a high bulk modulus, which simply means that it resists significant volume change. Contraction of circular, radial or transverse muscle fibers will decrease the diameter, thereby increasing the pressure, and because no significant change in volume can occur, this decrease in diameter must result in an increase in length. Following elongation, shortening can be caused by contraction of the longitudinal muscle fibers, re-expanding the diameter and thus re-elongating the circular, radial or transverse muscle fibers. The longitudinal muscle fibers and the circular, radial or transverse muscle fibers thus
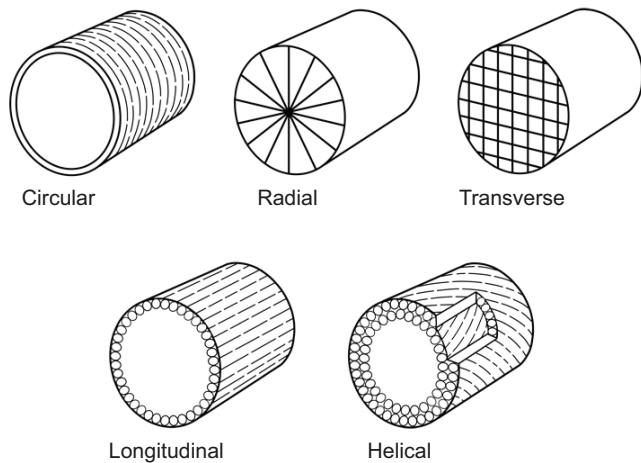
Fig. 1. Schematic diagram illustrating common muscle fiber orientations in hydrostatic skeletons. The cross-sectional area can be controlled by fibers oriented circumferentially, radially and transversely; fibers in these orientations are important for elongation and also support of bending movements. The length is controlled by longitudinal fibers, which shorten the organ or body and, through selective contraction, also create bending. Helically arranged muscle fibers are found in muscular hydrostats and create torsion or twisting around the long axis. Both right- and left-handed helical muscle fiber layers are typically present and create torsion in either direction.
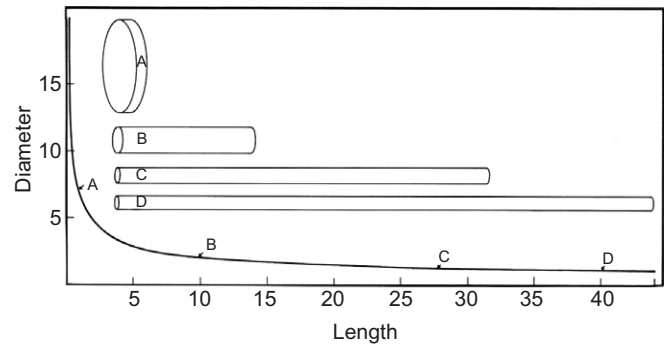

Fig. 2. Relationship between diameter and length of a constant volume cylinder. The positions on the graph of shapes A through D (drawn to scale) are indicated. A small decrease in diameter from shape B to D causes a large increase in length. From Kier and Smith (Kier and Smith, 1985).

function as antagonists, in a manner that is analogous to muscles on either side of a joint in an arthropod or vertebrate. The function of the system thus depends on the pressurized internal fluid.

Although hydrostatic skeletons lack the fulcrums and lever arms present in rigid skeletons that allow amplification of force, displacement and velocity, their geometry nevertheless provides a mechanism for mechanical amplification of muscle contraction. For example, consider the relationship between the diameter and length of the constant volume cylinder shown in Fig. 2. For an initially elongate cylinder, it is apparent that a given percentage decrease in diameter (caused by shortening of the circular, radial or transverse muscle fibers) will cause a larger percentage increase in length compared with a short cylinder (Chapman, 1950; Kier and Smith, 1985). More generally, the volume of a cylinder of length l and radius r is:

$$V = \pi r^2 l. \tag{1}$$

Assuming constant volume, Eqn 1 can then be rearranged and the radius differentiated with respect to the length (Alexander, 2003):

$$\frac{dr}{dl} = \frac{-r}{2l} . \tag{2}$$

As an example, the prey-capture tentacles of squid, which rely on a type of hydrostatic skeleton discussed below, require only a 25% decrease in diameter to generate nearly an 80% increase in length (Kier, 1982; Van Leeuwen and Kier, 1997). The displacement and the velocity of contraction of the radial, circular or transverse musculature can thus be amplified. Furthermore, since the strain in the longitudinal muscles is proportional to the overall longitudinal strain during elongation, length changes such as those of a squid tentacle require longitudinal muscle fibers that are capable of a greater range of shortening and elongation than is typical for most vertebrate and arthropod muscle fibers. As in the longitudinal muscles of the squid tentacle described above, the muscle fibers of many hydrostatic skeletons are obliquely striated and have the

capability of superelongation, most likely involving a mechanism of 'changing partners' as thick and thin filaments are pulled beyond overlap at extreme extensions (Lanzavecchia and Arcidiacono, 1981; Miller, 1975). Vertebrate tongues often rely on a form of hydrostatic support (see below) and in highly protrusible tongues, the longitudinal retractor muscles are either specialized for supercontraction, as is the case in the retractor muscles of the tongue of the chameleon (Herrel et al., 2001; Rice, 1973), or they have their origin outside of the tongue and are thus much longer than the tongue itself, reducing their strain as the tongue is protruded. Supercontracting muscle is also found in the some insect larvae, which rely on hydrostatic support and undergo greater deformation than the adults (Osborne, 1967; Hardie and Osborne, 1977).

Connective tissue fibre reinforcement

The walls of many hydrostatic skeletons are reinforced with layers of connective tissue fibers that control and limit shape change. The fibers are typically arranged as a 'crossed-fiber helical connective tissue array' in which sheets of connective tissue fibers (often collagenous) wrap the body or structure in right- and left-handed helices. Even though the connective tissue fibers are typically stiff in tension and are thus relatively inextensible, such an arrangement actually allows length change. Elongation and shortening is possible because the pitch of the helix changes during elongation (the fiber angle, which is the angle relative to the long axis, decreases) and shortening (the fiber angle increases) (Clark and Cowey, 1958; Shadwick, 2008). Reinforcement with this type of connective tissue fiber array limits and controls shape change, allows smooth bending to occur, and prevents torsion or twisting around the longitudinal axis (Fig. 3). As a comparison, consider the implications of wrapping the body wall with circular and longitudinal connective tissue fibers. Such an arrangement, termed an 'orthogonal' array, resists elongation because of the presence of inextensible longitudinal fibers and also resists shortening, as shortening requires an increase in diameter, which is resisted by the circular fibers. Orthogonal arrays also resist bending forces and will fail in bending by kinking. They also offer little resistance to twisting (Alexander, 1987; Alexander, 1995; Koehl et al., 2000; Wainwright, 1982).

The role that the crossed-fiber helical connective tissue array plays in controlling shape change in wormlike animals has been analyzed with a simple geometrical model (Clark and Cowey, 1958; Harris and Crofton, 1957; Seymour, 1983; Shadwick, 2008).
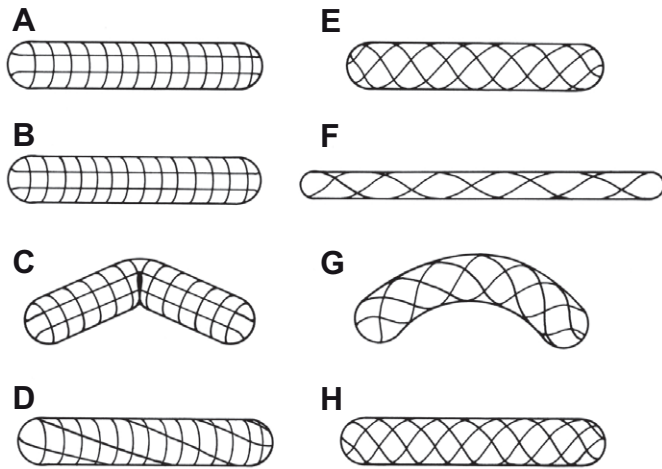
Fig. 3. Diagram illustrating the differences between a pressurized cylinder reinforced with fibers in an orthogonal array (A–D) and a cylinder reinforced with fibers in a crossed-fiber helical array (E–H). Orthogonal fiber reinforcement prevents length change (B), provides stiffness in bending until failure occurs by kinking (C), and allows torsion or twisting around the long axis (D). Cylinders reinforced with a crossed-fiber helical array can change length (F), bend in smooth curves (G) and resist torsion (H). After Wainwright (Wainwright, 1988).

The model considers a right circular cylinder wrapped with a single turn of an inextensible helical fiber and is used to solve for the enclosed volume of the cylinder as the fiber angle varies from 90 deg (an infinitely thin disk with a circumference equal to the helical fiber length) to 0 deg (an infinitely thin cylinder with a length equal to the helical fiber length). The volume approaches 0 as the fiber angle approaches 0 or 90 deg, with the maximum volume occurring at a fiber angle of 54 deg 44 min (Fig. 4). A worm with a volume equal to the maximum that could be enclosed by the fiber system at 54 deg 44 min would be unable to elongate or shorten significantly because any length change would entail a decrease in volume of an essentially incompressible fluid or strain in stiff connective tissue fibers. In reality, most worms enclose a volume of fluid and tissue that is less than the maximum, and thus at a fiber angle of 54 deg 44 min, they are flattened in cross-sectional shape and lack turgidity. Such a worm can change length, subject to the constraints of the helical fiber system. For instance, the worm can elongate, decreasing the fiber angle until it reaches the angle at which the volume contained by the helical fiber system equals the actual volume of the worm. No further elongation can occur beyond this angle because a decrease in the enclosed volume of fluid would be required. By examining Fig. 4 it should be apparent that worms that enclose a smaller relative volume (relative to the maximum that could be enclosed by the helical fiber system) should be capable of a greater range of elongation and contraction. This prediction was tested in a variety of worm species and was found to be an accurate predictor of extensibility, except in situations where the assumptions of the model were violated, for example when the worm's structure prevented the cross-section from becoming fully circular, or when other morphological components limited deformation (Clark and Cowey, 1958).

Examples of hydrostatic skeletons

A remarkable diversity of animals and animal structures rely on some form of hydrostatic skeletal support. In addition to variation in the arrangement of the musculature, considerable variation

exists in the form of the fluid-filled cavities, ranging from extensive cavities to solid musculature or tissue with minimal extracellular fluid. Below I review some examples of hydrostatic skeletons to provide an overview of their diversity of structure and function.

Polyps and vermiform animals

Polyps, such as sea anemones, are one of the classic examples of animals that rely on a hydrostatic skeleton. The body of a sea anemone is in the form of a hollow column that is closed at the base and equipped at the top with an oral disk that includes a ring of tentacles surrounding the mouth and pharynx (Fig. 5). By closing the mouth, the water in the internal cavity – the coelenteron – cannot escape and thus the internal volume remains essentially constant. The walls of an anemone include a layer of circular muscle fibers. Longitudinal muscle fibers are found on the vertical partitions called septa that project radially inward into the coelenteron, including robust longitudinal retractor muscles along with sheets of parietal longitudinal muscle fibers adjacent to the body wall. Additional radial muscle fibers occur on the septa and a large circular sphincter muscle is present surrounding the base of the tentacles of the oral disk (Batham and Pantin, 1950). With the mouth closed, contraction of the circular muscle layer decreases the diameter and thereby increases the height of the anemone. Contraction of the longitudinal muscles shortens the anemone and re-extends the circular muscle fibers. Bending of the column can be achieved by simultaneous contraction of the longitudinal bundles on one side of the anemone and contractile activity of the circular muscle fibers (to prevent shortening of the column due to compressional forces from the longitudinal musculature). Thus, with this simple muscular arrangement a diverse array of bending movements and height change can be produced. Most anemones can also expel the coelenteric fluid while retracting the tentacles, the oral disk and the column towards the base in response to disturbances such as
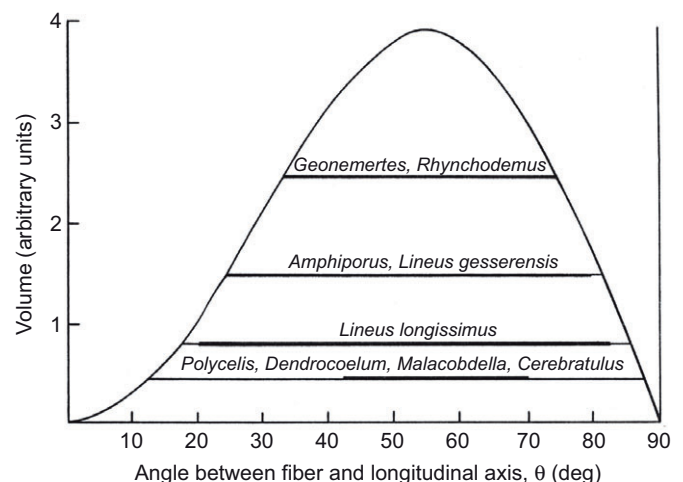

Fig. 4. Relationship between the volume contained by the crossed-fiber helical system and the fiber angle. The actual volumes of several nemertean and turbellarian worms are indicated with fine horizontal lines; the heavy lines show the measured range of elongation and contraction. Note that a worm with a smaller relative volume (e.g. *Lineus longissimus*) is typically capable of a greater range of elongation and shortening than a worm with a greater relative volume (e.g. *Geonemertes*). Some worms (e.g. *Polycelis*) do not reach the limits set by the crossed-fiber helical system because of other morphological constraints. From Clark and Cowey (Clark and Cowey, 1958).
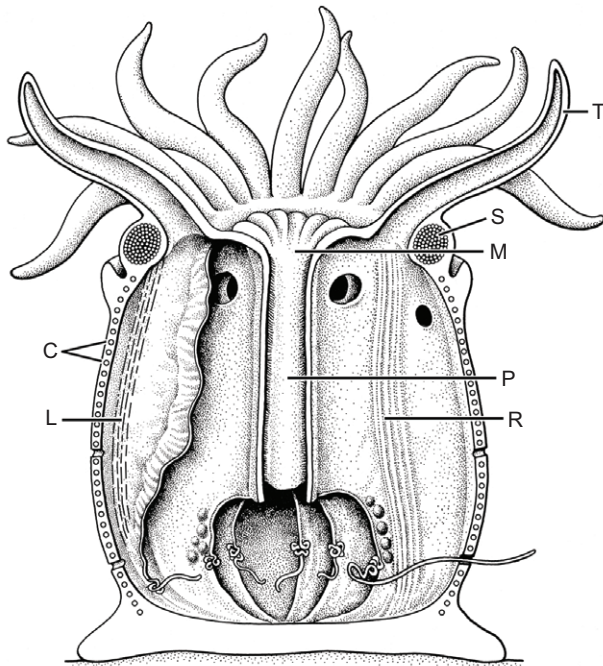
Fig. 5. Schematic cutaway view of a sea anemone showing the circular muscle fibers (C), parietal longitudinal muscle fibers (L), mouth (M), pharynx (P), retractor muscles (R), sphincter muscle (S), and tentacles (T). After Ruppert et al. (Ruppert et al., 2004).

This basic arrangement of circular and longitudinal muscle fibers characterizes the musculature of a diversity of worm-like animals including, for example, many annelids, sipunculids and holothurian echinoderms (Chapman, 1958; Chapman, 1975; Clark, 1964). The circular and longitudinal muscle fibers antagonize one another and, depending on the sequence of contraction, can be used to generate a diverse range of movements. The musculature can be used to produce alternating waves of elongation and shortening, for instance in the production of peristaltic movements used in crawling and locomotion (Fig. 6). In annelids such as the earthworm, the coelom is divided into segments by muscular septa, which prevent movement of the hydrostatic fluid from one segment to another during normal locomotion (Newell, 1950; Seymour, 1969; Seymour, 1976). Such subdivision of the coelom allows individual segments to operate independently, thereby facilitating localized action and a more complex and variable pattern of movement.

Septa are likely also crucial in allowing large lateral forces to be exerted during burrowing (Alexander, 1983; Chapman, 1950). If we consider the body of the worm to be a thin-walled pressurized cylinder of radius r and wall thickness t, we can derive expressions for the stresses in the longitudinal direction, which would tend to blow the ends off the cylinder, and stresses exerted in the circumferential direction, which would tend to split the cylinder longitudinally (Wainwright et al., 1976). The total force in the longitudinal direction is the area of the end of the cylinder with radius r times the pressure p, $F=\pi r^2 p$, and is resisted by the cross-sectional area of the cylinder wall, $A=2\pi rt$. The longitudinal stress (σ_L) in the wall is thus:

$$\sigma_L = \frac{F}{A} = \frac{\pi r^2 p}{2\pi rt} = \frac{pr}{2t} \ . \qquad (3)$$

The stress in the circumferential direction (σ_C) for an element of unit length is the force normal to the diameter, $F=2pr$, divided by the area, $A=2t$:

$$\sigma_C = \frac{2pr}{2t} = \frac{pr}{t} = 2\sigma_L \ . \qquad (4)$$

Thus, at a given pressure, the stresses in the circumferential direction are twice those in the longitudinal direction. Assuming that the circular and longitudinal muscles can exert similar peak stress, if they

predators. The process involves first opening the pharynx and mouth by contraction of the radial muscle fibers. Contraction of the longitudinal muscles then shortens the column and withdraws the oral disk and tentacles into the column. The sphincter finally contracts, reducing the diameter of the oral disk and closing off the top of the column. Reinflation occurs slowly as water is pumped into the column by a pair of ciliated grooves called siphonoglyphs that extend the length of the pharynx. Elastic energy storage in the fiber-reinforced gelatinous extracellular matrix called the mesoglea also aids restoration of shape (Alexander, 1962; Gosline, 1971).
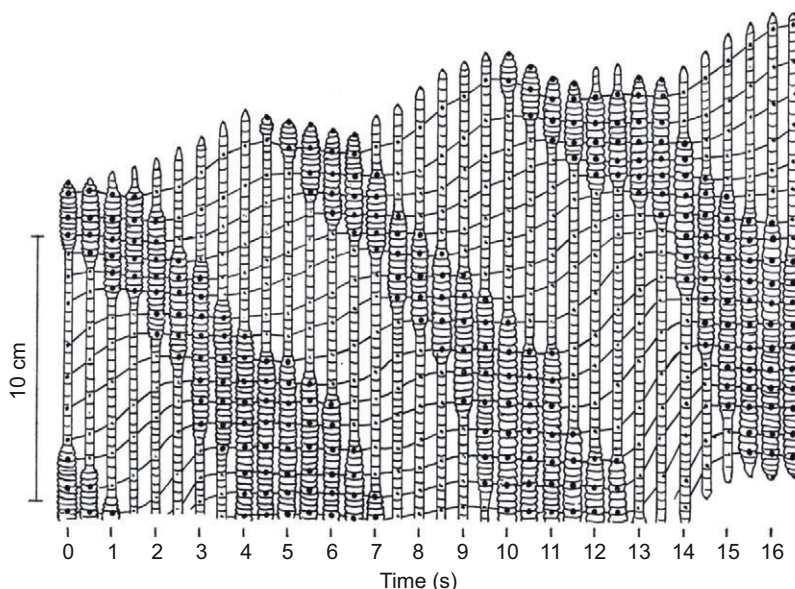

Fig. 6. Diagram showing the stages in locomotory cycle of an earthworm. Regions undergoing longitudinal muscle contraction are stationary (indicated by large dots) and are drawn twice as wide as those regions undergoing circular muscle contraction. The tracks of individual points on the body through time are indicated by the lines connecting each drawing, extending from left to right on the page. From Gray and Lissman (Gray and Lissman, 1938).

were to produce equal pressures in the body of the worm, the area of the circumferential muscles should thus be twice that of the longitudinal muscles. Measurements suggest, however, that the area of the longitudinal muscles is actually greater; therefore, the resulting pressures produced by the longitudinal muscles may be as much as five to 20 times greater than those produced by the circular muscles (Chapman, 1950; Seymour, 1969). The septa are thought to allow the pressure to be different in one location (or compartment) in the body compared with another (without septa an increase in pressure would be transmitted along the entire length of the body); thus the high pressure of a localized maximal contraction of the longitudinal muscle (perhaps required to enlarge the burrow) will not be transmitted down the length of the worm and overwhelm the circular muscle in another part of the body (Chapman, 1950). Subdivision of the coelom also provides protection from injury because rupture of the wall incapacitates an individual segment rather than the entire hydrostatic skeleton (Batham and Pantin, 1950; Chapman, 1958; Clark, 1964).

Nematode worms represent a particularly interesting example of the importance of connective tissues for the hydrostatic skeleton. Nematodes possess robust longitudinal muscle bundles, but they lack the circular muscle fibers that typically serve as antagonists in other hydrostatic animal skeletons. How, then, can the longitudinal musculature be antagonized? The answer lies in the structure of the cuticle, which includes robust fibers arranged as a crossed fiber helical connective tissue array. In *Ascaris lumbricoides*, the fibers are arranged at an angle of approximately 75 deg to the longitudinal axis (Harris and Crofton, 1957). Longitudinal muscle contraction exerts a force that tends to shorten the body and increase the fiber angle. Referring to Fig. 4, an increase in fiber angle from 75 deg would require a decrease in the enclosed volume and because the enclosed fluid is essentially incompressible and cannot escape, shortening of the body is resisted and the pressure (mean=9 kPa, range=2–30 kPa) in the worm is increased. In this way, the longitudinal muscle bundles on each side of the body can contract alternately, bending the body during undulatory locomotory movements and antagonizing the musculature on the opposite side (Harris and Crofton, 1957; Niebur and Erdös, 1991; Park et al., 2007). The fact that nematodes as a group are rather uniform in shape has been attributed to this characteristic form of support. Indeed their common name, roundworm, is a reflection of the pressurization resulting from the interaction between the longitudinal musculature and the crossed-fiber array.

Hydraulic mechanisms

In some hydrostatic skeletal support systems, movement or shape change occurs through a hydraulic mechanism, which involves displacement of fluid from one location in order to cause shape change or exert force elsewhere. An excellent example of such a mechanism is the tube-foot–ampulla complex of the water vascular system of echinoderms (McCurley and Kier, 1995; Woodley, 1967; Woodley, 1980). The tube feet of many echinoderms are used for locomotion, burrowing, and the movement of objects over the animal by elongation, shortening and bending movements. In many asteroids (starfish) the hollow, cylindrical tube feet are each connected to a muscular bulb (in some cases two) called an ampulla and are aligned in rows extending down the ambulacrum of the animal (Fig. 7). The tube-foot–ampulla complex is also connected to a radial canal, which supplies fluid to the complex through a one-way valve. The ampullae are equipped with muscle fibers oriented such that their contraction decreases the volume of the ampulla, expelling the water from the ampulla into the tube foot, and thereby
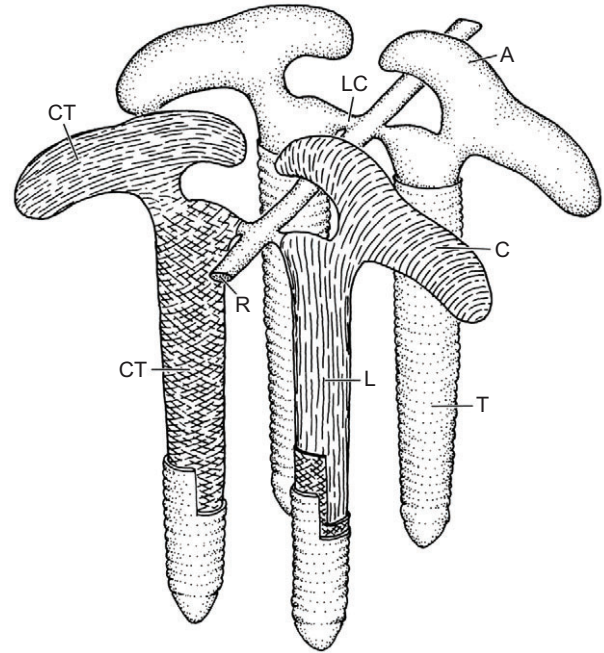

Fig. 7. Schematic cutaway diagram of the arrangement of the tube feet (T), ampullae (A), and the lateral (LC) and radial canals (R) of the starfish *Luidia clathrata*, showing the trajectories of the connective tissue fibers (CT), longitudinal muscle (L) of the tube feet, and circular muscle (C) of the ampullae. From McCurley and Kier (McCurley and Kier, 1995).

elongating it. The tube foot is equipped with longitudinal muscle fibers that can be contracted selectively on one side of the foot to create bending movements or can contract simultaneously to shorten the tube foot, forcing the water back into the ampulla. The musculature of the tube feet and ampullae thus serve as antagonists for one another.

The functioning of the tube feet as outlined above depends, however, on connective fiber reinforcement of the walls of the cylindrical tube foot. Eqn 4 shows that the circumferential stress in a pressurized cylindrical vessel is exactly twice the longitudinal stress. Without reinforcement of the tube foot wall, the pressure generated by the ampulla will cause an increase in diameter, rather than elongation of the tube foot. In fact, the tube feet of both brittlestars and starfish (and presumably other echinoderms as well) are reinforced with a crossed-fiber helical array of connective tissue (McCurley and Kier, 1995; Woodley, 1967; Woodley, 1980). By examining Fig. 4, it should be clear that an increase in volume of the tube foot will cause elongation only if the fiber angle of the connective tissue fibers is greater than 54 deg 44 min. This is indeed the case for brittlestar and starfish tube feet. The fiber angles in elongated tube feet of the brittlestar *Amphiura filiformis* and the starfish *Luidia clathrata* are 85 and 67 deg, respectively, and the must be even higher when the tube feet are retracted. Note that the deformation of the cylinder that results from inflation with fluid depends on the initial fiber angle: if this is less than 54 deg 44 min, an increase in volume will result in shortening rather than elongation, and no length change will occur at a fiber angle of 54 deg 44 min. Engineers have taken advantage of these properties in the design of pneumatic artificial muscles, which consist of a flexible tubular membrane reinforced with fibers, either embedded in the walls or wrapping the membrane like a sleeve (Daerden and Lefeber, 2002; Klute et al., 1999). Pressurization of the pneumatic
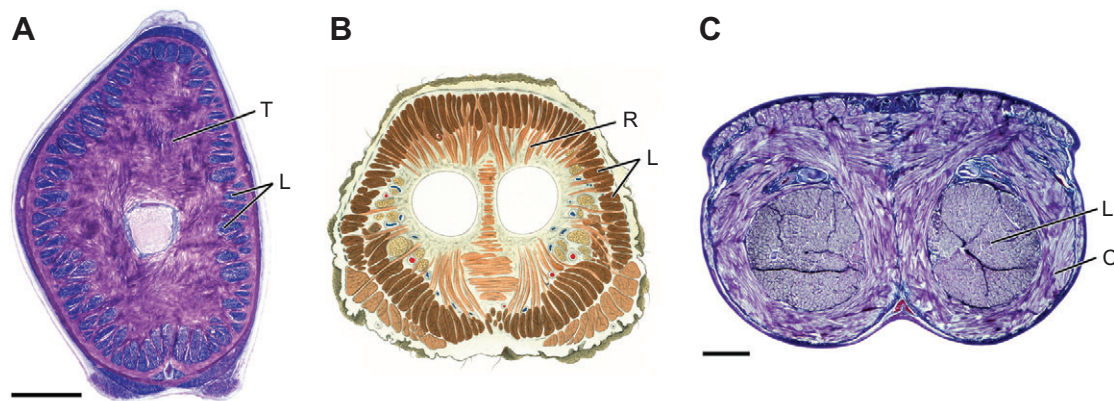
Fig. 8. Transverse sections showing the muscular arrangement of three examples of muscular hydrostats. (A) Transverse muscle fibers (T) occupy the core of the squid tentacle and extend to interdigitate with bundles of longitudinal muscle fibers (L) arranged near the surface. Scale bar, 1 mm. (B) Radial muscle fibers (R) extend from the center of the trunk of the elephant between bundles of longitudinal muscle (L). (C) Circular muscle fibers (C) surround two large bundles of longitudinal fibers (L) in the tongue of a monitor lizard. Scale bar, 1 mm. Panels A and C are histological sections stained with Masson's Trichrome. Panel B is after Boas and Paulli (Boas and Paulli, 1908).

artificial muscle causes it to change in length. Whether it shortens or elongates depends entirely on the initial fiber angle and both elongating and shortening pneumatic artificial muscles have been constructed (Pritts and Rahn, 2004).

Many mammalian penises also rely on a hydraulic mechanism and represent an interesting contrast to the generalization of wall reinforcement with cross-helical connective tissue fibers found in other hydrostatic skeletons. The hydraulic fluid in this case is blood, which is used to inflate the penis during erection. Once erect, if the penis is to be effective during copulation, it must resist length changes and must also be resistant to bending. In this regard, penile function represents a significant contrast to the function of the hydrostatic skeleton in many vermiform animals, where bending movements and cyclical length change often represent important aspects of the locomotory ability of the animal. How does the structure of the penis reflect this contrast in function? The primary erectile tissue of the penis is the corpus cavernosum, which is wrapped with a tough layer, the tunica albuginea, containing robust collagen fibers that do not follow helical paths around the penis, but instead are aligned both parallel and perpendicular to the longitudinal axis, i.e. fiber angles of 0 and 90 deg (Kelly, 1997; Kelly, 2002; Kelly, 2007). In the flaccid state, the tunica albuginea is highly folded. Upon inflation with blood, the penis enlarges, the tunica albuginea is placed in tension and the collagen fibers unfold. In contrast to the crossed-fiber helical reinforcement described above, this orthogonal arrangement of collagen fibers in the tunica albuginea makes the erect penis stiff in bending and resistant to changes in length, facilitating its use as an intromittent organ (Fig. 3) (Koehl et al., 2000). The orthogonal arrangement of collagen fiber reinforcement also evolved independently in the penises of turtles (Kelly, 2004).

In addition to the examples outlined above, hydraulic mechanisms are also employed in the foot of burrowing bivalves (Trueman, 1967; Trueman, 1968a; Trueman, 1975; Trueman et al., 1966) and some snails (Trueman, 1968b), as a mechanism to extend the legs of spiders (Parry and Brown, 1959), in the ligula (copulatory organ) of some octopuses (Thompson and Voight, 2003), and in the burrowing of many worm-like animals that lack segmentation, such as the lugworm *Arenicola* (Trueman, 1966; Seymour, 1970) or in priapulid worms that use the proboscis for burrowing (Hammond, 1970).

Muscular hydrostats

A diverse group of animal structures – including for instance the arms and tentacles of cephalopods (octopus and squid), the tongues of many vertebrates, and the trunk of the elephant – lack the fluid-filled cavities and fiber-reinforced containers that characterize the hydrostatic skeletal support systems described above. These structures, termed 'muscular hydrostats', instead consist of a densely packed, three-dimensional array of muscle and connective tissue fibers (Kier and Smith, 1985; Smith and Kier, 1989). The muscle fibers are typically arranged so that all three dimensions of the structure can be actively controlled, but in several cases such as the mantle of squid and some frog tongues, one of the dimensions is constrained by connective tissue fibers (Bone et al., 1981; Gosline and Shadwick, 1983; MacGillivray et al., 1999; Nishikawa et al., 1999; Thompson and Kier, 2001; Ward and Wainwright, 1972). Because muscle tissue, like most animal tissues lacking gas spaces, has a high bulk modulus, selective muscle contraction that decreases one dimension of the structure must result in an increase in another dimension. This simple principle serves as the basis upon which diverse deformations and movement of the structure can be achieved. For example, elongation is caused by contraction of muscle fibers arranged transversely, radially or circumferentially because their shortening decreases the diameter and thereby increases the length (Fig. 8). Shortening is caused by contraction of longitudinal muscle fibers, re-elongating the transverse, radial or circumferential muscle fibers. Muscular hydrostats are frequently capable of precise and complex bending movements, which require selective contraction of longitudinal muscle fibers on one side of the structure and simultaneous contractile activity in the transverse, circular or radial musculature. This simultaneous contractile activity is necessary to prevent the compressional forces generated by the longitudinal muscle from simply shortening the structure, rather than bending it, and can actually augment the bending by elongating the structure along the outside radius of the bend. The longitudinal muscle bundles are frequently located near the surface of the structure, as this placement away from the neutral plane increases the bending moment. Simultaneous contractile activity can also be used to control the stiffness dynamically. The musculature thus serves not only in the production of force, but also as the hydrostatic fluid.

In addition to the transverse, radial, circular and longitudinal muscle fibers, muscular hydrostats also commonly include helically arranged muscle fibers (Fig. 1). In the cases where helical muscle layers (or composite helical muscle and connective tissue layers) are present, the continuous crossed-fiber helical connective tissue arrays described above for conventional hydrostatic skeletons are absent, thus shape change is not limited and controlled by connective tissue fibers. The helical muscle layers can, by selective contraction, generate torsion or twisting of the structure around its long axis and may also alter the torsional stiffness of the structure. The direction of twisting depends on the handedness of the helical muscle layer contracting. Twisting in both directions requires both right- and left-handed helical muscle layers and helical muscle layers of each handedness are commonly present. They are typically located near the surface of the structure, rather than at its core, as this location increases the torsional moment for twisting. Active twisting movements are a common characteristic of muscular hydrostats (consider the diversity of movements of an elephant trunk or an octopus arm), in contrast to conventional hydrostatic skeletons in which twisting is resisted by the crossed-fiber helical connective tissue array.

Muscular-hydrostatic support is particularly common in the bodies of cephalopod molluscs (octopus, squid, cuttlefish and the chambered nautilus). The elongate arms and tentacles of squid (Kier, 1982; Van Leeuwen and Kier, 1997), the arms of octopuses (Kier and Stella, 2007), and the tentacles or cirri of the chambered nautilus (Kier, 1987) all depend on muscular hydrostatic support, with transverse (octopus arms, squid arms and squid tentacles), circular (squid tentacles), radial (chambered nautilus cirri), longitudinal (all), and helical or oblique muscle fibers (all) represented. In addition to these more or less cylindrical structures, muscular-hydrostatic support is also used to support and create substantial subambient pressures in the suckers (Kier and Smith, 1990; Kier and Smith, 2002), to support and actively bend the fins of squid and cuttlefish (Kier, 1989; Kier et al., 1989; Johnsen and Kier, 1993), to support and create the movement of the beaks (Uyeno and Kier, 2005; Uyeno and Kier, 2007), to provide muscular antagonism for the mantle during respiration and jet locomotion, with contributions from elastic energy storage in the connective tissues (Curtin et al., 2000; Gosline and Shadwick, 1983; Gosline et al., 1983; MacGillivary et al., 1999), and to provide support and antagonism for a variety of other structures and organs (Kier, 1988; Kier and Thompson, 2003).

The tongues of many vertebrates also rely on muscular-hydrostatic support, with examples from mammals, reptiles and amphibians. In mammalian tongues, the intrinsic musculature typically includes transverse muscle fibers in alternating sheets of parallel muscle fibers oriented more or less vertically and horizontally and longitudinal muscle fibers in bundles around the central core of transverse muscle fibers. Mammalian tongue deformations and many types of tongue movement are generated according to the general principles outlined above for muscular hydrostats (Bailey and Fregosi, 2004; Gilbert et al., 2007; Kier and Smith, 1985; McClung and Goldberg, 2000; Napadow et al., 1999). Muscular-hydrostatic mechanisms may also be important in the support and movement of many lizard tongues and some frog tongues (Chiel et al., 1992; de Groot et al., 2004; de Groot and van Leeuwen, 2004; Nishikawa et al., 1999; Smith and Mackay, 1990; Smith, 1986; van Leeuwen, 1997; van Leeuwen et al., 2000; Wainwright and Bennett, 1992a; Wainwright and Bennett, 1992b).

The trunk of the elephant also relies on a muscular-hydrostatic mechanism for support and exemplifies the remarkable diversity and complexity of movement of structures that rely on this form of support. The trunk includes radially arranged muscle fiber bundles, an array of longitudinal muscle bundles surrounding the central core of radial fibers, and both right- and left-handed helical muscle arrays (portions of the pars rimana and pars supralabialis muscles). Elongation, shortening, bending and torsion are probably generated in a manner similar to that outlined above for other elongate muscular hydrostats (Kier and Smith, 1985; Smith and Kier, 1989). The proboscis of tapirs (Witmer et al., 1999) and the vibrissal–fascial muscular complex of the manatee (Marshall et al., 1998) also function as a muscular hydrostat.

The remarkable diversity and complexity of movements observed in the elephant trunk, as well as in other muscular hydrostats such as the arms of octopus or mammalian tongues, may be facilitated by the muscular-hydrostatic mechanism of support and movement. In these structures, bending and other deformations can occur at any point along the length, so movement is not restricted only to joints as it is in organisms with rigid skeletons such as the vertebrates and arthropods. Likewise, unlike the situation in more conventional hydrostatic skeletons where localized muscle contraction increases the hydrostatic pressure throughout (Clark, 1964), the contraction of a small group of muscle fibers in the structure has a localized effect on the pressure and deformation, thereby providing these structures with the potential for much greater precision and intricacy of deformation. The limitation is the complexity of neural control that may be required in order to exploit the capabilities of these structures. Recent studies of the neuromuscular control of octopus arms suggest that various mechanisms exist that may simplify motor control of the arm, reducing the demands on the nervous system while still providing remarkable diversity of movement (Gutfreund et al., 1996; Sumbre et al., 2001; Sumbre et al., 2005; Sumbre et al., 2006).

The adaptability and the range and complexity of movement of hydrostatic skeletons, especially muscular hydrostats, have recently attracted the attention of robotics engineers, who are using these organs as inspiration for the design and construction of a new class of robotic manipulators and earthworm robots (Laschi et al., 2009; Trivedi et al., 2008; Vaidyanathan et al., 2000; Walker et al., 2005). These soft robots have the potential of providing greater dexterity and manipulability than conventional hard robots, but are more difficult to control and position accurately (Trivedi et al., 2008).

Additional examples

In addition to the examples presented above, hydrostatic skeletal support has been described for a number of additional animal and plant structures. The notochord of ascidians, cephalochordates, many larval and adult fish, and frog tadpoles (Adams et al., 1990; Grotmol, 2006; Koob and Long, 2000; Jiang and Smith, 2007) is considered to employ hydrostatic support. Support for movement of many larval insects, whose cuticle is soft and thus generally cannot bear compressive and bending forces, may also depend on a hydrostatic mechanism (Berrigan and Pepin, 1995; Brackenbury, 1999; Casey, 1991; Mezoff et al., 2004), although the mechanical properties of the body wall, air loss from the tracheal system and use of legs make the situation more complex (Lin et al., 2011).

Hydrostatic support is not restricted, however, to larval arthropods. As a crustacean such as a crab grows, it molts periodically, shedding its rigid exoskeleton. The newly molted cuticle is thin and flexible and cannot resist compressive and bending loads, yet the animals are still capable of rapid and forceful movements. The body of a newly molted 'softshell' crab is inflated with water (and also with air in
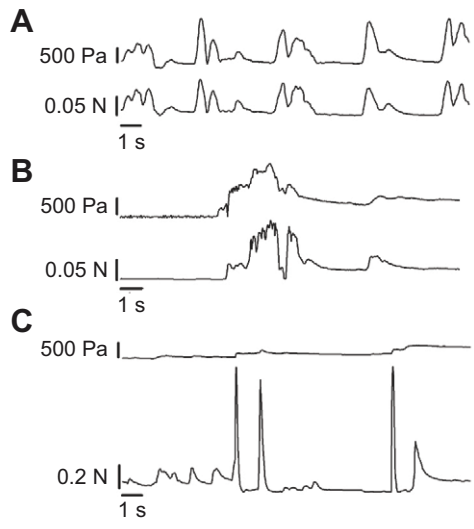
Fig. 9. Recordings of pressure (upper trace) and force (lower trace) from the crab *Callinectes sapidus* following a molt. (A) Recording from a soft-shell crab 1 h following exuviation, showing correlation between peaks of increased pressure and peaks of increased force. (B) Recordings from a paper-shell crab 12 h after exuviation. Correlation between force and pressure is still observed at this stage. (C) Recordings from a hard-shell crab 7 days after exuviation. Large forces are observed but there are no corresponding increases in pressure. Note that the scale for force in C is different. All traces represent approximately 19.5 s of recording. From Taylor and Kier (Taylor and Kier, 2003).

some terrestrial crabs). The longitudinal compressional forces resulting from muscle contraction can thus be resisted if the newly molted cuticle resists tension and increase in diameter. Simultaneous recordings of force and pressure (Fig. 9) show a strong correlation between the force exerted and the internal pressure, consistent with the use of hydrostatic skeletal support (Taylor and Kier, 2003; Taylor and Kier, 2006). These internal pressures disappear as the cuticle hardens. Mechanical testing shows that the flexural stiffness

(composite variable *EI*) of the postmolt cuticle is four orders of magnitude lower than that of the intermolt cuticle, but the breaking strength (stress at fracture in tension) is the same. Thus, although the postmolt cuticle is unable to bear compressive or bending loads, this thin membrane can support large tensile stresses as is required for hydrostatic skeletal support (Taylor et al., 2007). This alternation between the two categories of skeletal support may be widespread for arthropods.

Finally, hydrostatic skeletal support is not restricted to animals. Support of the herbaceous stems of plants depends on internal pressure and a tension-resisting outer layer (Hettiaratchi and O'Callaghan, 1978; Niklas, 1992; Vincent and Jeronimidis, 1991). The opening and closing of the stomata on the surface of leaves depends on changes in the internal pressure of the guard cells that flank the opening (Niklas, 1992).

Perspectives and conclusions

In this brief commentary on hydrostatic skeletons I have outlined the principles of function, described the general arrangement of muscle and connective tissue, and provided an overview of the diverse array of animals and animal structures that rely on hydrostatic skeletal support. The range of form and function is striking and the mechanism is remarkably widespread, including examples from both invertebrates and vertebrates, and even plants. Table 1 provides a summary of the salient characteristics of selected examples representing this considerable range.

The role of connective tissue in support and function in these systems is crucial, especially for reinforcement of the walls or container and for controlling and limiting shape change. Crossed-fiber helical connective tissue arrays are common, and are widespread in polyps and vermiform animals. They allow smooth bending and length change to occur and resist twisting or torsion. They are also important in hydraulic mechanisms where they reinforce the walls so that increases in pressure and volume cause the desired deformation. There are examples, however, of parallel connective tissue fiber arrays that are arranged orthogonally rather than helically. Such arrays are seen in mammalian penises and

Table 1. Selected examples of hydrostatic skeletons and their characteristics

Animal/Organ	Musculature	Connective tissue	Hydrostatic fluid/cavities	Movements
Polyps	Circumferential and longitudinal	Discontinuous fibers in mesoglea	Large, water-filled, undivided Closure of mouth to maintain volume	Elongation, shortening and bending Deflation with opening of mouth
Many vermiform animals	Circumferential and longitudinal	Crossed-fiber helical array	Range from large coelomic space to solid tissue Subdivided by septa in some cases	Elongation, shortening and bending No torsion Peristaltic movements common
Nematodes	Longitudinal only	Crossed-fiber helical array	Undivided coelomic space	Bending and undulatory waves, no length change
Echinoderm tube feet	Circumferential in ampulla, longitudinal in tube feet	Crossed-fiber helical array, fiber angle in tube feet greater than 55 deg 44 min	Undivided cavity, part of water vascular system	Elongation, shortening and bending Hydraulic mechanism
Mammalian penises	N/A, erection by inflation with blood	Orthogonal collagen fiber layers, folded in flaccid state	Erectile tissue (corpora cavernosa) filled with blood	Resistance to length change and bending when erect
Muscular hydrostats, e.g. cephalopod arms and tentacles, tongues, elephant trunk	Transverse, radial, circumferential, longitudinal, helical	No continuous crossed-fiber arrays Some with parallel fiber arrays controlling one dimension	Fluid-filled cavities absent Tightly packed three-dimensional array of muscle	Elongation, shortening, bending, torsion; variable stiffness in each Can be highly localized and complex
Post-molt crustaceans	Normal antagonistic and synergistic muscle groups	Newly secreted cuticle	Post-molt inflation of cuticle with water	Normal movements involving bending at joints with cuticle resisting pressure

provide an interesting contrast to the helical arrays; they play a crucial role in the function of the organ because they resist length change and bending. Connective tissue fibers sometimes are present in an orientation typically occupied by muscle fibers. For example, the connective tissue fibers in the cuticle of nematodes serve the role of circular muscle fibers in controlling the diameter, and connective tissue fibers may also be arranged to limit one dimension of muscular hydrostats, as observed in some tongues.

Although we normally associate hydrostatic skeletal support with soft-bodied invertebrates, a number of vertebrate animals possess structures that rely on hydrostatic support, including tongues and the elephant trunk. Furthermore, many arthropods, which we normally consider to have a stiff skeleton, rely on hydrostatic skeletal support as larvae and especially during molting, when the newly secreted cuticle is a thin and flexible membrane that cannot bear compressive or bending loads.

Although hydrostatic skeletons lack the rigid levers and fulcra that provide mechanical amplification in rigid skeletons, mechanical amplification can nevertheless occur. The amplification is a simple consequence of the relationship between dimensional changes in a structure that is essentially constant in volume. The form of amplification seen in hydrostatic skeletons has some interesting implications for the evolution of muscle. Unlike the situation with rigid skeletons, in which the displacement of muscle is amplified by the lever system and thus muscle strain is limited, many of the muscle fibers in hydrostatic skeletons (e.g. retractor muscles of elongate structures) are subjected to larger strains than could be accommodated by normal vertebrate skeletal muscle. This mechanical effect may be important in the evolution of the oblique striation pattern, which is common among animals with hydrostatic skeletons, and can function over a much wider range of strain than vertebrate skeletal muscle.

Although many hydrostatic skeletons include liquid-filled cavities, some may be partitioned by septa, which allows for independent operation of portions of a hydrostatic body or structure. Indeed, a range of relative hydrostatic fluid volume is observed, including muscular hydrostats such as tongues, cephalopod tentacles and the elephant trunk, which lack fluid-filled internal spaces. Such an arrangement allows much more highly localized control of deformations, with the potential for much greater diversity and complexity of movement. These characteristics have made muscular hydrostats appealing as inspiration for the development of robotic manipulators.

Although the basic arrangement and function of the muscle and connective tissue in hydrostatic skeletons has been examined and the movements of these bodies and structures have been characterized, much additional research is needed. We know relatively little about the neuromuscular control of hydrostatic skeletons. This is true of hydrostatic skeletons in general, but is of particular importance for muscular hydrostats, where the complexity of movement observed is expected to place significant demands on the nervous system. In addition, although the pressure and the forces produced during movement have been measured in some cases, the transduction of muscle contraction into bending, elongation and torsion of hydrostatic skeletons is not well understood. Additional quantitative models and experimental measurements are needed. Finally, with the exception of some interesting work on earthworms, we know relatively little about the effects of scaling on hydrostatic skeletons. The size range of these structures is, in many cases, quite large, yet we know little about how size affects the arrangement of the muscle and connective tissues, dynamics and mechanics of movement, and the modulation of muscle structure and properties.

Glossary

Ambulacrum
Each of the five radially arranged bands in echinoderms, together with their underlying structures, through which the double rows of tube feet protrude.

Antagonistic muscle
A muscle that opposes the action of another muscle, thereby allowing a shortened muscle to be re-elongated.

Bulk modulus
The ratio of the change in pressure acting on a volume to the fractional change in the volume.

Coelenteron
The central sac-like digestive cavity of animals in the Phylum Cnidaria.

Crossed-fiber helical array
An arrangement of connective tissue fibers, typically collagen, commonly found reinforcing the walls of hydrostatic skeletons and wrapping the body or organ in sheets of parallel fibers, in both right- and in left-handed helixes.

Mesoglea
A jellylike layer in cnidarians and ctenophores between the ectoderm and the endoderm.

Neutral plane
A surface in a bent beam along which the material is neither compressed nor extended.

Obliquely striated muscle
A striated muscle fiber type, common in invertebrates such as annelids, nematodes and molluscs, in which the thick and thin myofilaments and the dense bodies to which the thin filaments are anchored are arranged in a staggered pattern, forming oblique bands across the fiber.

Siphonoglyph
A ciliated groove found in sea anemones and some corals that extends from the mouth into the pharynx and generates a current of water directed into the coelenteron.

Stomata
One of the minute pores in the epidermis of a plant leaf or stem through which gases and water vapor pass.

Strain
A dimensionless number that characterizes the change in dimensions of an object during a deformation.

Stress
The force per unit area that tends to deform the body on which it acts.

Supercontraction
The natural contraction of a cross-striated muscle with a maximum length change greater than threefold effected by penetration of the myofilaments through perforated Z-discs.

Water vascular system
A system of water-filled canals derived from the coelom that connects the tube feet of echinoderms.

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