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The Arrangement and Function of Molluscan Muscle

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I. Introduction

The arrangement and function of the musculature of an animal is closely related to the skeletal support system. A skeletal support system allows muscles to be returned to their resting length by action of antagonistic muscles, transmits the force produced by muscle contraction, provides the support needed to resist the compressive and bending forces exerted by muscles, and may amplify the resultant force, speed, or displacement of muscle activity.

Molluscs exhibit a wide range of muscular arrangements and provide examples of the two general categories of skeletal support seen in animals. The first category of skeletal support is characterized by hardened skeletal elements with musculature typically arranged in distinct bundles. The adductor muscles of bivalves and the dorsal musculature of chitons are familiar examples. The second general category of skeletal support is the hydrostatic skeleton with musculature arranged in two-dimensional sheets or complex three-dimensional arrays. Hydrostatic skeletons are classically envisaged as including cavities filled with body fluid, but the relative proportion of the cavities and musculature is variable and ranges

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from the large fluid-filled hemocoel seen, for example, in the foot of many burrowing bivalves, to structures such as the arms and tentacles of cephalopods that are made up almost entirely of muscle with no hemocoelic cavities.

In spite of this range, hydrostatic skeletons share a common characteristic of being constant in volume. Hydrostatic structures with large fluid-filled cavities may utilize a hydraulic mechanism whereby localized contraction of musculature results in movement of fluid from one portion of the body or organ to another and thereby provides for the transmission of force for movement and muscular antagonism. The musculature of hydrostatic structures lacking large fluid-filled cavities does not create bulk movement of fluid from one portion of the structure to another; instead, it creates changes in the dimensions of the structure. It is the change in dimension that transmits the force of muscular contraction for movement and muscular antagonism.

The focus of this chapter will be on the arrangement and function of the musculature of structures and organs in molluscs that possess hydrostatic skeletons. Rather than reviewing the arrangement of the musculature of all molluscs, examples will be chosen of structures with hydrostatic skeletons in which the function of the musculature in the production of movement has been studied. The examples range from hydrostatic skeletons with complex three-dimensional arrays of tightly packed muscle fibers to structures with large fluid-filled cavities. Particular emphasis will be placed on hydrostatic skeletons with tightly packed muscle, because these are a more widespread and general feature of molluscs than is usually recognized.

II. Mechanics of Hydrostatic Skeletons

Hydrostatic skeletal support systems have been reviewed by a number of authors (Alexander, 1968; Chapman, 1958, 1975; Clark, 1964, 1981; Kier and Smith, 1985; Trueman, 1975; Wainwright, 1970, 1982; Wainwright et al., 1976), and a summary of the general characteristics of hydrostatic skeletons follows. The most important biomechanical feature of a hydrostatic skeleton is that it is constant in volume. The body fluid or aqueous liquid in hydrostatic cavities or muscles is practically incompressible at physiological pressures. In a 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 present analysis of arrangement and function of muscle in hydrostatic skeletons.

The musculature of a hydrostatic skeleton may surround a central fluid-

filled cavity or may be arranged in a three-dimensional array in the structure. The three-dimensional array of muscle fibers may form a solid mass of muscle termed a "muscular-hydrostat" (Kier and Smith, 1985), or the network of muscle fibers may pass through fluid-filled spaces and connective tissue, these two conditions representing end points on a continuum. The basic principles of support and movement in muscular-hydrostats and hydrostatic skeletons with large fluid-filled cavities are the same. Some of the capabilities, however, are different and will be mentioned below. Organs or bodies with hydrostatic skeletons are capable of four types of movement: elongation, shortening, bending, and torsion.

Contraction of muscles that decrease the cross-sectional area of a constant-volume structure must result in elongation of the structure. Three general arrangements of muscles—circular, transverse, or radial—will, on contraction, create a decrease in cross-sectional area. Circular muscle is typically arranged as a continuous layer at the circumference of the body or organ. Transverse muscles are defined here to include muscle fibers that run from one side of the body or organ to the other, perpendicular to the long axis of the structure. They may be oriented vertically and horizontally; in bodies or organs with fixed orientation, it is often convenient to refer to the vertical muscle fibers as dorsoventral and the horizontal muscle fibers as transverse. Elongation will occur even if vertical or horizontal muscles contract alone so long as tonus is maintained in the muscles of the other orientation. Radial muscles are defined here to include fibers that run perpendicular to the long axis from the central axis to the periphery of a structure of approximately circular cross section.

Mechanical amplification of muscle displacement or force is often provided by a lever system of hardened skeletal elements, but an analysis by Kier and Smith (1985) suggested that mechanical amplification analogous to leverage may also be possible for hydrostatic skeletons. Lever systems may be designed to increase mechanical advantage, so that the resultant force is greater than the applied force or, alternatively, the lever system may increase displacement so that the resultant displacement or velocity is greater than the applied displacement or velocity. The relationship between the length and diameter of a cylinder of constant volume is plotted in Fig. 1. In a constant-volume cylinder with a high initial length–width ratio, a small decrease in diameter will produce a large increase in length. Decrease in diameter may be created by contraction of circular, transverse, or radial muscles, and, in this case, the resultant displacement and velocity is greater than the applied displacement and velocity. This relationship may be important in protrusible hydrostatic organs. Shortening of a structure with a hydrostatic skeleton results from contraction of longitudinally arranged muscles.
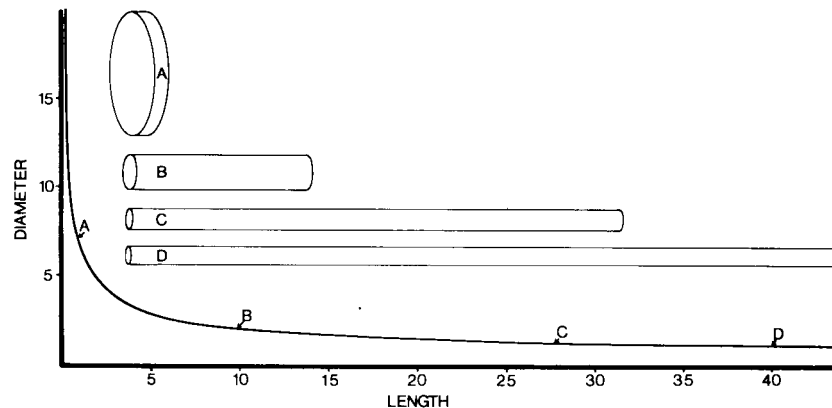
Fig. 1. Plot of relationship between length and diameter of a cylinder of constant volume. The positions on the graph of shapes A through D (drawn to scale) are indicated. A small decrease in diameter from shape B to D causes a large increase in length. [From Kier and Smith (1985), with permission of the *Journal of the Linnean Society*.]

Bending of a hydrostatic 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 body or organ is resisted. Without resistance to longitudinal compression, unilateral longitudinal muscle activity will cause shortening without bending. Shortening of a structure of constant volume must result in an increase in cross-sectional area. Shortening due to a longitudinal compressional force can therefore be prevented by resisting increase in cross-sectional area. Figure 2A illustrates bending of a cylinder of constant volume by unilateral decrease in length in combination with maintenance of constant cross-sectional area. In a structure with a hydrostatic skeleton, unilateral decrease in length may be created by contraction of longitudinal muscles on one side of the structure while constant cross-sectional area may be maintained by tonus in transverse, radial, or circular musculature. Without simultaneous activity of the musculature maintaining constant cross-sectional area, unilateral longitudinal muscle contraction causes little or no bending (Fig. 2B).

Bending of a hydrostatic structure may also be produced by a decrease in cross-sectional area in consort with maintenance of unilateral constant length (Fig. 3A). Decrease in cross-sectional area may be produced by circular, transverse, or radial muscle contraction, and unilateral constant length can be maintained by contractile activity of longitudinal muscles on one side of the cylinder. Without simultaneous longitudinal muscle activ-
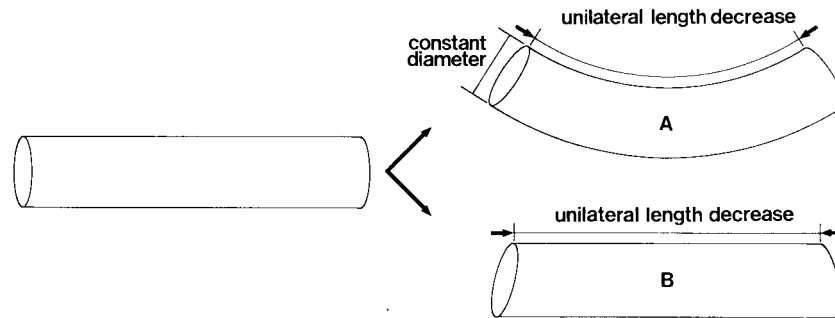
Fig. 2. Diagram illustrating the requirements for bending of a hydrostatic body or organ. Unilateral length decrease is caused by contraction of longitudinal muscle on one side of the structure. In case A, constant diameter is maintained thereby providing resistance to longitudinal compression and causing the structure to bend. Constant diameter is maintained by contractile activity of transverse, radial, or circular muscle. In case B, constant diameter is not maintained. Without resistance to longitudinal compression, the structure is shortened but not bent. [From Kier and Smith (1985), with permission of the *Journal of the Linnean Society*.]

ity, contraction of circular, radial, or transverse muscle will cause elongation without bending (Fig. 3B). Bending therefore requires simultaneous contractile activity of longitudinal muscle and the antagonistic transverse, radial, or circular muscle.

The longitudinal muscle masses have a greater moment arm available for bending the structure if they are situated peripherally away from the neutral axis, as they thus have greater mechanical advantage than more centrally located longitudinal muscles. In order for bending to occur in
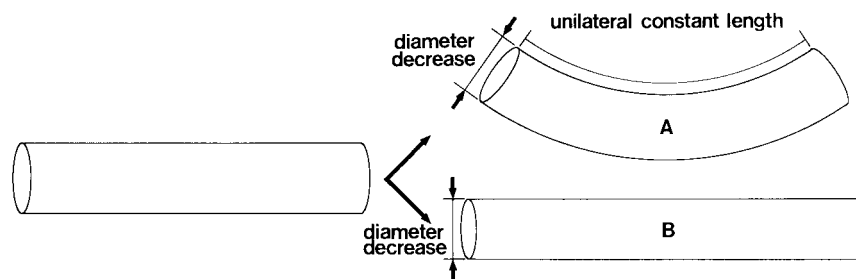

Fig. 3. Diagram illustrating the requirements for bending of a hydrostatic body or organ. Diameter decrease is caused by contraction of transverse, radial, or circular muscle. In case A, unilateral constant length is maintained by contractile activity of longitudinal muscle on one side of the structure and thereby causes bending. In case B, unilateral constant length is not maintained and diameter decrease simply causes elongation. [From Kier and Smith (1985), with permission of the *Journal of the Linnean Society*.]

any plane, many longitudinal muscle bundles must be arranged around the circumference of the structure. In hydrostatic skeletons with tightly packed three-dimensional arrays of muscle, localized bending is possible through contraction of longitudinal muscles and their antagonists in a restricted area of the structure. Contraction of the musculature of hydrostatic skeletons with large fluid-filled cavities increases the pressure in all portions of the structure and thus is correlated with less precise control of bending than is found in muscular-hydrostats. Note that the same arrangement of musculature used for bending can also be used for elongation and shortening by simply altering the sequence of contractile activity and relaxation, so that antagonistic muscles operate sequentially rather than simultaneously.

Many hydrostatic structures are also capable of torsional movements. (The term "torsion" is used in this case to denote the twisting of a structure around its longitudinal axis and does not refer to the developmental process of torsion in the Gastropoda.) Torsion of a hydrostatic structure is created by obliquely or helically arranged muscle (Kier, 1982; Kier and Smith, 1985). The direction of torsion created by helically or obliquely arranged muscle depends on the handedness of the helical system. For instance, contraction of a left-handed helical muscle layer will cause clockwise torsion of the free end of a structure relative to its base when viewed from base to free end (Fig. 4). Torsion in either direction requires separately acting right- and left-handed helical or oblique muscle layers. Helically or obliquely arranged mucle fibers may also create force for elongation or shortening, depending on the fiber angle of the helical or oblique layers (the fiber angle is the angle that a helical or oblique muscle fiber makes with the long axis of the structure). Contraction of muscle fibers with fiber angle of 54°44' will cause torsion without creating force for elongation or shortening. Contraction of helical or oblique muscle fibers with a fiber angle >54°44' will create force for elongation, while contraction of muscle fibers with a fiber angle <54°44' will create force for shortening of the hydrostatic structure (Kier and Smith, 1985).

In addition, hydrostatic structures with tightly packed musculature can create deformations that do not fit precisely into the above-mentioned categories of elongation, shortening, bending, and torsion. For example, two-dimensional "bulging" of a block of muscle of a given orientation can be used to exert force perpendicular to the long axis of the muscle for use in movement or muscular antagonism. The importance of the work done in radial expansion of a contracting muscle has been suggested by Wainwright et al. (1978) and will be emphasized further in this chapter.
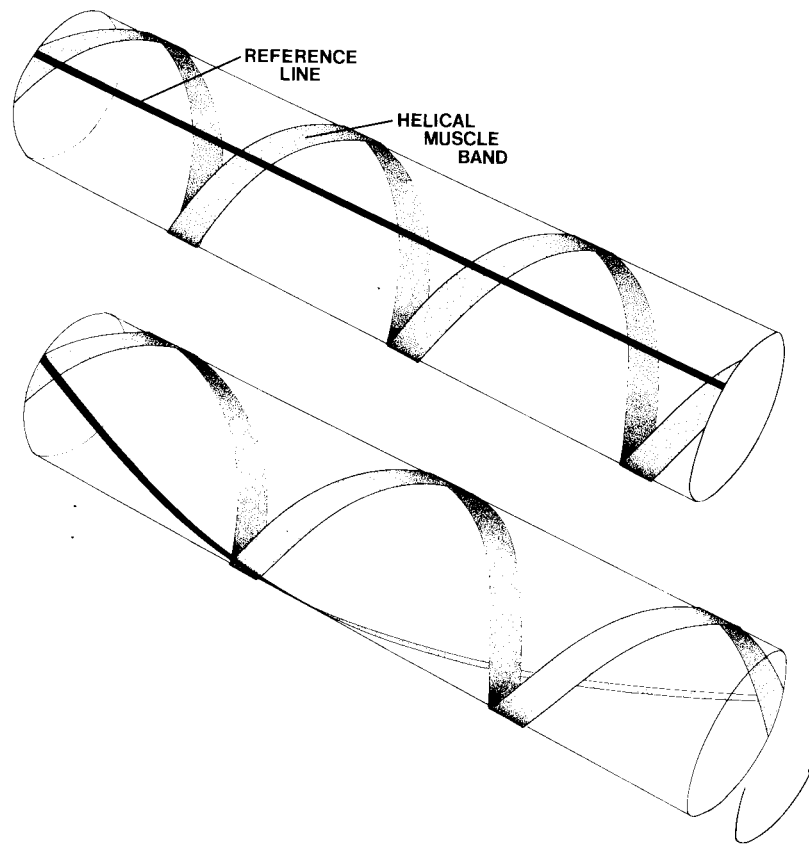
Fig. 4. Diagram illustrating the effect of contraction of a single helical muscle band (in this case, a left-handed helix). The black line is a reference line. Contraction of the helical muscle band causes the cylinder to twist. [From Kier (1982), with permission of the publisher.]

III. Examples of Muscular-Hydrostats

A. Gastropod Columellar Muscles

Columellar muscles of many species of gastropods utilize a muscular-hydrostatic system that both withdraws the animal into the shell and pushes it out of the shell. A careful description of the anatomy of the columellar muscle of *Nassarius* (= *Nassa*) *mutabilis* L. was provided by Rotarides (1941) and is summarized below (see also Weber, 1926). Trueman and Brown (1976) described the anatomy and function of a
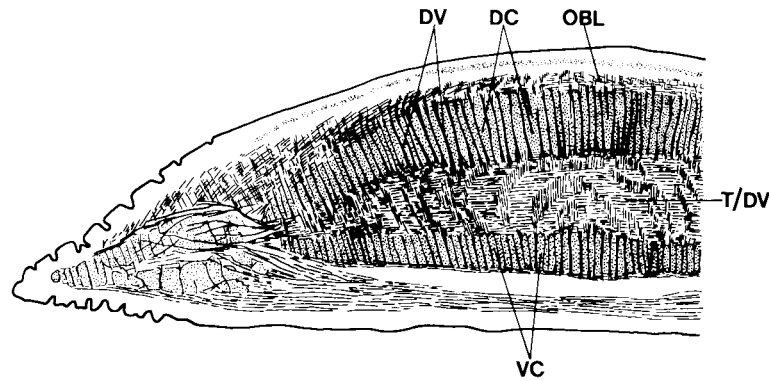
Fig. 5. Transverse section of the foot of *Nassarius* (= *Nassa*) *mutabilis*, showing arrangement of muscle fibers in the columellar muscle mass. DC, Dorsal portion of columellar muscle; DV, dorsoventral muscle fibers; OBL, oblique muscle layer formed of two systems of obliquely arranged muscle fibers; T/DV, transverse and dorsoventral muscle fibers; VC, ventral portion of columellar muscle. [After Rotarides (1941).]

similar system in *Bullia digitalis*. Brown and Trueman (1982) examined the columellar muscles of a variety of gastropods including the prosobranchs *Turbo samaticus* L., *Oxystele variegata* (Anten), *Gibbula rosea* (Wood), *Argobuccinum argus* (Gmelin), and *Burnupena cincta* (Bolten), in addition to a freshwater snail *Planorbis corneus* L. and a terrestrial pulmonate *Theba pisana* (Muller). A similar muscular-hydrostatic system was consistently seen in each species, and Brown and Trueman (1982) suggested that this mechanism of extension of the foot is in fact widespread in gastropods. [See Dale (1974) for an investigation of a different mechanism of extension in the terrestrial pulmonate *Helix pomatia*.]

The morphology of the columellar muscle of the foot of *N. mutabilis* is shown in Fig. 5. The thick columellar muscle is divided into two principal parts, an anterior and posterior stem. The anterior stem extends anteriorly and laterally in the propodium toward the sole of the foot and, after interdigitating with muscle fibers of the foot, inserts as single fibers near the epithelium of the sole. The posterior stem of the columellar muscle is considerably longer and is divided into dorsal and ventral portions that run posteriorly in the metapodium to insert on the operculum. Between the dorsal and ventral portions of the posterior stem of the columellar muscle is a central mass of tightly packed dorsoventral and transverse muscle fibers that show a striking resemblance in sections to the arrangement of the transverse muscle masses of the arms and tentacles of loliginid and ommastrephid squids (compare Figs. 5 and 9). The dorsoventral fibers extend from the central mass of transverse and dorsoventral fibers
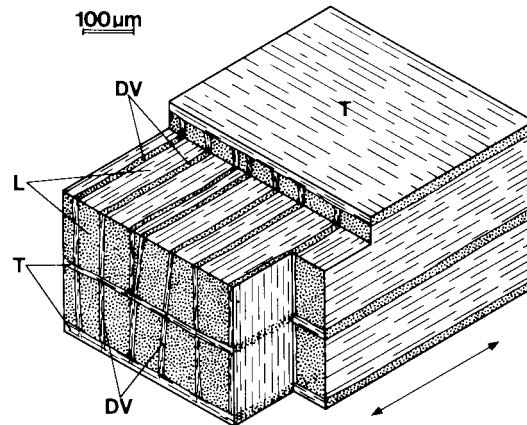
Fig. 6. Schematic diagram of posterior stem of columellar muscle in the metapodium of *Bullia digitalis*. Dorsoventral muscle fibers (DV) extend through the columellar muscle, dividing it into longitudinal muscle bundles (L). Transverse muscle fibers (T) extend through the longitudinal and dorsoventral muscle fibers and are present on the dorsal and ventral surfaces of the columellar muscle. The arrow indicates the orientation of the long axis of the columellar muscle. (From histological material provided by courtesy of E. R. Trueman.)

through the dorsal and ventral portions of the longitudinally oriented posterior stem of the columellar muscle, dividing the columellar stem into many longitudinal bundles (Fig. 5). The transverse muscle mass is thickest along the midline and tapers as the transverse muscle fibers extend laterally in the foot (Rotarides, 1941).

A similar arrangement of the columellar muscle of *Bullia digitalis* is seen, although there are some differences with respect to the arrangement of the posterior stem and transverse muscles (Trueman and Brown, 1976). The columellar muscle of *Bullia* extends from the columella of the second whorl of the shell into the foot where it divides into an anterior stem which sends radiating muscle fibers into the propodium, and a single posterior stem or opercular muscle, which extends longitudinally through the metapodium to insert on the operculum. Dorsoventrally oriented muscle fibers extend through the opercular muscle, dividing it into numerous longitudinal bundles (Fig. 6). In addition, transverse muscle fibers extend through the opercular muscle and are also present on its dorsal and ventral surfaces.

Küttler (1913) described briefly the columellar muscle of *Oliva peruviana* (L.) and noted that it was divided into bundles by muscle fibers oriented perpendicularly to the longitudinal axis of the columellar muscle fibers. Brown and Trueman (1982) noted a similar arrangement of the

columellar muscle in a variety of gastropod species (listed above) and suggested that this arrangement is common in gastropods.

The functional significance of this system of closely packed muscle fibers is as follows (Brown and Trueman, 1982; Trueman and Brown, 1976, 1985a). The columellar muscle, with its closely packed dorsoventral and transverse muscle fibers, forms a three-dimensional muscular network or muscular-hydrostat. Because this three-dimensional muscular network is constant in volume, any decrease in one dimension must result in an increase in at least one other dimension. It is by virtue of this principle that muscular antagonism of all three muscle fiber orientations is possible. Retraction of a snail into the shell is brought about by contraction of the longitudinally arranged columellar muscle fibers. Relaxation of the muscle fibers in either the lateral or dorsoventral orientations (or both) is required during retraction, because the system must increase in either the transverse or dorsoventral dimension (or both) as it shortens. An increase in length of the system may be brought about by a decrease in cross section, and therefore extension of the snail may occur as a result of contraction of the dorsoventral and transverse muscle fibers with relaxation of the longitudinally arranged fibers. Additionally, with one of the dimensions held constant, muscle fibers in the two remaining orientations can antagonize one another. For example, the foot could be broadened by contraction of the dorsoventral muscle fibers (see Fig. 5 for *Nassarius*) if the longitudinal fibers maintain the length and the transverse fibers are relaxed.

Brown and Trueman (1982) have noted that during emergence of *Bullia* the dorsal surface of the foot does not press against the shell, as would be required if emergence was caused by the foot dragging the animal out of the shell as a result of inflation with hemolymph, as was suggested by Brown (1964). In addition, after emergence the shell is held above the foot, without contact with the dorsal surface of the foot, and thus it seems likely that elongation of the columellar muscle by contraction of the dorsoventral or transverse muscle fibers (or both) causes emergence in *Bullia* (Brown, 1964; Brown and Trueman, 1982). Trueman and Brown (1985a) have provided direct experimental evidence that the columellar muscle of *Haliotis midae* functions as a muscular-hydrostatic system in the manner outlined above. The columellar (or shell) muscle of *H. midae* has muscle fibers arranged in a tightly packed three-dimensional array that includes longitudinal retractor muscle fibers, circular muscle fibers, and radial muscle fibers. During pedal extension and elevation of the shell, an increase in pressure was recorded in the proximal region of the columellar muscle, but no pressure pulses were observed in the mantle cavity, cephalopedal venous sinus, or ventricle. The force for elongation is pro-

vided by the columellar muscle, and the pressure observed is likely the result of contraction of the circular and radial muscles. The presence of similar arrangements of muscle fibers in the columellar muscles of the gastropods listed above suggests that this mechanism of emergence may be common in gastropods.

An obliquely arranged muscle layer surrounding the columellar muscle of *N. mutabilis* was identified by Rotarides (1941) as an oblique circular layer. It consists of two systems of helically arranged fibers that cross one another at an angle of ~90°. Each forms an angle of ~45° with the longitudinal axis of the foot, and the layer thus constitutes both a left-handed and a right-handed helical arrangement of muscle fibers surrounding the columellar muscle. The contraction of one or the other of the helical arrangements may cause twisting or rotation of the shell relative to the foot. The direction of rotation would depend on the handedness of the contracting muscle fibers (Kier, 1982; Kier and Smith, 1985). Jones and Trueman (1970), citing Weber (1926), suggested that "spiral muscles" of the foot of the limpet *Patella vulgata* L. are responsible for the rotation of the shell commonly seen in response to predators. The ability to twist the shell relative to the foot is common in gastropods, and it is thus likely that helically arranged muscle fibers surrounding the columellar muscle are also common.

B. Squid and Cuttlefish Mantle

The muscular mantle of squid and cuttlefish is used in jet propulsion and respiration and is an example of a muscular-hydrostatic system. The functioning of the tightly packed muscles is affected to a considerable degree by connective tissue fibers that are present in various orientations in the mantle tissue. The arrangement and function of the muscles and connective tissue fibers of a variety of squid species and a cuttlefish species were studied recently by several authors (Bone et al., 1981; Gosline and Shadwick, 1983a,b; Gosline et al., 1983; Mommsen et al., 1981; Packard and Trueman, 1974; Ward, 1972; Ward and Wainwright, 1972), and a summary of the results follows (see also Wells, Chapter 11 this volume).

The anatomy of the mantle of the squid species *Lolliguncula brevis* and *Loligo pealei* was studied by Ward and Wainwright (1972) and is illustrated diagrammatically in Fig. 7. Underlying the skin on the inner and outer surfaces of the mantle are layers of connective tissue fibers called the inner and outer tunics. In between the inner and outer tunics is a thick layer of circularly oriented muscle fibers divided up into more-or-less regular bands by thin partitions of radially oriented muscle fibers that
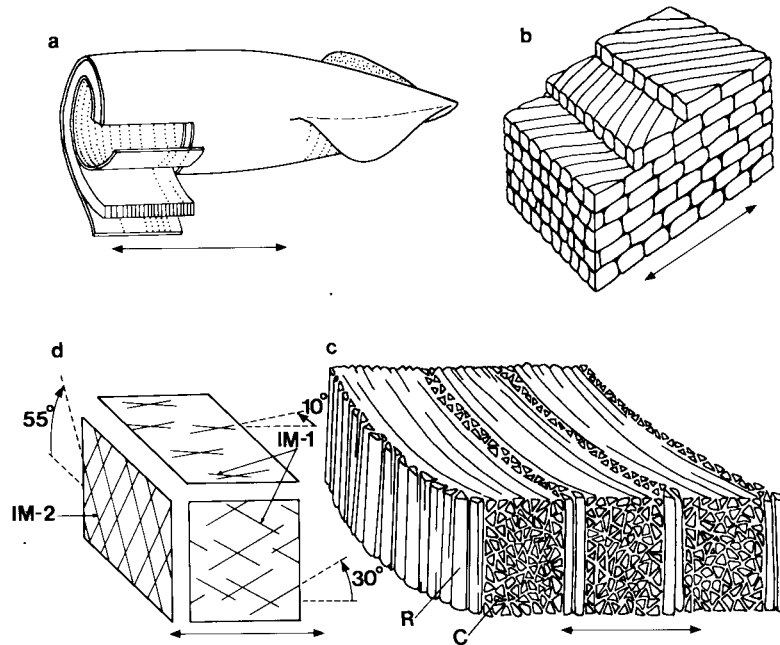
Fig. 7. Diagrams showing arrangement of muscle fibers and connective tissue fibers in squid mantle. (a) Diagram of mantle of *Lolliguncula brevis* with skin and pen removed. A thick muscle layer is sandwiched in between the inner and outer tunics. (b) Diagram showing arrangement of collagen fibers in the outer tunic of *L. brevis*. Each of the seven layers is one fiber thick. (c) Diagram showing arrangement of circular muscle fibers (C) and radial muscle fibers (R). (d) Diagram showing arrangement and angles of intermuscular connective tissue fibers. The fibers of intermuscular fiber system one (IM-1) are visible in radial and tangential section planes. The fibers of intermuscular fiber system two (IM-2) are present in the radial muscle partitions and are thus visible in transverse section planes. The arrows indicate the orientation of the long axis of the mantle. [Figure adapted, with permission of the Zoological Society of London, from Ward and Wainwright (1972).]

extend from the inner to the outer surface of the mantle. The radial muscle partitions are sometimes discontinuous and, as was noted by Bone et al. (1981) (for *Alloteuthis subulata* and *Loligo forbesi*), the partitions interdigitate rather than being continuous around the mantle. No large spaces are present in the mantle tissue, and the muscle fibers are closely packed (Ward and Wainwright, 1972).

Studies by Bone et al. (1981) on the mantle muscle of the squids *Alloteuthis subulata* L. and *Loligo forbesi* L. and the cuttlefish *Sepia officinalis* L. and by Mommsen et al. (1981) on the squids *Loligo opalescens, Illex illecebrosus, Ommastrephes* sp., *Berryteuthis magister,* and *Symplectoteuthis oualaniensis* indicated that the circular muscle fibers of the mantle

are differentiated into an inner, middle, and outer zone. The circular muscle fibers of the inner and outer zones are rich in mitochondria while those of the central zone are poor in mitochondria. Histochemical localization of succinic dehydrogenase (SDH) activity shows the same pattern; the inner and outer layers are strongly SDH positive compared to the middle zone (Bone et al., 1981; Mommsen et al., 1981). Mommsen et al. (1981) also measured enzyme activities from the three zones and found that the ratio of oxidative to glycolytic enzyme activities in the inner and outer layers was high while the ratio in the middle layer was low. The vascularity of the zones also reflects these differences, for the inner and outer zone show dense capillary plexuses while the middle zone shows a sparse capillary plexus. The radial muscle fibers are similar in structure and mitochondrial content to the circular muscle fibers of the central zone (Bone et al., 1981).

The metabolic differentiation of the muscle fibers of the mantle is thought to be analogous to the red and white muscle of vertebrates. The circular muscle fibers of the middle zone probably produce the escape jet. The circular muscle fibers of the inner and outer zone may produce the respiratory movements (Bone et al., 1981; Mommsen et al., 1981). The similarity between the radial muscle fibers and the circular muscle fibers of the middle zone, where the ratio of oxidative to glycolytic enzymes is low, is at first sight perplexing, because the radial muscle fibers are thought to be antagonizing the circular muscles and therefore should have the oxidative capacity of the inner and outer zones. Work by Gosline and Shadwick (1983a,b) and Gosline et al. (1983) suggests, however, that connective tissue fibers of the mantle may store elastic energy and provide antagonism for the circular muscles. In addition, flow-induced pressure differences may aid in mantle refilling and antagonism of the circular muscles during high-speed swimming (Vogel, 1987).

The connective tissue of the mantle includes the inner and outer tunics and intermuscular connective tissue fibers. The tunics consist of closely packed layers of collagenous connective tissue fibers (Fig. 7) (Ward and Wainwright, 1972; Gosline and Shadwick, 1983a). A single row of parallel connective tissue fibers forms each layer, and the fibers in alternate layers run in right- and left-handed helixes around the mantle. Ward and Wainwright (1972) and Bone et al. (1981) observed several orientations of intermuscular connective tissue fibers that extend through the mantle musculature as a meshwork. These fibers have been classified by Gosline and Shadwick (1983a) as intermuscular fiber sets 1, 2, and 3 (IM-1, IM-2, IM-3). IM-1 and IM-2 are shown schematically in Fig. 7. IM-3 consists of coiled or buckled connective tissue fibers that are oriented parallel to the circular muscle fibers.

Some of the connective tissue fibers of the mantle may be elastic fibers, because they show staining reactions typical of elastic fibers and, in addition, lack the typical 68-nm repeat of collagen fibers when observed by electron microscopy (Bone et al., 1981). Gosline and Shadwick (1983a) reported that the fibers of IM-1 are probably collagen because they measured the same birefringence as the collagen of rat tail tendon for these fibers and did not observe the optical isotropy that is typical of elastic fibers. Gosline and Shadwick (1983a) were unable to measure the birefringence of the fibers of IM-2 and IM-3 due to masking by parallel birefringent muscle fibers. Calculations of strain energy storage in the intermuscular systems suggested that the fibers of IM-2 may also be collagen, but a decision on the makeup of these fibers and those IM-3 awaits further study.

The function of the muscle and connective tissue fibers of the mantle in producing both the powerful jet used in locomotion and the rhythmic respiratory movements depends on the muscular hydrostatic system of the mantle. The mantle is constant in volume and has been found to be essentially constant in length (Packard and Trueman, 1974; Ward, 1972). The tunics probably play an important role in limiting length changes of the mantle (Ward and Wainwright, 1972). Contraction of the circular muscles of the mantle causes a decrease in the diameter of the mantle and expels water from the mantle cavity. Because the mantle is constant in volume and does not change length, circular muscle contraction causes thickening of the mantle and extension of the radial muscle fibers. Similarly, contraction of the radial muscle fibers causes the mantle wall to become thinner, extending the circular muscles and refilling the mantle cavity. Studies by Gosline and Shadwick, (1983a,b) and Gosline et al. (1983) demonstrated that refilling of the mantle cavity also involves elastic recoil of the mantle wall, and they suggested that the intermuscular connective tissue fibers are responsible for the elastic properties of the mantle. Mechanical tests of whole mantle showed that the tissue is indeed stiff enough to store a significant amount of elastic energy and, in addition, that the efficiency of energy storage (resilience) is high enough. Using dimensional changes of the mantle during jetting reported by Ward (1972), Gosline and Shadwick (1983a) calculated the amount of strain that would occur in the intermuscular connective tissue fiber systems IM-1 and IM-2. The calculations suggested that the angles of the fibers of IM-1 and IM-2 allow the extensibility of the fibers to be matched precisely to the thickness changes of the mantle wall. The calculations also suggested that the intermuscular connective fibers are responsible for the elastic properties of the mantle because the stiffness of the mantle can be predicted based on the calculated strain in the intermuscular fiber systems

IM-1 and IM-2, the stiffness of collagen, and the percentage of the volume of mantle tissue made up of the intermuscular fiber systems (Gosline and Shadwick, 1983a). The intermuscular fiber system IM-3 may provide an upper limit to mantle expansion (Gosline and Shadwick, 1983b).

The roles of the radial muscle, circular muscle, and connective tissue fibers of the mantle in the production of mantle movement have been further elucidated by simultaneously recording electromyograms of the radial and circular muscle, changes in mantle pressure, and change in mantle diameter (Gosline et al., 1983). These results indicated that the locomotory jet is divided into three phases. During the first phase, hyperinflation of the mantle cavity occurs as a result of contraction of the radial muscles evidenced by strong EMG traces of these muscles. This phase is referred to as "hyperinflation," because the mantle is expanded to a larger diameter than the expanded diameter (resting diameter) seen in respiratory movements. The second phase, "the jet," occurs as the circular muscles of the mantle contract. The final phase, "refilling," occurs as the mantle cavity reexpands, primarily due to the elastic recoil of the connective tissue fiber lattice (see also Trueman, 1983). In addition, a low level of radial muscle fiber EMG activity was often observed, suggesting that the radial muscles may contribute to refilling by increasing the rate of refilling.

Respiratory movements of the mantle occur in the anterior half of the mantle (Packard and Trueman, 1974). Two patterns of muscular activity are observed during respiratory movements. In one pattern, radial muscle activity is observed during mantle expansion but no muscle activity is observed as water is expelled, suggesting that the radial muscles are antagonized by mantle elasticity. In the other pattern, circular muscle activity is observed as water is expelled and reexpansion is caused by mantle elasticity (Gosline et al., 1983). Connective tissue fibers therefore play an important role in the muscular-hydrostatic system of the squid mantle and may actually provide antagonism for the musculature.

C. Squid Arms and Tentacles

Squid and cuttlefish capture and subdue live prey with an array of 10 muscular appendages. One pair of appendages, termed tentacles, are used to capture prey by rapid elongation, while the remaining four pairs of appendages, termed arms, subdue and orient the captured prey with bending and grasping movements. The tentacles are elongated with remarkable rapidity during prey capture, reaching the prey in as little as 15 msec (Kier, 1982; Messenger, 1968, 1977). The terminal portion of the tentacle, the "club," is equipped with suckers that attach to the prey and allow the

tentacles to withdraw the prey within reach of the arms. The arms then subdue the prey and orient it for ingestion with bending and grasping movements using suckers present on the oral surface of the arms (surface facing the mouth). In addition to elongation and shortening of the tentacles and bending movements of the arms, torsional movements in either direction have been observed in both appendage types in *Sepioteuthis sepioidea* (Blainville), *Loligo pealei* (LeSueur), *Loligo plei* (Blainville), and *Lolliguncula brevis* (Blainville) (Kier, 1982). The following is an outline of the arrangement of the musculature of the arms and tentacles and a summary of its possible functional role in movement. The same arrangement of musculature has been observed in *Sepioteuthis sepioidea* (Blainville), *Loligo opalescens* (Berry), *Loligo media* (Linné), *Illex illecebrosus* (LeSueur), *Lolliguncula brevis* (Blainville), and *Sepia officinalis* (Guérin, 1908, Kier, 1982, 1983).

The tentacular stalk is made up of closely packed muscle fibers that are present in a variety of orientations shown schematically in Fig. 8. The
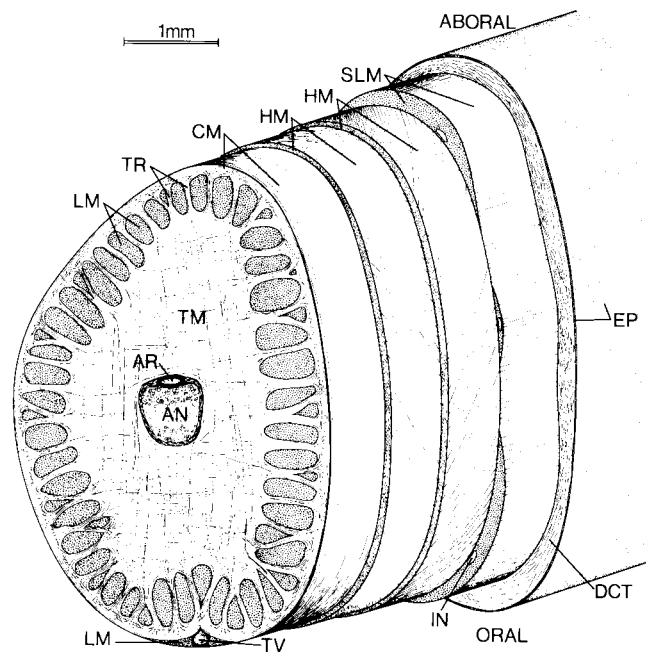

Fig. 8. Schematic diagram of left tentacular stalk of a loliginid squid. AN, Axial nerve cord; AR, artery; CM, circular muscle; DCT, dermal connective tissue; EP, epithelium; HM, helical muscle; IN, intramuscular nerve cord; LM, longitudinal muscle; SLM, superficial longitudinal muscle; TM, transverse muscle; TR, trabeculae of transverse muscle; TV, superficial tentacular vein. [From Kier (1982), with permission of the publisher.]

axial nerve cord and associated artery run longitudinally down the central axis of the tentacle and are surrounded by an extensive mass of transverse muscle fibers. Muscle fibers within the transverse mass are oriented perpendicularly to the long axis of the tentacle. Bundles of longitudinal muscle fibers are situated around the periphery of the tentacle. Groups of muscle fibers from the transverse muscle mass radiate between the longitudinal muscle bundles and flare out into a layer of circular muscle. The groups of transverse muscle fibers running between the longitudinal muscle bundles are termed trabeculae (Graziadei, 1965). The circular muscle layer is wrapped by two thin muscle layers made up of helically oriented muscle fibers. The two helical layers are opposite in handedness, and their fiber angle (the angle a muscle fiber makes with the long axis of the tentacle) varies with the degree of extension of the tentacle from a maximum of ~67° measured in a retracted tentacle to a minimum of ~36° in an extended tentacle (*Loligo pealei*). The helical muscle layers are, in turn, surrounded by a layer of superficial longitudinal muscle (Kier, 1982).

The possible functional role of the musculature of the tentacular stalk in producing elongation, shortening, and torsion is as follows. As in other muscular-hydrostatic systems, the volume of the tentacle can be considered to be essentially constant at physiological pressures. Contraction of the extensive transverse muscle mass and associated circular muscle layer will cause a decrease in the cross section of the tentacle. If the tentacle is constant in volume, then any decrease in cross section must result in elongation of the tentacle. Thus, the transverse and circular muscle masses probably are responsible for elongation. It is likely that shortening of the tentacle is brought about by contraction of the longitudinal muscle bundles that run the length of the tentacle (Kier, 1982).

As discussed earlier, the relation between the diameter and length of a cylinder of constant volume may provide a muscular-hydrostatic system with a mechanism for mechanical amplification analogous to leverage. An analysis of the relation between the diameter and length of a constant-volume cylinder with an initial length–diameter ratio and elliptical cross section that approximate those of the tentacular stalk was performed (Kier, 1982). This analysis revealed that a 70% elongation (a typical elongation observed in prey capture by the tentacles) results from only a 23% decrease in width. This relation could have important implications for the function of the circular and transverse muscles of the tentacles, because it implies that the displacement and speed of their contraction is amplified and may therefore be important in producing the rapid and considerable elongation of the tentacles observed (Kier, 1982; Kier and Smith, 1985).

Torsion of the tentacles in either direction was often observed during prey capture. The two helical muscle layers are probably responsible for creating torsion. The direction of torsion depends on the handedness of
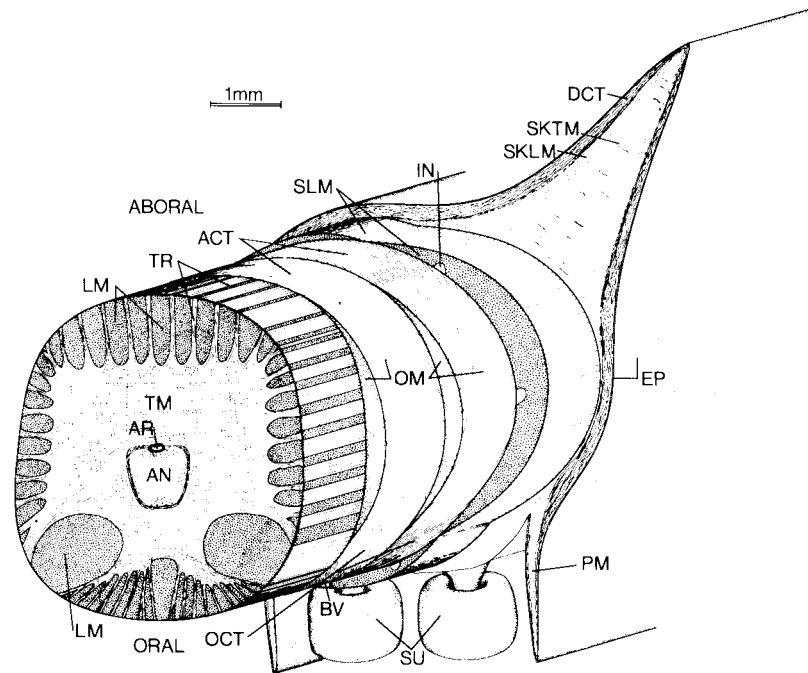
Fig. 9. Schematic diagram of left arm of a loliginid squid. ACT, Aboral connective tissue (fibrous); AN, axial nerve cord; AR, artery; BV, superficial brachial vein; DCT, dermal connective tissue; EP, epithelium; IN, intramuscular nerve cord; LM, longitudinal muscle; OCT, oral connective tissue (fibrous); OM, oblique muscle; PM, protective membrane; SKLM, swimming keel longitudinal muscle; SKTM, swimming keel transverse muscle; SLM, superficial longitudinal muscle; SU, suckers; TM, transverse muscle; TR, trabeculae of transverse muscle. [From Kier (1982), with permission of the publisher.]

the helical muscle layer contracting. Antagonism of each helical muscle layer is provided by the other layer (Kier, 1982).

Figure 9 is a schematic view of the anatomy of the musculature of the arm. A central core of transverse muscle surrounds the axial nerve cord. As in the tentacle, the muscle fibers of the transverse muscle mass are oriented perpendicularly to the long axis of the arm. The transverse muscle fibers extend out in trabeculae to insert orally and aborally on fibrous connective tissue sheets and laterally on connective tissue lining the inner member of a pair of oblique muscles on each side of the arm. Longitudinal muscle fibers run in bundles between the trabeculae formed by the transverse muscles. The pair of oblique muscles each insert on the oral and aboral connective tissue sheets. Connective tissue fibers in the sheets are

in a crossed-fiber arrangement with a fiber angle (angle that a fiber makes with long axis of the arm) of ~72° (*Loligo pealei*). The oblique muscle pairs are opposite in handedness and are composed of muscle fibers with the same fiber angle as the connective tissue fibers of the oral and aboral sheets to which they are attached. Surrounding the oblique muscles and connective tissue sheets are superficial longitudinal muscle fibers (Kier, 1982).

Bending movements and torsional movements of the arms have been observed (Kier, 1982). Bending presumably results from selective contraction of longitudinal muscles on the side of the arm representing the concave radius of the bend. As outlined earlier, the longitudinal compressive force created by this unilateral longitudinal muscle contraction must be resisted, otherwise the arm will be shortened with little or no bending. The transverse muscle mass of the arm is arranged such that it could provide this resistance to longitudinal compression. Contractile activity of the transverse muscle fibers will resist the increase in diameter that must result from longitudinal compression of this constant volume structure. It is likely, therefore, that bending of the arms involves contractile activity of both the transverse muscle mass and longitudinal muscles on one side of the arm. The location of the large longitudinal muscle masses on the oral side of the arm is interesting in this context, because forceful bending of the arms orally is important in handling and subduing struggling prey during ingestion (Kier, 1982). The oblique muscles are probably responsible for torsional movements of the arms. The oblique muscles and the connective tissue sheets to which they are attached can be considered to be two helical systems of opposite handedness. Each system is a composite of connective tissue fibers alternating with muscle fibers. Contraction of the muscles of the composite results in torsion of the arm, and the direction of torsion depends on the handedness of the composite (Kier, 1982).

The descriptions of the muscular morphology of the arms and tentacles above (compare Figs. 8 and 9) show a number of similarities, in particular with respect to the arrangement of the transverse muscle mass. In spite of the similarity in arrangement, the functional proposals outlined above suggest that the transverse muscle masses of the arms and tentacles are serving different functional roles: the transverse muscles of the tentacle probably create rapid extension of the tentacles during prey capture while the transverse muscles of the arm are involved in bending movements. This paradox can be explained by examination of the ultrastructure of the transverse muscle masses of the arms and tentacles (Kier, 1985). Muscle cells of the transverse muscle mass of the arms (*Loligo pealei, Illex illecebrosus*) are obliquely striated, the most prevalent muscle type in cephalo-

pods (Amsellem and Nicaise, 1980; Hanson and Lowy, 1960; Hoyle, 1964; Nicaise and Amsellem, 1983). The muscle cells of the transverse and circular muscle masses of the tentacle, however, are cross-striated. The difference in ultrastructure has important physiological implications, because the shortening speed of molluscan cross-striated muscles is typically higher than that of molluscan obliquely striated muscles (Millman, 1967). Structural parameters of the cross-striated muscle fibers also suggest that these muscle fibers have a high shortening speed relative to other cross-striated muscles (Kier, 1985). Thus, in spite of the difference in function, the similarity in arrangement of the transverse muscles of the arms and tentacles is understandable because of the difference in the muscle fiber types of these muscle masses.

D. Octopus Arms

Octopuses possess four pairs of arms that project from the head and encircle the mouth. The arms are tapered, muscular organs and (in species of *Octopus*) are equipped on their oral surface with a double row of unstalked suckers. Octopuses use their arms for locomotion, prey capture, rejection of unwanted objects, and sensory functions (Wells, 1978). The arms are capable of a remarkable range of movements including elongation, shortening, and bending in any plane. Observations of *Octopus joubini* and *Octopus bimaculoides* suggest that bending may occur either sharply at one point on the arm or gently over the entire length. In addition, bending is not restricted to a single location and can occur at any position along the arms. Torsional movements of the arms are also common and can occur in either direction. Bending and torsion are sometimes produced simultaneously, creating a helical configuration of the arms, particularly in the terminal portions (Kier, 1983).

The following summary of the arrangement and function of the muscles of the octopus arm is taken from histological examination of the microanatomy of the arms of *Octopus bimaculoides* and *Octopus joubini* (Kier, 1983). Similar muscular anatomy has been reported for *Octopus vulgaris* and *Eledone moschata* by Colasanti (1876) and Guérin (1908). The muscles of the arms can be divided into three groups: (1) the intrinsic muscles of the sucker, (2) the acetabulobrachial muscles linking the sucker and arm musculature, and (3) the intrinsic muscle of the arms (Graziadei, 1971). The intrinsic musculature of the arms and its possible role in creating the observed movements will be discussed here.

Figure 10 is a schematic diagram of an octopus arm. The axial nerve cord and an associated thick-walled artery are arranged on the central axis of the arm and are surrounded by the transverse muscle mass. This
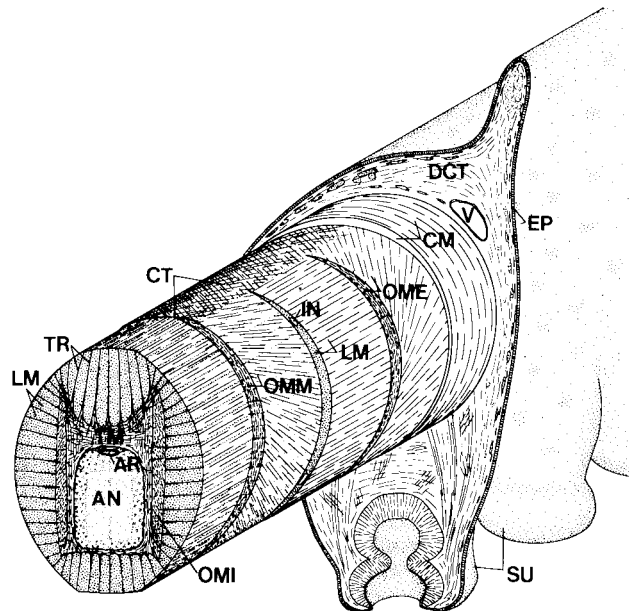
Fig. 10. Schematic diagram of the arm of *Octopus*. AN, Axial nerve cord; AR, artery; CM, circumferential muscle; CT, connective tissue sheath; DCT, dermal connective tissue; EP, epidermis; IN, intramuscular nerve; LM, longitudinal muscle; OME; external oblique muscle; OMI, internal oblique muscle; OMM, median oblique muscle; SU, sucker; TM, transverse muscle; TR, trabeculae; V, vein.

muscle mass is thickest aborally above the axial nerve cord, of intermediate thickness laterally on each side of the nerve cord, and thinnest orally beneath the nerve cord. Muscle fibers within the transverse muscle mass are tightly packed and oriented perpendicularly to the long axis of the arm. The transverse muscle bundles extend out from the center in trabeculae in between peripheral bundles of longitudinally arranged muscle fibers. The trabeculae running orally and aborally insert directly on a fibrous connective tissue sheath that encloses most of the intrinsic musculature and is especially thick orally and aborally. The trabeculae of the transverse muscle mass extending laterally pass through three oblique muscle layers (discussed below) before inserting on the thin lateral portion of a connective tissue sheath. The trabeculae branch as they pass through the oblique muscle layers (Kier, 1983; Tittel, 1961, 1964).

The octopus arm is equipped with three sets of oblique muscle layers; the internal oblique muscles, the median oblique muscles, and the external

oblique muscles. In all three oblique muscle pairs, the handedness of one side of the pair is opposite that of the other. For example, the external oblique muscle on one side is arranged as a subset of a right-handed helix, while the external oblique muscle on the opposite side is arranged as a subset of a left-handed helix. In addition, the three layers on the same side do not all have the same handedness. The handedness of the external oblique muscle layer is opposite to that of the median oblique muscle layer but the same as the internal oblique muscle layer. The external and median oblique muscle layers are separated from one another by a crescent-shaped layer (when viewed in transverse section) of longitudinal muscle and insert on the oral and aboral connective tissue sheets. The fiber angle of the connective tissue fibers and oblique muscles in a relaxed octopus arm is ~60°. A thin layer of circumferentially arranged muscle fibers covers the aboral surface of the intrinsic musculature. The circumferentially arranged muscle layer is thickest aborally and thinner laterally.

The muscle cells of the intrinsic musculature of the arm of *Octopus joubini* and *Octopus bimaculoides* have the appearance in the light microscope of obliquely striated muscle fibers. A central core, presumably of mitochondria, is surrounded by myofilaments that show a banded appearance in transverse sections at high power. Obliquely striated muscle has been found by Socastro (1969) and Gonzalez-Santander and Socastro Garcia-Blanco (1972) in electron-microscopic studies of the arm musculature of *Octopus vulgaris* and *Eledone cirrhosa*.

The muscular-hydrostatic system of the octopus arm shows many similarities to the arms and tentacles of squid and cuttlefish discussed previously, and proposals for the functional role of the musculature are similar. As in the squid tentacle, the transverse muscle fibers are probably responsible for elongation, because their contraction would decrease the cross section of this constant-volume structure and therefore increase its length. Shortening is presumably caused by contraction of the longitudinal muscles of the arm. The longitudinal muscle may also be involved in bending movements. As discussed earlier, bending may be caused by unilateral longitudinal muscle contraction in association with contractile activity of muscle capable of resisting longitudinal compression; in this case, the transverse muscle mass. Thus, in the octopus arm, the same musculature may create both changes in length and bending movements depending on the sequence of contractile activity. The variety of bending movements observed, from a slight bend of the entire arm to localized sharp bends at any point along the arm, is an example of the local control of movement possible in a muscular-hydrostatic system.

Torsional movements of the arms are likely the result of contraction of the oblique muscle layers. The median and external oblique muscle layers

in conjunction with the oral and aboral connective tissue sheaths represent a composite helical connective tissue–muscle array similar to that discussed earlier in the squid arm. This array represents both a right-handed and a left-handed helical system, and could therefore provide a torsional force in either direction. The median and external oblique muscles are peripherally arranged in the arm musculature and therefore have a larger torsional moment available through which to apply torque than a more central location. In this regard, the functional role of the inner oblique muscles is perplexing. Although they could apply a torsional force, their central location makes them less effective than the more peripheral median and external oblique muscles.

E. Bivalve Siphon: Scrobicularia plana

The siphons of the bivalve Scrobicularia plana (Tellinacea) are used in deposit feeding and show considerable extensibility and mobility. Elongation of the siphons of S. plana has been shown to involve both a muscular-hydrostatic and a hydraulic mechanism. Chapman and Newell (1956) found that initial elongation involves contraction of the musculature of the wall of the siphon. Further elongation is the result of pumping water into the siphons from the mantle cavity by slight adductions of the valves (Hodgson and Trueman, 1981).

The inhalant and exhalant siphons of Scrobicularia are separated throughout their length; a diagrammatic view of their microanatomy is shown in Fig. 11 (Chapman and Newell, 1956; Yonge, 1949). Underneath the epithelium of the exterior of the siphon is a thin layer of collagen fibers (orientation not stated), and beneath this is a thin layer of longitudinal muscle fibers. Chapman and Newell (1956) reported that beneath the longitudinal muscle layer is a thick layer of collagen fibers (with a few intermingled muscle fibers) that appear in cross sections of contracted siphons to be arranged as a latticework, whereas in cross sections of elongated siphons the fibers appear circular in arrangement.

In a subsequent study, Hodgson and Trueman (1981) stated that they identified a much larger proportion of muscle fibers within this layer, in particular at the tips of the siphons. They therefore referred to this layer as a circular muscle layer rather than a connective tissue layer. They noted tissue surrounding the muscle fibers that they suggest is collagen because it stains blue in trichrome stain. This layer probably contains a significant proportion of circularly arranged connective tissue fibers, because pressure applied to anesthetized, ligated siphons causes the siphons to elongate but not to increase in diameter (Hodgson and Trueman, 1981). Beneath this layer are two thick layers of longitudinal muscle that are
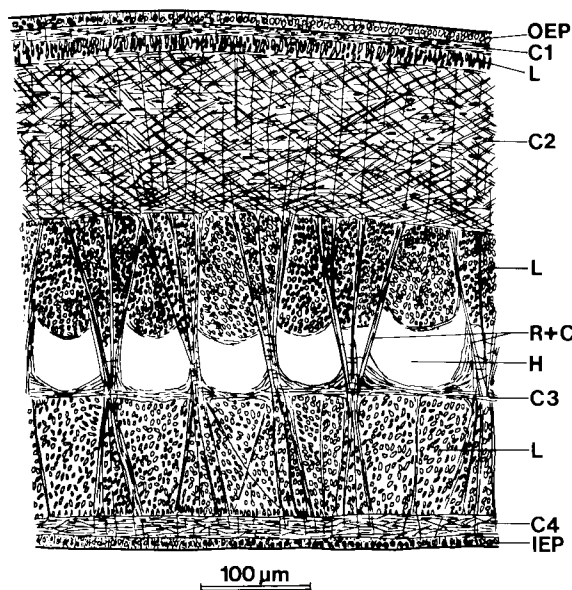
Fig. 11. Diagram of transverse section of siphon wall of *Scrobicularia plana* in a partly contracted state. C1, Outer collagen layer; C2, thick collagen layer with muscle fibers; C3, third collagen layer; C4, innermost collagen layer; H, hemocoel; IEP, inner epithelium; L, longitudinal muscle; OEP, outer epithelium; R+C, radial muscle fibers and collagen fibers. [After Chapman and Newell, (1956).]

separated from one another by a hemocoelic space and a thin layer of collagen fibers. Radially arranged muscle and collagen fibers cross the two thick longitudinal muscle layers. The radial collagen fibers extend beyond the longitudinal muscle layers to insert on the epithelium of the siphonal canal and the outer epithelium. Inside the longitudinal muscle layers is an additional thin layer of collagen fibers covered by the epithelium that lines the siphonal canal (Chapman and Newell, 1956).

Initial elongation of the siphons occurs smoothly, with the tips of the siphons open. Chapman and Newell (1956) and Green (1967) observed that the tips of the siphons remained open until the siphons were extended to lengths of 10–12 cm. Hodgson and Trueman (1981), however, did not observe the tips of the siphons to remain open beyond lengths of 2 cm. It is thus difficult to be certain of the importance of this initial elongation in producing the total elongation of 20–25 cm (shell length 4 cm) observed by Hodgson and Trueman (1981).

The initial elongation will occur even if one valve is removed, and Chapman and Newell (1956) therefore concluded that it cannot be due to

water being pumped by muscular activity of the adductors from the mantle cavity into the siphonal canal. Chapman and Newell (1956) also rejected the hypothesis that elongation of the siphons is due to pumping of blood by the heart into the coelomic spaces of the siphonal wall, because siphonal elongation occurs even if the heart is removed. They therefore suggested that the intrinsic musculature of the siphons is responsible for elongation and noted a number of observations that support this hypothesis. A siphon can still elongate, even if it is removed from the animal or a ligature is placed around its base. In addition, elongation and shortening can occur simultaneously in different regions of the siphon. Finally, the walls of the siphon become thinner during elongation. If the walls of the siphons are constant in volume, then the decrease in thickness accompanying increase in length can be predicted theoretically and compared with actual measurements taken from elongating siphons and sections of siphons fixed at various states of elongation. Chapman and Newell (1956) found that the correspondence between actual and theoretical dimensional changes was close enough to support the view that the walls are indeed constant in volume.

Chapman and Newell (1956) suggested therefore that initial elongation of the siphons occurs as a result of contraction of the radial muscles of the wall of the siphon. The thick layer of circularly arranged collagen and muscle fibers allows thinning of the wall and enlargement of the lumen, but does not allow an increase in the overall diameter of the siphon. Because the siphon wall is constant in volume and constant in external diameter, any decrease in thickness caused by contraction of the radial muscle fibers must result in elongation. In order for the walls to be maintained at a constant volume, blood in the hemocoelic spaces of the siphon wall must be prevented from escaping into the general circulation. Hodgson and Trueman (1981) stated that no valves are found in the hemocoelic spaces at the base of the siphons and suggested that the circular muscles at the base may contract to prevent loss of blood from the hemocoelic spaces into the general circulation. It is also likely that the size of the hemocoelic spaces observed in paraffin sections is exaggerated, because considerable shrinkage of the musculature is apparent in the published micrographs (Chapman and Newell, 1956).

After initial elongation, further extension of the siphons occurs with the tips of the siphons closed. Water is pumped from the mantle cavity into the siphonal lumen at low pressure (0.3–0.4 kPa) by small valve adductions, extending the siphons in a stepwise manner by 0.5–1.5 cm at each step. The ventral mantle margins come together to keep the mantle cavity watertight during valve adductions. Experiments on anesthetized, isolated siphons show that elongation occurs more rapidly if the pressure is

applied intermittently (as it is in the animal) rather than constantly. In addition, the siphons do not shorten if the pressure is removed, suggesting that shortening of the siphons is a result of contraction of the longitudinal musculature only (Hodgson and Trueman, 1981).

The siphons of *Scrobicularia plana* are also capable of bending movements that occur when the siphons are used in deposit feeding. Hodgson and Trueman (1981) suggested that bending of the siphons will result from contraction of the longitudinal muscles on one side of the siphonal wall and relaxation of the longitudinal muscle in the opposite wall. As discussed above for bending movements in other muscular-hydrostats, it is likely that the radial muscles of the siphon wall are also involved in bending movements, because they can resist the increase in siphonal wall thickness that must result from the longitudinal compressional force created by the longitudinal muscles. Bending may therefore involve both contraction of longitudinal muscle on one side of the siphon and contraction of the radial musculature on the opposite side. The rather sharp bends of the siphons illustrated by Hughes (1969) may be the result of localized contraction of the radial muscles of the siphon wall on the outer radius of the bend with simultaneous contraction of the longitudinal muscles of the opposite wall. The arrangement of musculature of the siphonal walls may thus allow local control of movement not possible in a hydrostatic system with large fluid-filled cavities.

F. Gastropod Foot

Many gastropods use muscular waves of the pedal sole for locomotion (Clark, 1964; Elves, 1961; Lissmann, 1945a,b; Miller, 1974; Morton, 1964; Trueman, 1975, 1983; Trueman and Jones, 1977; Vlés, 1907). Support for this movement and antagonism of the musculature is provided by a hydrostatic skeletal support system. The relative proportion of the foot occupied by muscle and fluid-filled hemocoelic spaces varies widely. Tightly packed pedal musculature has been reported for the limpet *Patella vulgata* (Trueman and Jones, 1977) and the marine snails *Thais rustica* and *Neritina reclivata* (Gainey, 1976). Voltzow (1985) reported an intermediate level of packing in the pedal musculature of *Busycon contrarium*, and more loosely packed musculature was observed in the pedal sole of the terrestrial pulmonates *Agriolimax reticulatus* and *Ariolimax columbianus* (Denny, 1981; Jones, 1973). (Much more extensive fluid-filled cavities are seen in the foot of several burrowing gastropods; see section IV.) Although a range of muscle packing and hemocoelic space is seen in the pedal musculature of gastropods, J. Voltzow (personal communication) suggests that much of the hemocoelic space described in earlier studies is
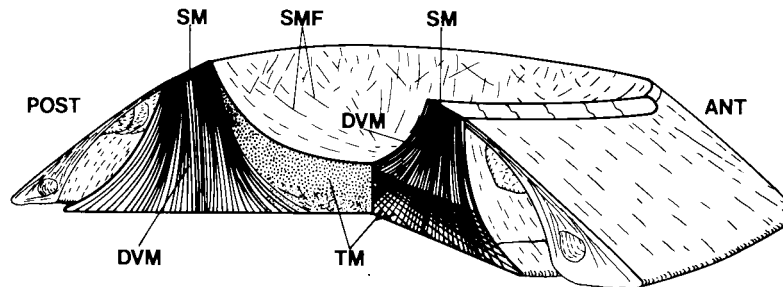
Fig. 12. Schematic diagram of foot and mantle of *Patella* showing the orientation of the muscle fibers of the foot. ANT, Anterior; DVM, dorsoventral muscle; POST, posterior; SM, shell muscle; SMF, shell muscle fibers visible through the floor and side of the visceral cavity; TM, transverse muscle. [After Jones and Trueman (1970).]

an artifact of paraffin processing for sectioning. Tightly packed three-dimensional arrays of pedal musculature may thus be more common in gastropods than previously realized. Emphasis has been placed previously on the role of the pedal hemocoel in the production of pedal waves (Trueman, 1983), and this discussion will therefore focus on the production of pedal waves in tightly packed pedal musculature.

Jones and Trueman (1970) investigated the production of locomotory waves in the foot of the limpet *Patella vulgata* L. in relation to the anatomy of the musculature of the foot. They divided the muscle fibers of the foot into four categories of orientation (Fig. 12). The first category consists of dorsoventral muscles that originate on the shell and insert on the epithelium of the foot on the same side of the animal as their origin and at a right angle to the sole. Dorsoventral muscle accounts for 70% of the foot musculature. The second category consists of transverse muscles that originate on the shell and cross to the opposite side of the body to insert on the sole and lateral margin of the foot. The transverse muscle fibers run from their origins as a compact layer that forms the ventral boundary of the visceral sinus and crosses at the midline of the foot with the transverse muscles from the opposite side. After crossing the midline, the transverse muscle fibers spread out to insert on the sole and lateral margin of the foot. The transverse muscles constitute 25% of the pedal musculature.

The third category consists of longitudinal muscle fibers. Some of the longitudinal muscle fibers originate near the anterior margin of the shell muscle and insert on the posterior margin of the foot, while others originate near the posterior margin of the shell muscle and run to the anterior margin of the foot. No longitudinal muscle fibers are seen immediately above the sole. The fourth category consists of spiral muscles that run in

both right- and left-handed helixes from their origin on the shell to their insertion on the pedal sole. The spiral muscles run as compact bundles from their origin and spread out before inserting on the sole. The longitudinal and spiral muscles together constitute only 5% of the musculature of the foot. The foot has very little hemocoelic space. In fact, spherical "spaces" in a thin region above the epithelium of the sole that were originally suggested to be hemocoelic spaces by Jones and Trueman (1970) have now been identified to be mucopolysaccharide-secreting glands (Grenon and Walker, 1978, 1982). Histochemical tests (orcinol–new fuchsin) did not reveal elastic tissue within the foot of *Patella* (Jones and Trueman, 1970; Trueman, 1969). The musculature of *Patella vulgata* was briefly described by Davis and Fleure (1903) and the musculature of the foot of *Patella coerula* L. by Rotarides (1945). Both descriptions are similar to that of Jones and Trueman (1970).

Patella uses retrograde ditaxic pedal locomotory waves for forward movement. [As originally proposed by Vlés (1907), locomotor waves that pass along the sole of the foot in the opposite direction to the movement of the animal are classified as retrograde waves. Two parallel systems of waves on the foot are classified as ditaxic.] As a retrograde wave passes, the sole of the foot in the wave is elongated in an anterior–posterior direction. Jones and Trueman (1970) suggested that the sole of the foot is lifted off the substratum as the wave passes. A study by Denny (1981) on the role of mucus in locomotion of a terrestrial slug showed that very little lifting occurs, and thus the lifting of the foot of *Patella* should perhaps be reexamined in the light of this study (Trueman, 1983). Although the sole is elongated in an anterior–posterior direction in each wave, it does not increase in width. In fact, a slight narrowing of the foot occurs as each wave passes (Jones and Trueman, 1970). The transverse muscles probably control the width of the foot. Anterior–posterior elongation of the sole in the wave is thought to be a result of contraction of the dorsoventral muscles of the foot (Jones and Trueman, 1970; Trueman, 1969, 1975, 1983). The musculature of the foot is essentially constant in volume. Dorsoventral muscle contraction decreases the vertical dimensions of the foot and, because lateral expansion does not occur, must therefore longitudinally extend the sole in the wave. The elongation of the anterior margin of the foot at the start of a pedal wave is probably brought about by a similar mechanism.

Because longitudinal muscle fibers are not present in the sole of the foot, anterior–posterior compression of the sole and reextension of the dorsoventral muscles after a wave passes must occur by some other means. Jones and Trueman (1970) suggested that contraction of the dorsoventral muscles created an increase in pressure in the hemocoelic

"spaces" of the foot. The increased pressure was thought to be responsible for reextending the dorsoventral muscles of the foot at the trailing edge of the wave. As mentioned earlier, hemocoelic spaces are not present in the sole. The absence of hemocoelic spaces in the sole suggests that the foot of *Patella* may function as a muscular-hydrostat and requires a slight modification of the proposal for reextension of the dorsoventral muscles. The modification does not affect the proposal that the force for reextending the dorsoventral muscle fibers at the trailing edge of the wave is transferred from the contracting dorsoventral muscle fibers at the leading edge of the wave, and the dorsoventral muscles therefore antagonize one another (Trueman, 1969, 1975, 1984). Reextension of the dorsoventral muscles at the trailing edge of the wave can be visualized if the passage of a wave is considered with reference to the forces developed in the wave. The pedal sole on either side of the wave is fixed in position relative to the substratum. The anterior–posterior elongation of the sole caused by contraction of the dorsoventral muscles at the leading edge of the wave will exert a longitudinal compressional force on the sole at the trailing edge of the wave. The now-relaxed muscle fibers in the zone at the trailing edge of the wave will be reextended because the longitudinal compressional force will shorten the sole (anterior–posteriorly) in this zone, and—because the tissue is constant in volume and cannot expand laterally—the vertical dimension must increase, thereby reextending the dorsoventral muscle fibers.

The spiral or helical muscles of the foot probably rotate the shell of *Patella* relative to the foot. Jones and Trueman (1970) noted that *Patella* exhibits a defense reaction to predators that involves, in part, rotation of the shell as much as 90°. Citing Weber (1926), they suggested that the spiral muscles are responsible for rotating the shell. The presence of both left- and right-handed helical or spiral muscles allows rotation to be produced in either direction and, in addition, provides for muscular antagonism.

G. Other Examples of Muscular-Hydrostats

Structures with tightly packed three-dimensional arrays of muscle are a common and perhaps characteristic feature of molluscs. In addition to the variety of examples presented above, a brief discussion of other molluscan structures that may also be examples of muscular-hydrostats is presented below.

Structures that consist of tightly packed three-dimensional arrays of muscle are especially common in cephalopods. The mantle of *Octopus vulgaris* is made up of muscle fibers arranged in three orientations: circu-

lar, radial, and an outer longitudinal layer (Wilson, 1960). The function of the circular and radial musculature in respiratory mantle movements and escape jetting in *Octopus* is probably similar to that described earlier for squid and cuttlefish, although it is not known whether elastic energy storage occurs in the mantle of octopuses. In addition, mantle length is probably controlled by the longitudinal muscle layer rather than by connective tissue fiber tunics such as those seen in the mantle of squid and cuttlefish.

The retractor muscles of the head and funnel of squid (*Loligo pealei*) provide another example, as they are made up of longitudinal muscle fibers that are divided up into blocks by transverse muscle fibers arranged perpendicularly to the long axis of the retractor muscle masses (Young, 1938). Muscle fibers in these two orientations can presumably antagonize one another and thereby cause both elongation and shortening of the retractor muscle masses. A similar situation obtains in the head retractor and funnel muscles of *Nautilus macrocephalus*, described by Packard et al. (1980) as being made up of muscle fibers running in all three planes.

The musculature of the lateral fins of squid provides yet another example. The fins of *Loligo pealei* are composed of tightly packed muscle fibers in three orientations enclosed between three connective tissue fasciae. Two of the fasciae form the upper and lower surfaces of the fin, and the third lies between them in the middle of the fin. Longitudinal muscles are arranged in thin sheets on the upper and lower surfaces of the middle fascia and extend parallel to the base of the fin from one free edge of the fin to the other. Thick transverse muscle bundles are arranged perpendicularly to the base of the fin and parallel to the surface of the fin. The transverse muscle bundles are sandwiched between the middle and superficial fasciae and thus form an upper and lower layer of transverse muscle bundles. Between the transverse muscle bundles are vertical muscle fibers that extend from the middle to the upper and lower fasciae and form partitions between the transverse muscles extending from the base to the free edge of the fin (Williams, 1909). Although the function of the various muscle fiber orientations in the production of fin movements has not been studied, it is likely that the muscles can antagonize one another in a manner similar to that described for other muscular-hydrostats. The arrangement of muscle fibers of the fin in vertical, transverse, and longitudinal directions allows control of all dimensions of this constant-volume structure. As the fin is bent up and then down, presumably by contraction of the upper and then lower transverse muscles, the length and thickness of the fin could be controlled by the longitudinal and vertical muscles. Details of the function of the muscles of the fin in production of fin movements deserve further study.

The suckers of many cephalopods are also made up of tightly packed muscle fibers (Girod, 1884; Guérin, 1908; Niemiec, 1885; Nixon and Dilly, 1977; Williams, 1909). The details of the arrangement of the musculature in the various types of stalked and unstalked suckers are beyond the scope of this review, but several generalizations can be made. Two muscle fiber orientations are usually seen in the wall of the sucker: radial and circular. The radial muscles run from the inner to the outer surface of the sucker. The circular muscles may be arranged around the sucker as a distinct sphincter muscle and/or as numerous small muscle bundles. It is likely that the radial muscles produce suction because their contraction would result in a thinning of the sucker wall with a resultant increase in the volume of the acetabulum or chamber of the sucker. The circular muscles may antagonize the radial muscles because circular muscle contraction would cause thickening of the sucker wall and a decrease in the volume of the acetabulum. Suckers attached to the arms and tentacles with muscular stalks are seen in many sepioids and teuthoids (Guérin, 1908; Nixon and Dilly, 1977; Williams, 1909). The sucker stalks of *Loligo pealei* are made up of longitudinal muscles divided up into bundles by transverse muscle fibers (Williams, 1909) and thus probably also function as muscular-hydrostats. The suckers of many gymnosomatous pteropods are also made up of tightly packed radial muscle fibers and may function in a manner similar to those of cephalopods (Lalli, 1970; Meisenheimer, 1905).

Yet another example of a muscular-hydrostatic system is seen in the digital tentacles of the chambered nautilus, *Nautilus pompilius*. Each tentacle consists of an extensible muscular cirrus that can be retracted completely into a protective sheath. The cirri are approximately cylindrical and are equipped on the oral side with adhesive annular ridges that aid in attachment to surfaces and seizure of food. The cirri are capable of considerable elongation (up to 100%), shortening, bending movements in any plane, and torsional movements in both directions (Kier, 1987).

Three orientations of muscle fibers are seen in the digital cirri of *Nautilus:* radial, longitudinal, and oblique (Fernandez, 1907; Griffin, 1900; Kier, 1987; Owen, 1843; Willey, 1897). The radial muscle fibers are oriented perpendicularly to the long axis of the cirrus and extend radially from a central meshwork of muscle fibers and branch to insert on connective tissue immediately beneath the epidermis. Longitudinal muscle fibers are located around the central meshwork of radial muscle fibers. As the radial muscle fibers extend out from the center, they divide the surrounding longitudinal muscle fibers into bundles. A layer of oblique muscle fibers is located on each side of the cirrus, overlying the longitudinal muscles. The handedness of the oblique muscle fibers on one side of the

cirrus is opposite to that of the oblique muscle fibers on the opposite side of the cirrus (Kier, 1987).

Elongation of the cirrus is probably caused by contraction of the radial muscle fibers. The retracted length–width ratio is high, approximately 25 : 1, and suggests that mechanical amplification of radial muscle contraction (see Fig. 1) may be important in creating the elongation observed. Shortening is presumably brought about by longitudinal muscle contraction. Bending movements are probably created in a manner similar to that discussed earlier and involve unilateral contraction of longitudinal muscle in consort with contractile activity of the radial muscle. As in the octopus arm, the same musculature can create changes in length and bending movements by simply altering the sequence of contractile activity. Finally, torsional movements of the cirri probably result from contraction of the oblique muscle fibers. The direction of torsion once again depends on the handedness of the contracting oblique muscle fibers (Kier, 1987).

In addition to the columellar system of gastropods, other gastropod structures show muscular arrangements that suggest that they may function as muscular-hydrostats. For example, the extensible cephalic tentacles of *Haliotis tuberculata* are described by Crofts (1929) as being composed of both longitudinal and transverse muscle bundles. The transverse muscle bundles are oriented perpendicularly to the long axis of the tentacle and branch as they pass between the longitudinal muscles. Elongation of the tentacles may result from transverse muscle contraction. Retraction is probably caused by longitudinal muscle contraction (Crofts, 1929). Another possible example is seen in the penis of *Oliva peruviana,* which is described by Küttler (1913) as being an especially muscular structure. Küttler (1913) describes three orientations of tightly packed muscle fibers in the penis: circular, transverse, and longitudinal. The longitudinal muscle is divided into bundles by the transverse and circular muscle fibers. The circular muscles are arranged as two thin layers around the circumference and are separated from one another by longitudinal muscle fibers. The movements of the penis and the functional role of the musculature are not described by Küttler (1913), but the arrangement of the muscle suggests that the penis too may function as a muscular-hydrostat. The foot of a variety of chitons has been reported to be made up of a three-dimensional array of musculature (Henrici, 1912; Plate, 1897; Sampson, 1895). Muscle fiber orientations of the foot include dorsoventral, transverse, longitudinal, and oblique fibers (Sampson, 1895). A three-dimensional array of musculature is also seen in the mantle margin of chitons (Henrici, 1912; Sampson, 1895). It is possible that the mantle margin and foot of chitons may also function using direct muscular antagonism. Morton (1964) noted that the compressed foot of cardiacean bivalves is a tongue-

like muscular organ and suggested that the foot is deformed by antagonism between muscles within the foot.

From the examples presented above and in the previous sections, it is obvious that tightly packed three-dimensional arrays of muscle are more common in molluscs than previously recognized. These muscular-hydrostats are perhaps a characteristic of molluscs in general and certainly deserve further study.

IV. Hydrostatic Skeletons with Extensive Fluid-Filled Cavities

A variety of molluscs possess hydrostatic skeletons with extensive fluid-filled cavities unlike the muscular-hydrostats discussed earlier. These "classical" hydrostatic skeletons have received attention previously and so will be referred to only briefly here.

The fluid-filled cavities present in the foot of many burrowing molluscs serve an important function in movement during burrowing. An extensive fluid-filled cavity allows force to be transmitted over large distances in addition to allowing large-scale change in shape (Packard and Trueman, 1974). Both of these attributes are apparently important for burrowing and may explain why such cavities are often present in the foot of burrowing molluscs.

The hemocoelic cavity of the foot of bivalves serves as a hydraulic system that transmits force produced by the powerful shell adductor muscle and provides for antagonism of the muscles of the foot (Trueman, 1968a). Descriptions of the dynamics of burrowing and the anatomy of the foot musculature of a number of bivalve species are provided by Ansell and Truemen (1967), Graham (1934), Morton (1964), Trueman (1967), Trueman and Brown (1985b), and Trueman et al. (1966). An extensive fluid-filled cavity is also found in the foot of the burrowing scaphopod *Dentalium* and probably serves a similar hydraulic role in burrowing (Trueman, 1968c). A hydraulic mechanism is also used for elongation of some bivalve siphons and involves pumping of water from the mantle cavity into the siphonal canals by contraction of the shell adductor muscles (Chapman and Newell, 1956; Trueman, 1966).

The burrowing gastropod *Bullia digitalis* possesses extensive fluid-filled hemocoelic cavities in the foot that serve to transmit force during burrowing and provide for muscular antagonism (Hodgson and Trueman, 1985; Trueman and Brown, 1976). Extrusion of the proboscis of *Bullia* also involves an extensive fluid-filled hemocoelic cavity (Trueman and Brown, 1987). Other burrowing gastropods such as some members of the family Naticidae also possess extensive fluid-filled spaces, although in this

group, seawater in aquiferous tubules of the foot may supplement the blood in its hydraulic role during locomotion (Bernard, 1968; Morris, 1950; Russell-Hunter and Russell-Hunter, 1968; Trueman, 1968b).

Fluid-filled cavities are also found in many pelagic gastropods and presumably serve as a hydrostatic skeletal support system (Satterlie et al., 1985; van der Spoel, 1982). For example, the wings of many thecosomatous pteropods have muscular walls enclosing a hemocoelic space (Meisenheimer, 1905; Pafort-Van Iersel and van der Spoel, 1979). The hemocoelic fluid may inflate the wings and, once inflated, may then provide skeletal support for the musculature as the wings are bent up and down during swimming (Satterlie et al., 1985; Satterlie and Spencer, 1985).

Extensive fluid-filled cavities that may serve as a hydrostatic skeletal support system are also seen in another group of pelagic gastropods, the heteropods (Kalide, 1888; Reupsch, 1912). In many instances, however, the·fluid-filled cavities seen in pelagic molluscs such as heteropods and oceanic squid contain liquids that are less dense than seawater and therefore serve as a mechanism providing neutral buoyancy (Clarke et al., 1979; Denton and Gilpin-Brown, 1973; Denton and Shaw, 1961; Denton et al., 1969). While the fluid-filled cavities of pelagic molluscs may be utilized as a hydrostatic skeleton, it is likely that in many forms they are primarily an adaptation for the maintenance of neutral buoyancy.

The hemocoel of many pulmonate gastropods is thought to act as a hydrostatic skeleton, providing for antagonism of the musculature, support of the shell and viscera, and erection of the tentacles (Dale, 1973; Jones, 1975, 1978; Plesch et al., 1975). The musculature of the body wall of terrestrial pulmonates tends to be more strongly developed than that of aquatic forms (Plesch et al., 1975, Trappman, 1916). The difference in muscular development is thought to reflect the greater hydrostatic pressure required to support the body of the terrestrial snail (Plesch et al., 1975). In addition to maintaining hydrostatic pressure, the musculature of the body wall is probably involved in producing movements and deformations of the body (Carlson, 1905). The support for these movements is presumably provided by the enclosed body cavity that serves as the hydrostatic skeleton.

Studies of pedal locomotion in the terrestrial pulmonates *Agriolimax reticulatus* and *Ariolimax columbianus* have emphasized the importance of the pedal hemocoel in the production of locomotory pedal waves (Denny, 1981; Jones, 1973). A muscular-hydrostatic system may, however, be present in the pedal musculature of some pulmonates. Jones (1975) noted the lack of a large hemocoel in the pedal musculature of *Helix* and suggested that its absence was an artifact of fixation proce-

dures. The presence of muscle fibers in the foot oriented in all three planes suggests that muscular antagonism could be provided by the muscles themselves as outlined previously, and it thus may not be necessary that a large, fluid-filled hemocoelic cavity be present.

V. Summary and Perspectives

The overview presented in this chapter suggests that muscular-hydrostats are a widespread and general feature of molluscs. Muscular-hydrostats, hydrostatic skeletons with tightly packed three-dimensional arrays of muscle, are characterized by a number of features of mechanical significance. In muscular-hydrostats there is no extensive fluid-filled cavity, and localized muscle contraction has a localized effect because the fluid and musculature are highly partitioned. Localized muscle contraction in a hydrostatic skeleton with an extensive fluid-filled cavity has a generalized effect due to the transmission of pressure throughout the cavity. In such hydrostatic skeletons localized or differential bending will not occur. The muscular-hydrostat represents a highly partitioned system in which muscles of different orientations interact in a variety of ways. Muscles alternately support the structure and deform it. Muscles have different effects depending on the activity of antagonistic muscles. Localized, diverse, and complex movements are therefore possible and are well illustrated by the arms of squids and octopuses and the siphons of the deposit-feeding bivalve *Scrobicularia*. Many gastropod feet also exhibit the characteristics of muscular-hydrostats. The locomotory waves of the foot of gastropods such as *Patella* provide another example of the localized effect of muscle contraction in muscular-hydrostats.

Hydrostatic skeletons with extensive fluid-filled cavities are present in the foot of a variety of burrowing molluscs including burrowing bivalves, scaphopods, and gastropods. This type of hydrostatic skeleton employs a hydraulic mechanism whereby localized muscle contraction causes displacement of the hydraulic fluid, providing force for movement and muscular antagonism. A hydraulic mechanism is thought to be important for burrowing, because such a system allows the force of muscle contraction to be transmitted over large distances and allows major change in shape (Packard and Trueman, 1974). For instance, the dilation and resultant anchoring of the distal portion of a burrowing bivalve foot would not be easily accomplished with a muscular-hydrostatic system. Dilation of the tip (increase in diameter) of a muscular-hydrostatic structure would require shortening, and because of the geometric relations of a constant-volume, long and narrow foot (see Fig. 1), a relatively large decrease in

length would be required for a given increase in diameter. With a hydraulic mechanism, however, dilation of the tip occurs by displacement of fluid and once anchorage is established, shortening then occurs. The use of such a hydraulic mechanism for burrowing is not unique to molluscs and is seen in a variety of vermiform burrowers (see, e.g., Clark, 1964; Trueman, 1975).

In future studies of the musculature and hydrostatic skeletons of molluscs, particular attention should be paid to the role of connective tissue in transmitting force, limiting deformation, and providing for anisotropy of tissues. For example, the connective tissue fibers of the tunics and intermuscular fiber systems of the squid mantle play an extremely important role in the functioning of this hydrostatic system. The importance of connective tissue fibers in the functioning of many other hydrostatic skeletons has been recognized (Clark and Cowey, 1958; Clark, 1964; Cowey, 1952; Seymour, 1983), and it is likely that connective tissue serves an important role in other molluscan hydrostatic skeletons.

Investigations of the neural control of the musculature should also provide additional insight into the functioning of muscular-hydrostatic structures and organs in molluscs. As noted by Trueman and Ansell (1969), the coordination of the simple system of mutually antagonistic circular (or transverse) muscles and longitudinal muscles in invertebrates with extensive fluid-filled cavities makes relatively slight demands on the nervous system. A more complex neural organization is required, however, for muscular-hydrostats. In muscular-hydrostats, the action of a particular muscle fiber or group of muscle fibers is localized. The complex and diverse movements that characterize muscular-hydrostatic structures are made possible by the localized action of the musculature and suggest that a highly subdivided and complex neural system is present. Because little is known about the control and integration of movement of muscular-hydrostatic structures, this is therefore an important area for future research.

The commonly held belief that the functioning of a hydrostatic skeleton requires fluid-filled cavities has in part led to the view that blood pressure in the hemocoel of molluscs causes reextension of the musculature. While blood pressure may in a few cases serve in this role (e.g., in pulmonates), such a mechanism has not been demonstrated in most molluscs. The notion of the requirement of fluid-filled cavities in hydrostatic skeletons has prevented many muscular-hydrostatic systems in molluscs from being recognized, and it is likely that many other molluscan structures and organs operate in a similar manner. Indeed, Trueman and Brown (1985a) suggested that such a system may have evolved early in molluscan evolution as a means to antagonize the shell or pedal retractor muscles. It is

hoped that this chapter will generate further interest in this important aspect of support and movement of the Mollusca.

Acknowledgments

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