The Arrangement and Function of Octopus Arm Musculature and Connective Tissue

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ABSTRACT The morphology of the musculature and connective tissues of the arms of *Octopus bimaculoides* was analyzed with light microscopy. We also studied *O. briareus* and *O. digueti*, which possess relatively more elongate and less elongate arms, respectively. The morphology of the arms was found to be remarkably uniform among species. The arms consist of a densely packed three-dimensional arrangement of muscle fibers and connective tissue fibers surrounding a central axial nerve cord. Three primary muscle fiber orientations were observed: 1) transverse muscle fibers oriented in planes perpendicular to the long axis of the arm; 2) longitudinal muscle fibers oriented parallel to the long axis; and 3) oblique muscle fibers arranged in helixes around the arm. The proportion of the arm cross section occupied by each of these muscle fiber groups (relative to the total cross sectional area of the musculature) remains constant along the length of the arm, even though the arm tapers from base to tip. A thin circular muscle layer wraps the arm musculature on the aboral side only. Much of this musculature has its origin and insertion on several robust connective tissue sheets including a layer surrounding the axial nerve cord and crossed-fiber connective tissue sheets located on the oral and the aboral sides of the arm. An additional thin layer of connective tissue wraps the arm musculature laterally and also serves as a site of origin and insertion of some of the muscle fibers. The fibers of the oral and aboral crossed-fiber connective tissue sheets are arranged oblique to the long axis of the arm with the same fiber angle as the oblique muscle layers that originate and insert on the sheets. The oblique muscle layers and the crossed-fiber connective tissue sheets thus form composite right- and left-handed helical fiber arrays. Analysis of arm morphology from the standpoint of biomechanics suggests that the transverse musculature is responsible for elongation of the arms, the longitudinal musculature is responsible for shortening, and the oblique muscle layers and associated connective tissues create torsion. Arm bending may involve unilateral contraction of longitudinal muscle bundles in combination with resistance to arm diameter increase due to contraction of the transverse musculature or passive stiffness of the arm tissues. The arms may also be bent by a combination of decrease in diameter due to contraction of the transverse musculature and maintenance of constant length on one side of the arm by unilateral activity of longitudinal muscle bundles. An increase in flexural stiffness of the arm may be achieved by cocontraction of the transverse and longitudinal muscle. Torsional stiffness may be increased by simultaneous contraction of both the right- and left-handed oblique muscle layers. J. Morphol. 268:831–843, 2007. © 2007 Wiley-Liss, Inc.

The eight arms of octopuses are capable of a remarkable diversity and complexity of movement and they serve a wide range of functions. The arms are used in prey capture, locomotion, manipulation, grooming, burying, copulation, defense, chemosensing, and tactile sensing. The adaptability of the arms to such a wide range of tasks has attracted considerable attention recently from robotics engineers who are using them as a source of inspiration for the design and construction of a new class of robotic arms (McMahan et al., 2005, 2006; Walker et al., 2005; Jones and Walker, 2006a,b). Such robotic arms have significant potential advantages over more conventional "vertebrate-like" robotic arms. For instance, they more readily adapt to unstructured and cluttered environments and they do not require a specific "end effector" for each type of manipulated object; instead, the entire arm itself can be used for object manipulation.

Although the general arrangement of the musculature of octopus arms has been known for some time (Cuvier, 1817; Colasanti, 1876; Guérin, 1908; Tittel, 1961, 1964; Socastro, 1969; Graziadei, 1971; Browning, 1980; Kier and Smith, 1985; Kier, 1988; Kier and Thompson, 2003), a detailed description of arm morphology is lacking, in particular with respect to muscle fiber trajectories and the arrangement of connective tissues. The goal of this paper, therefore, is to provide a precise description of the three-dimensional arrangement and form of the musculature and the connective tissues of the arms. This morphology is of particular interest because the arms are examples of a group of animal structures, termed "muscular-hydrostats," which

lack both the fluid-filled cavities that characterize the hydrostatic skeleton of many invertebrates and the rigid skeletal elements present in other animals (Kier and Smith, 1985; Smith and Kier, 1989). The three-dimensional arrangement of the musculature of these structures serves both to generate the force for movement and to provide skeletal support. We therefore analyze the biomechanics of the arms to predict the functional role of the various muscles and connective tissues in support and movement. To explore potential variation in arm structure and function, we sampled several octopus species representing a range from relatively short to relatively elongate arms. In addition to the inherent biological interest in these structures, we hope that the insights gained from the analysis of their structure and function will be helpful in the design and construction of robotic arms with greater diversity and complexity of movement.

MATERIALS AND METHODS
Experimental Animals

The focus of our investigation was the Californian Two-Spot Octopus, *Octopus bimaculoides* Pickford and McConnaughey, 1949. Specimens were obtained from the National Resource Center for Cephalopods (Galveston, TX) or from Aquatic Research Consultants (San Pedro, CA) and maintained until use in a recirculating artificial seawater system housed in the Department of Biology, University of North Carolina, Chapel Hill, NC. In addition to the detailed morphological analysis of arms of this species, arms of the Caribbean Reef Octopus, *O. briareus* Robson, 1929, and Diguet's Pygmy Octopus, *O. digueti* Perrier and Rochebrune, 1894, were also analyzed. Specimens of the latter two species were provided by R. Hanlon, Marine Biological Laboratory, Woods Hole, MA. They were included in this study because they represent species that possess relatively longer (*O. briareus*) and relatively shorter (*O. digueti*) arms, compared with *O. bimaculoides* and with other species in the Octopodidae. In addition to the species described above, previously prepared but undescribed histological material of the arms of the Caribbean Pygmy Octopus *O. joubini* Robson and the Mediterranean Musky Octopus *Eledone moschata* (Lamarck, 1798) was also examined.

Histology

Portions of the arms were removed from specimens that had been anesthetized using 2.5% ethanol in seawater (O'Dor et al., 1990) or a 1:1 mixture of 7.5% $MgCl_2 \cdot 6H_2O$ and seawater (Messenger et al., 1985) and fixed for 24–48 h in 10% formalin in seawater. Smaller blocks (3–4 mm thickness) were cut from the fixed arm tissue, dehydrated in ethanol, cleared in Citri-Solv (Fisher Scientific, Fair Lawn, NJ), and embedded in Paraplast Plus (MP 56°C) (Tyco Healthcare/Kendall, Mansfield, MA). The blocks were sectioned on a rotary microtome. Serial sections were obtained in three mutually perpendicular planes. The sections were stained with Picro-Ponceau with Weigert iron hematoxylin or with Milligan's Trichrome (Kier, 1992) and examined with brightfield and polarized light microscopy.

Morphometrics

For measurements of fiber angles, digital micrographs were taken of grazing sections of the connective tissue sheets or muscle layers. The angles formed with the longitudinal axis of the arm by connective tissue fibers or muscle fibers were measured using morphometrics software (SigmaScan Pro; Systat Software, Point Richmond, CA). The software was also used to measure the areas of components of the intrinsic muscle mass along the length of the arm. For these measurements, an entire arm was fixed and cross-sectional slices of the arm were removed from five equally spaced intervals covering the entire length of the arm. These tissue slices were then processed as described earlier and transverse sections of the arm were obtained from each sample. The total area of the transverse, longitudinal, and oblique musculature, and the axial nerve cord was measured from each of these transverse sections. The relative area of each of these components in the cross section was calculated by dividing the measured area by the total area of the intrinsic arm musculature.

RESULTS
Arm Gross Morphology

The following definitions of section planes and arm orientation will be used in the morphological descriptions below. Given the significant rearrangement of the arm crown in late embryonic development (Budelmann et al., 1977) these definitions are not necessarily related to the morphological orientation (in general understood as equivalent to "embryological orientation") of the cephalopod body. The oral surface of the octopus arm is defined as the surface bearing suckers. If the eight arms of an octopus are brought together (as happens for instance when the animal uses the mantle to swim backwards by jet locomotion) the oral surfaces of the arms face one another surrounding the mouth. Transverse section planes are defined here as planes perpendicular to the longitudinal axis of the arm. Frontal section planes are defined here as planes parallel to the longitudinal axis and to the oral surface. The sagittal plane is defined here to be at the center of the arm in a plane parallel to the longitudinal axis and perpendicular to the frontal plane.

In the description of arm morphology that follows, sections from the arms of *Octopus bimaculoides* are included in all figures. In spite of the differences in the relative length of the arms of the various octopus species analyzed in this study, the morphology we observed was remarkably uniform. Thus, although the figures are of only one of the species, the description that follows applies to all species studied. Our decision to use material from *O. bimaculoides* for the illustrations was based simply on the quantity and the quality of the preparations of this species. This similarity in morphology was also apparent in the arms of a single individual, in spite of differences in the relative lengths of the four pairs of arms. It is of interest that in a recent parallel study, Hanlon et al. (personal communication) have not observed any difference in the behavior of the arms among these species even though the differences in arm proportions are dramatic.

The musculature of the arm was classified by Graziadei (1965, 1971) into 1) the intrinsic muscu-

lature of the suckers, 2) the intrinsic musculature of the arms, and 3) the acetabulo-brachial musculature that connects the suckers to the arm musculature (Fig. 1A). The intrinsic musculature of the suckers and the acetabulo-brachial musculature has been described in detail elsewhere (Guérin, 1908; Tittel, 1964; Kier and Smith, 1990, 2002) and the focus of the current study is therefore on the intrinsic musculature of the arms.

The arm intrinsic musculature consists of a densely packed, three-dimensional array of muscle fibers surrounding a large central axial nerve cord that extends the length of the arm (Figs. 1B and 2). The axial nerve cord includes nerve cell bodies located along the lateral sides and oral side, numerous axons of a range of sizes in a tract on the dorsal surface of the cord, and a central core of neuropile (see Guérin, 1908; Rossi and Graziadei, 1954; Graziadei, 1971; Matzner et al., 2000; Sumbre et al., 2001 for detailed descriptions of arm neuroanatomy). A thick-walled artery extends longitudinally down the aboral surface of the axial nerve cord. Four intramuscular nerve cords (Guérin, 1908; Rossi and Graziadei, 1956) extend the length of the arm at locations towards the periphery of the dense core of musculature (Fig. 2).

The arm is covered by a simple epithelium and an underlying thick, loose fibrous dermal connective tissue layer that includes blood vessels, scattered muscle bundles, chromatophores, leucophores, and reflective cells (see Cloney and Brocco, 1983; Budelmann et al., 1997).

Connective Tissues of the Arm

A thick connective tissue layer surrounds the axial nerve cord of the arm and is formed of fibers that show staining reactions typical of collagen (Fig. 2). When viewed in grazing frontal or parasagittal sections, the birefringent fibers appear to be arranged as a feltwork and polarized light microscopy suggests a slight degree of preferred orientation in the circular and longitudinal directions. Many of the muscle fibers of the transverse muscle mass (see later) insert on this layer.

Additional thick crossed-fiber connective tissue sheets are present orally and aborally in the arm and serve as the site of origin and insertion for much of the intrinsic musculature of the arm (Figs. 1B and 2). The fibers of these layers are also highly birefringent and exhibit staining reactions typical of collagen. Frontal sections show the fibers to be in two sets of highly organized parallel arrays, one arranged as a right-hand helix and the other arranged as a left-hand helix (Fig. 3). The fiber angle (angle that the fibers make with the longitudinal axis) was measured to be 68°–75°. Although the animals were anesthetized when the arms were removed, the state of elongation or shortening of the arm is difficult to assess. Some of the

variation in fiber angle reported here may reflect differences in the state of elongation or shortening of the arms since the fiber angle is increased by shortening and decreased by elongation.

A thin layer of connective tissue wraps the intrinsic musculature laterally on each side of the arm and also serves as the site of origin and insertion of some of the intrinsic muscle fibers, in particular, transverse muscle fibers extending across the arm.

Intrinsic Musculature of the Arm

Transverse muscle mass. The transverse muscle mass is located at the core of the arm, surrounding the axial nerve cord (Figs. 1B and 2). The transverse muscle fibers are oriented in planes perpendicular to the longitudinal axis of the arm. They are oriented in an approximately orthogonal array, i.e., the fibers of the mass are either oriented approximately parallel to the sagittal plane (and thus extending from oral to aboral) or approximately parallel to the frontal plane (and thus extending from side to side).

The transverse muscle fibers extending approximately parallel to the sagittal plane originate on the thick crossed-fiber connective tissue sheets located on the oral and the aboral side of the arm and extend towards the central axis of the arm in longitudinal sheets between bundles of longitudinal muscle (Fig. 4). These longitudinal sheets are termed "trabeculae" (Graziadei, 1965), but in this location they are in the form of layers or plates of muscle fibers as opposed to isolated bundles. Many of the transverse muscle fibers insert on the connective tissue layer surrounding the axial nerve cord. Some of the transverse muscle fibers pass to the side of the axial nerve cord and either insert on the side of the connective tissue layer surrounding the axial nerve cord or extend to insert on the crossed-fiber connective tissue sheet on the opposite side.

Transverse muscle fibers extending from side to side parallel to the frontal plane originate on the thin layer of connective tissue surrounding the external oblique muscle layers. They extend through the oblique muscle layers and longitudinal musculature laterally and some insert on the connective tissue layer surrounding the axial nerve cord. Others pass oral and, especially, aboral to the axial nerve cord and extend to insert on the connective tissue surrounding the external oblique muscle layer on the opposite side of the arm (Fig. 5). They form trabeculae in the form of parallel sheets of muscle fibers as they extend between the fibers of the longitudinal muscle bundles, and bundles of fibers as they extend between the fibers of the oblique muscle layers (Fig. 6).

Longitudinal musculature. Longitudinal muscle fibers surround the central core of transverse
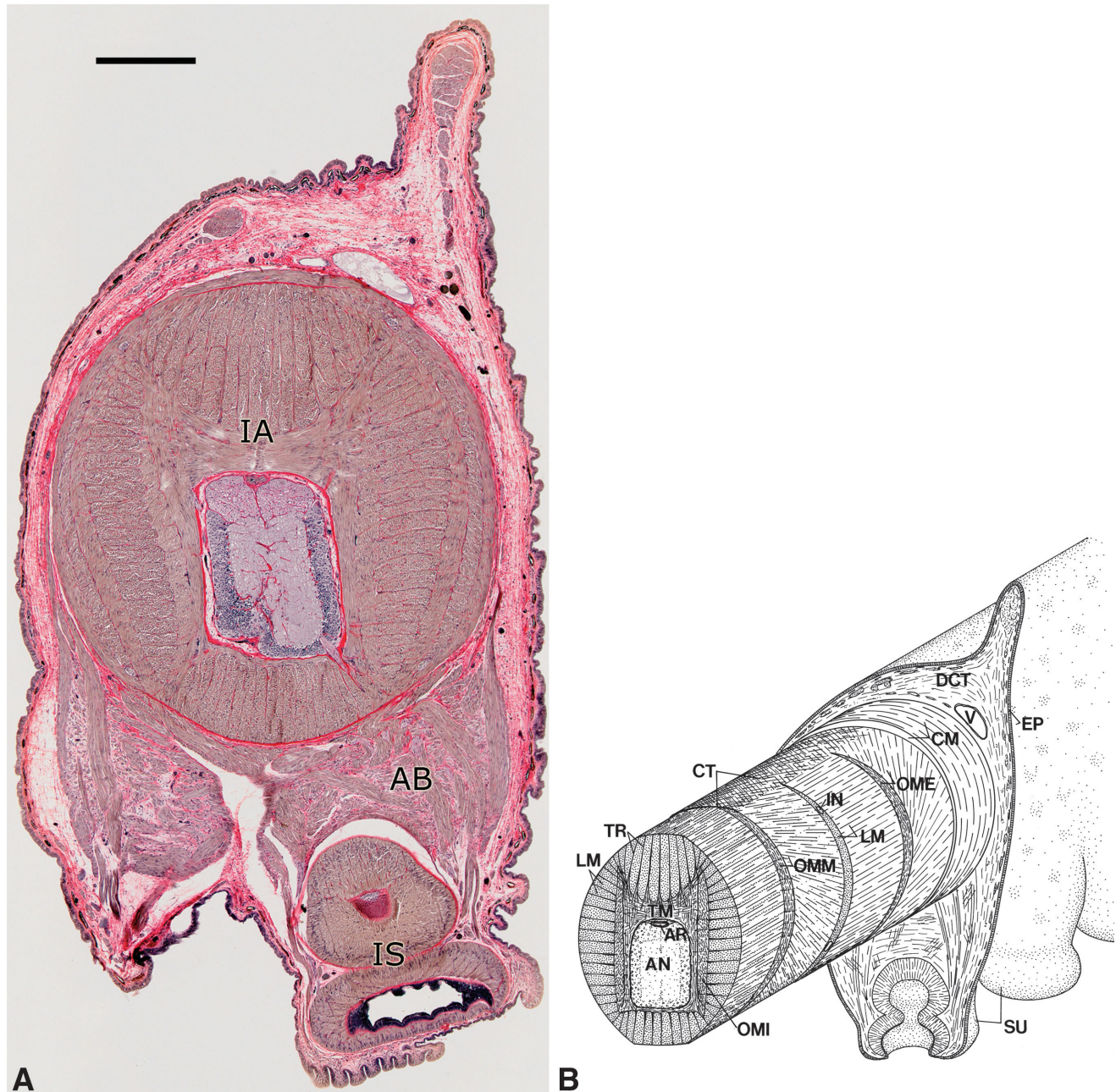
Fig. 1. **A**: Transverse section of the arm of *Octopus bimaculoides* showing the three major subdivisions of the arm musculature: the intrinsic arm musculature (IA); the intrinsic sucker musculature (IS); and the acetabulo-brachial musculature (AB) connecting the arm and sucker musculature. Scale bar: 0.5 mm. Brightfield microscopy of 10-μm-thick paraffin section stained with Picro-Ponceau and hematoxylin. **B**: Diagram of the arm of *Octopus* showing three-dimensional arrangement of muscle fibers and connective tissue fibers. AN, axial nerve cord; AR, artery; CM, circumferential muscle layer; CT, connective tissue; DCT, dermal connective tissue; EP, epidermis; IN, intramuscular nerve; LM, longitudinal muscle fibers; OME; external oblique muscle layer; OMI, internal oblique muscle layer; OMM, median oblique muscle layer; SU, sucker; TM, transverse muscle fibers; TR, trabeculae; V, vein. [Reproduced with permission from Kier, The Mollusca, Form and Function (Trueman ER, Clarke MR, editors), 1988, Vol. 11, pp 211–252, ©Academic Press].

musculature and are oriented parallel to the longitudinal axis of the arm. The fibers extend longitudinally as bundles between the trabeculae of the transverse muscle mass. Longitudinal muscle fibers are distributed orally, aborally, and laterally relative to the transverse muscle mass so that essentially the entire outer perimeter of the arm includes longitudinal muscle fibers, although the cross-sectional area of longitudinal muscle fibers is larger in the aboral quadrant of the arm, compared with the lateral and oral quadrants. A layer of longitudinal fibers is situated between the median and external

Fig. 2. Transverse section of the arm of *Octopus bimaculoides* showing the major components of the intrinsic arm musculature. Connective tissues are stained red and muscle tissue is stained brown in this preparation. AN, axial nerve cord; ACT, aboral crossed-fiber connective tissue sheet; AR, artery; CT, connective tissue; IN, intramuscular nerve; LM, longitudinal muscle fibers; OCT, oral crossed-fiber connective tissue sheet; OME, external oblique muscle layer; OMI, internal oblique muscle layer; OMM, median oblique muscle layer; TM, transverse muscle fibers; TR, trabeculae. Scale bar: 200 μm. Bright-field microscopy of 10-μm-thick paraffin section (same preparation as Fig. 1B) stained with Picro-Ponceau and hematoxylin.

oblique muscles and has a crescentic shape in cross section (Figs. 1B, 2, and 5). It, too, is further subdivided by trabeculae of transverse muscle fibers.

Oblique musculature. In addition to the longitudinal and transverse musculature, three sets of obliquely oriented muscle layers are present in the octopus arm (Figs. 1B, 2, and 5). The names of the oblique muscles used here follow Graziadei (1965). A pair of external oblique muscle layers is the most superficial, occupying a lateral position and enclosing the remainder of the intrinsic musculature. A pair of median oblique muscle layers is located closer to the central axis of the arm and is separated from the external oblique muscle pair by the crescent-shaped longitudinal muscle masses described earlier. The internal oblique muscle layers are the most central and are located on each side of the central core of transverse musculature.

The handedness of a given oblique muscle layer (external, median, or internal) is opposite to the handedness of the other member of the pair on the opposite side of the arm. For instance, if the external oblique muscle layer on one side of the arm is wrapped as a right-hand helix, the external oblique muscle layer on the opposite side is left-handed. In addition, on one side of the arm, the handedness of the external and internal oblique

muscle layers are the same but that of the median oblique muscle layer is opposite (Fig. 7). The external and median oblique muscle layers have their origin and insertion on the oral and aboral crossed-fiber connective tissue sheets and thus are restricted to the sides of the arm (Figs. 1B and 2). The fiber angles of the median and external oblique muscle layers are similar to those of the oral and aboral crossed-fiber connective sheets to which they attach [53°–72° for external oblique muscle (mean = 63°, SD = 5°); 52°–69° for median oblique muscle (mean = 61°, SD = 5°); 68°–75° for connective tissue sheets (mean = 74°, SD = 3°)]. The fibers of the internal oblique muscle layers appear to interdigitate with the transverse and longitudinal musculature and do not show as distinct an origin and insertion as is observed for the external and median oblique muscle layers. The fiber angle of the internal oblique muscle layers appears to be lower than that of the other oblique muscle layers and fibrous connective tissue layers and showed more variation between species [*Octopus briareus*: 39°–45° (mean = 42°, SD = 2°); *O. digueti*, 47°–65° (mean = 56°, SD = 6°)].

Circular muscle layer. A thin layer of muscle fibers arranged circumferentially is also present. This layer is thickest on the aboral side and covers
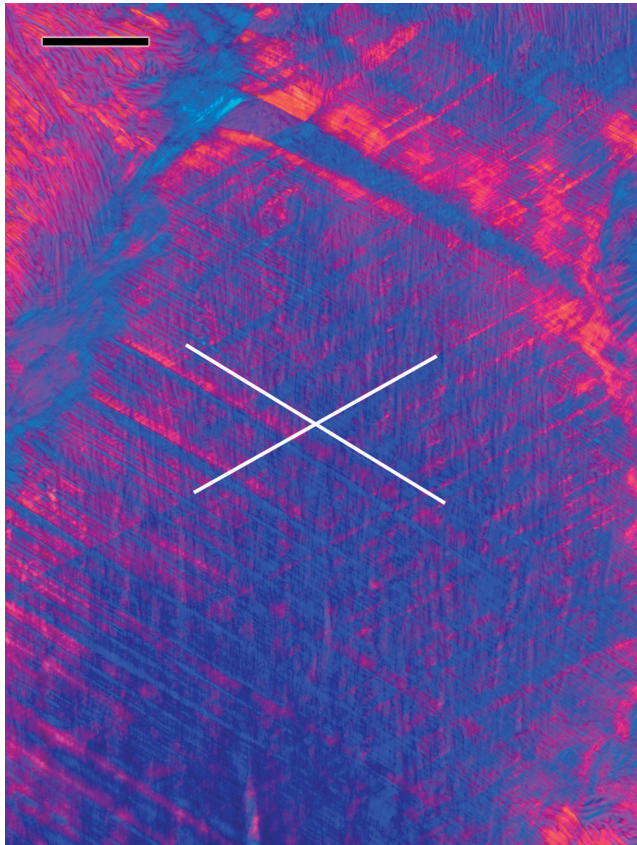
Fig. 3. A grazing frontal section of the oral crossed-fiber connective tissue sheet of the arm of *Octopus bimaculoides*. The fibers of this sheet are arranged as a highly ordered fiber array. The white lines are drawn parallel with the right- and left-handed fibers of the sheet. Longitudinal muscle fibers can be seen beneath the crossed-fiber connective tissue sheet. Scale bar: 100 μm. Polarized light microscopy with first order red filter of 10-μm-thick paraffin section stained with Milligan's trichrome.

the aboral crossed-fiber connective tissue layer (Fig. 4). It extends down each side of the arm as a thin layer (Fig. 5), wrapping the external oblique muscle layers, and then inserts on the oral crossed-fiber connective tissue layer. The interface between the circular muscle layer and the external oblique muscle layer is difficult to resolve in transverse sections because there is relatively little connective tissue separating the two components. In grazing parasagittal sections, however, the difference in muscle fiber orientation makes the interface between the two layers quite obvious (Fig. 7).

Arm Taper and Morphology

By sampling a series of locations along the arm of *Octopus bimaculoides*, we examined potential differences in the relative proportions of the various muscle masses as the arm tapers. Although the total cross-sectional area of the intrinsic arm musculature and axial nerve cord of the sample from the base of the

arm was 144 times the total cross-sectional area of the sample from the tip, the area that the longitudinal, transverse, and oblique musculature occupies in the cross section (expressed relative to the total cross-sectional area of the intrinsic musculature at a given location) was remarkably similar (Fig. 8). The longitudinal musculature occupies ∼0.56 of the total area of the intrinsic musculature in a cross section, and the oblique and transverse musculature occupy ∼0.21 and 0.17, respectively (mean of measurements taken at each location along the length). Note that these proportions are expressed relative to the total cross-sectional area of the intrinsic musculature and thus exclude the area occupied by the axial nerve cord.

Although the relative proportions of the various muscle masses were similar along the length, the relative proportion of the cross section occupied by the axial nerve cord (expressed relative to the total cross-sectional area of the intrinsic muscle) was almost an order of magnitude greater at the tip compared with the base. For instance, the axial nerve cord represented an area of 0.59 at the tip of the arm and only 0.07 at the base.

DISCUSSION
Principles of Support and Muscular Antagonism

Cephalopod arms and tentacles, many mammalian and lizard tongues, and the trunk of the elephant are members of a unique class of soft tissue structures, termed "muscular hydrostats" (Kier and Smith, 1985; Smith and Kier, 1989). These structures consist primarily of a dense, three-dimensional arrangement of muscle fibers and thus lack the characteristics of other forms of skeletal support observed in animals. Specifically, they lack the rigid internal or external skeletal elements seen in arthropods, echinoderms, and vertebrates, as well as the fluid-filled cavities enclosed by a container reinforced with connective tissue (typically the body wall) that characterize the hydrostatic skeleton of the diverse vermiform animals (Chapman, 1950, 1958, 1975; Clark, 1964, 1981; Gutman, 1981; Wainwright, 1970, 1982).

The basic principle of support and movement in muscular hydrostats is straightforward. Muscle tissue, like most tissues lacking gas-filled spaces, is characterized by a high bulk modulus and thus it resists volume change. Because the volume of the structure is approximately constant, any decrease in a given dimension must result in an increase in another dimension. In muscular hydrostats, the muscle fibers are typically arranged in multiple orientations so that all three dimensions can be actively controlled. Thus, by selectively activating specific muscle fiber orientations, these structures can create a wide diversity and complexity of movements. This fundamental principle serves as the foundation for the mechanical analysis and the pre-
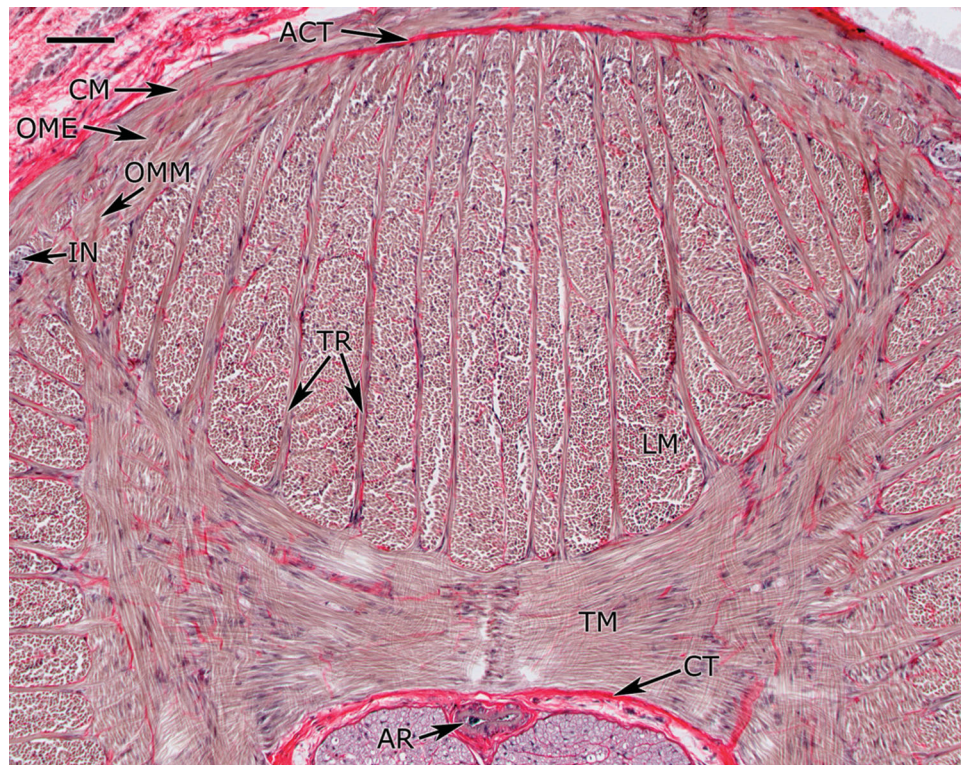
Fig. 4. Transverse section of the arm of *Octopus bimaculoides* aboral to the axial nerve cord showing the details of the musculature and the connective tissue arrangement. Connective tissues are stained red and muscle tissue is stained brown in this preparation. Fibers of the transverse musculature originate on the aboral connective tissue sheet and extend through the longitudinal musculature, dividing it into elongate bundles. Many of the transverse muscle fibers are visible as they extend through the transverse muscle mass to insert on the connective tissue surrounding the axial nerve cord. ACT, aboral crossed-fiber connective tissue sheet; AR, artery; CM, circular muscle layer; CT, connective tissue; IN, intramuscular nerve cord; LM, longitudinal muscle fibers; OME, external oblique muscle layer; OMM, median oblique muscle layer; TM, transverse muscle fibers: TR, trabeculae. Scale bar: 100 μm. Brightfield microscopy of 10-μm-thick paraffin section (same preparation as Figs. 1B and 2) stained with Picro-Ponceau and hematoxylin.
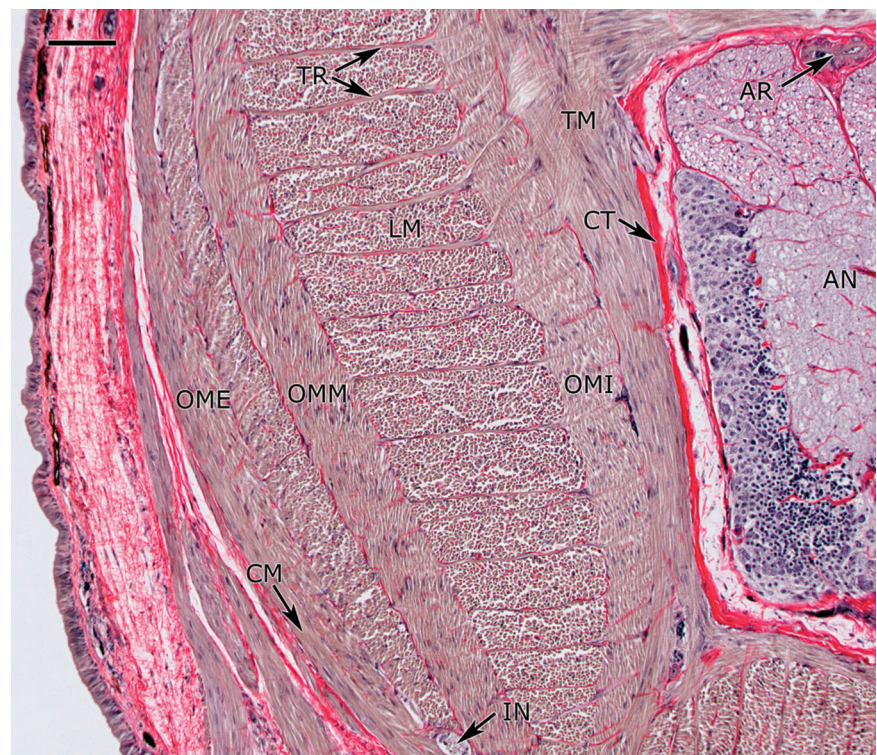

Fig. 5. Transverse section of the arm of *Octopus bimaculoides* lateral to the axial nerve cord showing the details of the musculature and connective tissue arrangement. Connective tissues are stained red and muscle tissue is stained brown in this preparation. The fibers of the transverse muscle mass are visible as they extend to the periphery of the arm, penetrating the surrounding oblique and longitudinal musculature. AN, axial nerve cord; AR, artery; CM, circular muscle layer; CT, connective tissue; IN, intramuscular nerve cord; LM, longitudinal muscle fibers; OME, external oblique muscle layer; OMI, internal oblique muscle layer; OMM, median oblique muscle layer; TM, transverse muscle fibers; TR, trabeculae. Scale bar: 100 μm. Brightfield microscopy of 10-μm-thick paraffin section (same preparation as Figs. 1B, 2, and 4) stained with Picro-Ponceau and hematoxylin.
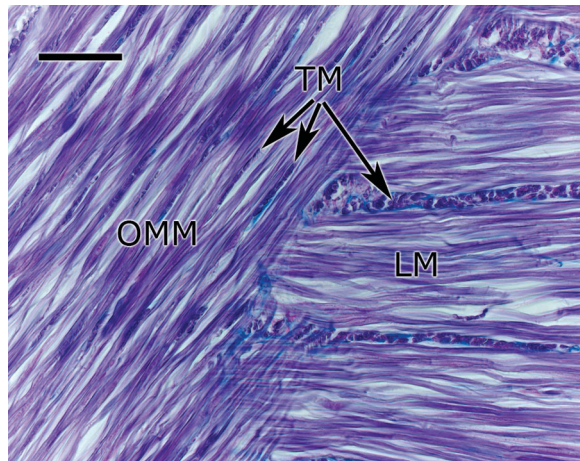
Fig. 6. Grazing parasagittal section of the arm of *Octopus bimaculoides* showing arrangement of transverse muscle fibers as they penetrate the oblique and longitudinal musculature. The section is slightly oblique to the long axis of the arm and the right side of the section cuts deeper into the arm musculature. The transverse muscle fibers are grouped as a plate or layer as they extend between the longitudinal fibers and are arranged as a series of bundles as they pass through the oblique muscle layers. LM, longitudinal muscle fibers; OMM, median oblique muscle layer; TM, transverse muscle fibers. Scale bar: 50 μm. Brightfield microscopy of 10-μm-thick paraffin section stained with Milligan's Trichrome.
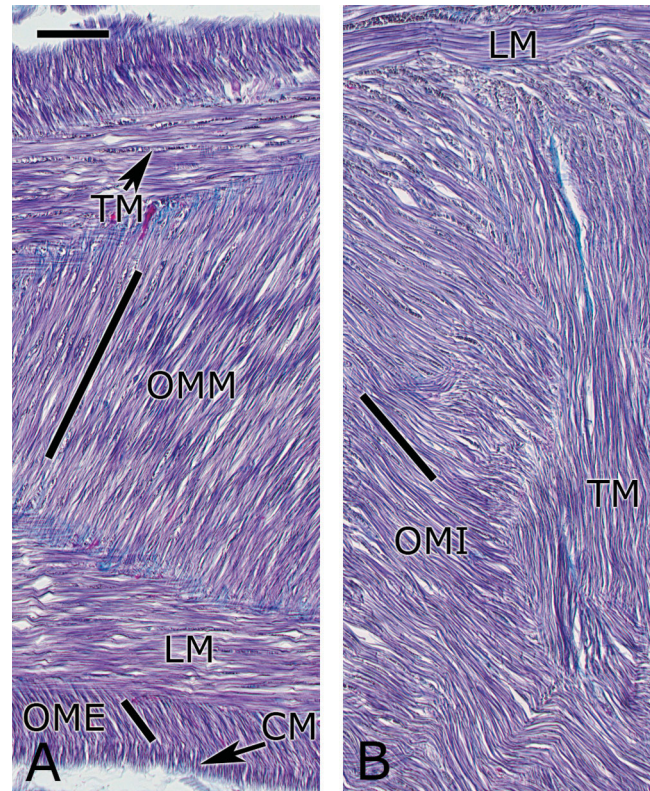

Fig. 7. Grazing parasagittal sections of the arm of *Octopus bimaculoides* showing the arrangement of the oblique muscle layers on one side of the arm. The section shown in (B) is deeper in the arm musculature than the section shown in (A) and both are from the same side of the arm. **A**: The thin circular muscle layer surrounding the external oblique muscle layer is apparent because of the difference in fiber orientation between the two layers. Note that the handedness of the external oblique muscle layer is opposite to that of the median oblique muscle layer, which the section grazes in the center of the micrograph. The lines are drawn parallel to the fibers of the external oblique and internal oblique muscle layers. **B**: The section is deeper on the right side of the micrograph and grazes the transverse muscle mass, which is adjacent to the internal oblique muscle layer visible on the left side of the micrograph. The line is drawn parallel to the muscle fibers of the internal oblique muscle layer. Note that the handedness of the internal oblique muscle layer is the same as that of the external oblique muscle layer on the same side of the arm shown in (A). CM, circular muscle layer; LM, longitudinal muscle layer; OME, external oblique muscle layer; OMI, internal oblique muscle layer; OMM, median oblique muscle layer; TM, transverse muscle fibers. Scale bar: 100 μm. Brightfield microscopy of 10-μm-thick paraffin section stained with Milligan's Trichrome.

diction of the functional role of the various muscle groups below.

Summary of Octopus Arm Movements and Biomechanics

As part of an ongoing collaborative project to design and build robotic arms inspired by octopus arms (Walker et al., 2005), Hanlon et al. (personal communication) are analyzing the behaviors of a number of octopus species with the goal of categorizing the movements of the arms. They have observed that the majority of arm movements appear to serve to place the suckers on objects in the environment. They have identified three general categories of arm movement. The first category, termed "Reach," is defined as an increase in distance between the proximal and distal portions of the arm. Reaches can be executed in several ways. One common form has been studied in considerable detail (Gutfreund et al., 1996, 1998; Yekutieli et al., 2005a,b) and involves a propagating wave of stiffening and straightening of the arm from the base to the tip, forming a passive bend at the transition between the stiffened base and relaxed terminal portion of the arm. Also observed are a progressive uncurling and straightening of a spirally curled arm and elongation of the entire arm in a straight configuration. The second category, termed "Pull," is defined as a decrease in the distance between the proximal and

distal portions of the arm. Pulls can be created using many forms of movement including curling of the arm from tip to base, overall shortening of the arm in a straight configuration, and localized bending of the arm at "pseudo joints," termed a "fetching" movement, so that the arm does not change length and behaves as if it were articulated (Sumbre et al., 2005, 2006). The third category, termed "Search/Grope/Explore" involves no significant change in distance between the proximal and
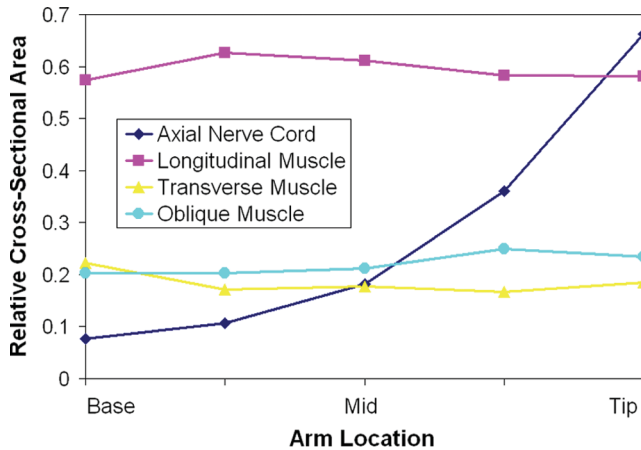
Fig. 8. Plot of areas of the axial nerve cord, longitudinal musculature, transverse musculature, and oblique musculature divided by the total area of the intrinsic arm muscle (excluding the axial nerve cord) as observed in transverse sections obtained at identically spaced intervals down the length of an arm of *Octopus bimaculoides*. Note that the relative proportions of a transverse section of the various muscle masses remain relatively constant along the length of the arm. In contrast, the area of the axial nerve cord, expressed as a proportion of the intrinsic arm musculature, increases dramatically from the base to the tip of the arm.

distal portions of the arm and is characterized by small- or large-scale lateral movements of the arms and by localized sharp bending, aboral flexion, and arm torsion.

From a biomechanical standpoint, all of the movements described earlier are produced by some combination of four basic arm deformations: elongation, shortening, bending, and torsion. These deformations may be highly localized, or they may occur generally over the entire length of the arm. Additionally, they may occur singly on the arm or at multiple locations along the length. Bending movements can also occur in any direction and torsional movements occur in either a clockwise or a counterclockwise direction. In addition to deformations and changes in the shape of the arm, changes in tensile, compressional, flexural, and torsional stiffness are important in producing the observed movements.

Given the basic principle of support and movement in muscular hydrostats outlined earlier, we can hypothesize the muscle activation that is required to generate the individual arm deformations that create the observed movements.

Elongation. Since the arm tissue resists volume change, any decrease in cross-sectional area must result in an increase in length. Given their orientation and attachments, a decrease in cross-sectional area can be created by shortening of the transverse muscle fibers and thus it is likely that the force for elongation is generated by these fibers. The decrease in cross section and consequent elongation can either be highly localized,

involving only a portion of the transverse musculature, or it may occur more generally in the arm, resulting in elongation throughout. Note that this represents an important distinction from the mechanics of classic hydrostatic skeletons with large fluid-filled cavities where muscle contraction increases the pressure throughout and localized deformations are thus more difficult to achieve. The evolution of metamerism provided a means for deformation of individual segments or groups of segments, thus providing for more localized deformation of classical hydrostatic skeletons (Clark, 1964). The effect of muscle contraction in the octopus arm (and in other muscular hydrostats in general) is even more highly localized.

The role of the thin circular muscle layer is less certain. While it is oriented such that its contraction will decrease the arm cross section and thereby elongate the arm, its cross-sectional area is relatively small and thus the force that it can produce for elongation is limited. One potential role could be in maintaining tonus in the arm for postural positioning. Additional experiments involving electromyography are needed to explore its function.

Shortening. Shortening requires the contraction of muscle fibers oriented to produce a longitudinal compressional force. The bundles of longitudinal muscle fibers are in the appropriate orientation to exert a longitudinal compressional force. Again, because the tissue resists volume change, shortening of the arm due to longitudinal muscle fiber contraction must result in an increase in the cross-sectional area. Contraction of the longitudinal muscle fibers will reelongate the transverse muscle fibers and vice versa. The longitudinal and transverse musculature of the arm can thus operate as antagonists, providing the force required for reelongation of each muscle fiber orientation.

Bending. Active bending of the arm involves a potentially more complex sequence of muscle activity than that required for elongation and shortening. Active bending requires selectively contracting the longitudinal muscle fibers along one side of the arm, creating an asymmetrical longitudinal compressional force that shortens one side of the arm and thus causes bending. But for this to be effective in generating bending, the opposite side of the arm must resist this compressional force, otherwise this unilateral longitudinal muscle fiber contraction will shorten the arm and will thereby be less effective in generating a bend. Since arm shortening results in an increase in cross section and the transverse muscle fibers are oriented to control the diameter, resistance to longitudinal compression can be provided by cocontraction of the transverse muscle fibers. Thus, bending may involve simultaneous contraction of the longitudinal and transverse musculature. In this example, the transverse muscle fibers serve simply to maintain the cross-sectional area constant while the

longitudinal muscle fibers on one side of the arm shorten. Resistance to longitudinal compression might also be provided by passive stiffness from transversely or circularly arranged connective tissues or the passive stiffness of the musculature, as long as they are capable of resisting the increase in diameter that results from the longitudinal compression. The limitation of a passive mechanism such as this, however, is that bending could be produced at only one arm length since passive components are fixed in length. The potential involvement of transverse muscle fibers in bending, as described earlier, would allow bending to occur at a range of arm lengths as the arm elongates and shortens.

Bending can also occur in situations where the transverse muscle fibers shorten while selected longitudinal muscle fibers maintain a constant length (Kier and Smith, 1985). In this case, contractile activity in the longitudinal muscle fibers must occur along one side of the arm to resist elongation of that side, and shortening of the transverse muscle fibers elongates the opposite side, creating a bend. Note that this mechanism and the mechanism outlined earlier actually represent endpoints in a continuum of relative shortening of the transverse and longitudinal musculature in bending. Localized bends of even smaller radius of curvature can be produced by unilateral shortening of the longitudinal musculature, decreasing the length of one side of the arm, simultaneous with shortening of the transverse musculature, increasing the length of the opposite side of the arm. As before, the extent of the bending (gentle vs. abrupt) depends on how much of the arm musculature is recruited; highly localized bending, as observed in the bending pulls or "fetch" behaviors (Sumbre et al., 2005, 2006), might involve this more localized longitudinal and transverse muscle fiber activity.

Forceful bending of the arm is aided by placement of the longitudinal muscle bundles as far as possible from the neutral plane of the arm (the neutral plane of a beam in bending is usually in the center and is where all bending stresses are zero). Bending in any plane requires that the longitudinal muscle bundles be situated around the entire periphery of the cross section. As seen in Figure 2, both of these conditions are met in the arm as the longitudinal muscle is indeed situated away from the central axis of the arm and it is also present around the entire periphery. As noted earlier, the cross-sectional area of the longitudinal muscle fibers in the aboral quadrant of the arm is greater than that of the other quadrants, suggesting that aboral bending movements of the arm may be more forceful than bending in other directions.

Stiffening. An increase in flexural stiffness of the arm can be caused by cocontraction of the transverse and longitudinal musculature. This pattern of activation is commonly observed and is an important component of the reaching behavior that has been the subject of an elegant series of experimental and theoretical studies by Hochner, Flash, and coworkers (Gutfreund et al., 1996, 1998; Yekutieli et al., 2005a,b). Based on these studies it was suggested that during reaching, a wave of cocontraction of the transverse and longitudinal musculature passes from the base to the tip of the arm. As this stiffening propagates from the base of the arm outward it forms a passive bend at the transition between the stiffened base and relaxed terminal portion of the arm, which trails behind the advancing wave of cocontraction. A similar wave of stiffening is observed in other octopus behaviors and may represent an important stereotyped component of many octopus arm movements (Gutfreund et al., 1996, 1998).

In some arm behaviors, a significant portion of the arm, particularly at the base, may be stiffened and the arm "swept" by rotation of the base in a manner analogous to rotation around a vertebrate shoulder joint. Such a behavior probably involves cocontraction of the transverse and longitudinal musculature of the intrinsic muscle mass of the arm to stiffen it, while contraction of the musculature of the web at the base of the arms could cause, or at least enhance, the sweeping motion. The fiber trajectories of this web musculature have been well described by Guérin (1908) and include muscle fibers that, depending on activation, could rotate the arm bases aborally, orally, and laterally.

Torsion. Torsion or twisting of a muscular hydrostat results from shortening of helically arranged muscle fibers (Kier, 1982; Kier and Smith, 1985). The arrangement and distribution of the oblique muscle layers and their associated connective tissues provides just such a helical array. Because the oblique muscle layers have their origin and insertion on the oral and aboral connective tissue sheets, and because their fiber angles are similar, a composite helical system is formed. Thus, the force produced by an oblique muscle fiber is transmitted to a connective tissue fiber and then to an oblique fiber on the opposite side of the arm, and then to another connective tissue fiber, and so on, along a helical path down the arm.

The arrangement of oblique muscle fibers observed in this study suggests that a nonsymmetrical pattern of activation occurs on opposite sides of the arm during torsional movements. As described earlier, for all three pairs of oblique muscle layers, the handedness of the helix of one member of the pair is opposite to that of its pair on the other side of the arm. To generate a torsional force, there must be a continuous helical force trajectory down the length of the arm. The handedness of this helical trajectory determines the direction of torsion. For instance, clockwise torsion of the tip of the arm relative to the base (when

viewed from base to tip) requires the contraction of a left-handed helical muscle system. If the external oblique muscle layer on one side of the arm is left-handed, then it must be coactivated with the median oblique muscle layer on the opposite side of the arm in order to form the appropriate helical force trajectory. We thus predict a non-symmetrical pattern of activation of the oblique muscle layers during torsional movements. Simultaneous contraction of the oblique muscle layer pairs on each side of the arm (e.g., both left and right median oblique muscle layers) is predicted to occur when an increase in torsional stiffness of the arm is required, perhaps in combination with coactivation of the transverse and longitudinal musculature for increased flexural stiffness.

The torsional moment of the oblique muscle layers is dependent on the product of the force they produce (which is a product of the inherent peak tension of the muscle fibers and their physiological cross-sectional area) and their distance from the neutral axis of the arm (the neutral axis is usually located at the center of a beam in torsion and is not subject to shear stress). It is thus interesting that the external and median oblique muscle layers are located away from the neutral axis, thereby providing a relatively large moment arm for application of torsional forces. In this regard the functional role of the internal oblique muscle layers is uncertain, given their location nearer to the central transverse musculature. While they possess the same handedness as the external oblique muscle layers on the same side of the arm and thus might augment the force of external oblique muscle fiber contraction in torsion, their smaller torsional moment suggests that they possibly serve some other function in the arm. In addition to their more central location, they appear to possess also a lower fiber angle than that of the median and external oblique muscle layers, but the significance of this difference is unclear. It is worth noting that the arms and the tentacular clubs of decapod cephalopods (squid and cuttlefish) include oblique muscle layers similar to the external and median layers of octopus arms, but they lack the inner oblique muscle layers observed in the octopus arm (Kier, 1982, 1988; Kier and Thompson, 2003). The general pattern of movement of squid arms and tentacular clubs is similar to that of octopus arms. Octopus arms elongate and shorten to a greater extent, but the significance of the inner oblique muscle layer in this difference is unclear. In this regard, future studies involving electromyographic recordings from specific arm muscle groups during movement and force generation would be of great interest.

Although the transverse musculature is likely to play a major role in arm elongation, there is the possibility that some force for elongation may be generated by the external and median oblique muscles. Oblique muscle fibers with a fiber angle equal to $54°44'$ generate torsional forces only. Oblique muscle fibers with a fiber angle less than $54°44'$ generate force for shortening in addition to torsion, while those with a fiber angle greater than $54°44'$ generate force for elongation in addition to torsion (Kier and Smith, 1985). Because the fiber angle of the oblique muscle fibers in the relaxed octopus arms was measured to be greater than $54°44'$, a component of the force creating torsion will also generate a force for elongation of the arm. As the arm extends, however, the fiber angle will decrease and consequently the component of this force that elongates the arm will decrease as well. If sufficient elongation of the arm occurs so that the fiber angle falls below $54°44'$, contraction of the oblique muscle layers will then generate force for shortening the arms in addition to generating a torsional force (Kier and Smith, 1985).

Implications of Octopus Arm Structure and Function for Motor Control

Compared with more conventional hydrostatic skeletons that include large fluid-filled cavities, octopus arms and muscular hydrostats in general have the potential to generate highly localized movements and deformations by selectively contracting small groups of muscle fibers. Experimental studies on the neuromuscular system suggest that octopus arms do indeed have the neuromuscular control required for localized movement; the motor units of the transverse and longitudinal musculature of the arm are small and there is little evidence for electrical coupling between the muscle fibers (Matzner et al., 2000). Such localized deformations are essential for the production of the complex and diverse movements observed in the octopus arm and in other muscular hydrostats.

The problem with such a system, however, is the potential complexity of motor control that is required. Deformations in any direction can potentially occur at any location, or at multiple locations, along the length of the arm. Recent studies on the neuromuscular control of octopus arms suggest that various mechanisms exist that may simplify arm control. For instance, Gutfreund et al. (1996) have studied the reaching behavior (described earlier) in *Octopus vulgaris* as the arm is extended toward a target. Their analyses revealed that certain features of the movement are stereotyped and they suggest that this simplifies the motor control. Indeed, in a later study, Sumbre et al. (2001) showed that arm extensions with typical kinematics could be produced by arms isolated from the brain, suggesting that a motor program for arm extension is present in the neural circuitry of the arm, thereby simplifying its motor control. Recently, Sumbre et al. (2005, 2006) have analyzed

a pulling behavior in *O. vulgaris* that they term "fetch." The movement is used to transfer prey to the mouth and involves stiffening of the arm and the formation of a highly localized bend that forms a "joint" at half the distance from the mouth to the point where the prey is held by the suckers. They suggest that this strategy provides an optimal solution for point to point transfer and also reduces the number of variables that must be controlled, in this case only three degrees of freedom, again simplifying the motor control.

The remarkable similarity in the relative proportions of the cross section of the various muscle masses along the length of the tapering arm is also of interest from the standpoint of neuromuscular control. Such constancy in the relative size, and thus the force that the various components of the musculature can produce along the length of the arm, might also be important in simplifying the control of arm movement. This arrangement allows a given motor command involving some subset of the arm musculature to elicit similar arm deformations at any position along the length of the arm.

Implications of Octopus Arm Structure for Mechanics

The arrangement and relative proportions of the musculature of the arms have several interesting mechanical implications. As described earlier, many of the transverse muscle fibers insert on the dense connective tissue sheet surrounding the axial nerve cord. When the transverse musculature contracts to generate elongation, provide support for bending, or to stiffen the arm, the intrinsic musculature will be pressurized. Will this pressurization compress the axial nerve cord? A preliminary mechanical analysis suggests that the balance of forces is such that the connective tissue surrounding the axial nerve cord will be placed in tension. It is perhaps easiest to envision this if the system is imagined as a cylinder within a cylinder, both consisting of flexible tension-resisting membranes. In between is a fluid of high bulk modulus and the two flexible membranes are connected by muscle fibers that pressurize the fluid when they contract. (Alternatively, it is perhaps easier to think about the muscle fibers as tension-resisting cables and then pressurize the fluid in the space independently.) In this situation, the total outwardly radial force (per unit length of arm) will be greater than the inwardly radial force because while the pressure will be the same, the total area of the outer membrane subjected to that pressure is greater. Thus, even during the generation of large forces in the arm, it is likely that the axial nerve cord will not be subjected to the pressures that are present in the surrounding musculature. An analogous situation occurs in the trunks of ele-phants, which are also muscular hydrostats, because the radial muscle of the trunk inserts on dense connective tissues surrounding the nasal passages. Pressurization due to contraction of the musculature of the trunk also places the connective tissues in tension and keeps the nasal passages open (Kier and Smith, 1985). In the octopus arm it is unclear whether pressurization of the axial nerve cord is potentially damaging, given the high bulk modulus of tissue and the lack of gas-filled cavities. The arrangement might, however, reduce the potential shear stresses on the axial nerve cord, which could indeed be harmful.

CONCLUSIONS

The arms of octopus show remarkable diversity and complexity of movement and thus represent a particularly interesting example of the dynamic musculoskeletal system provided by muscular hydrostatic support. A group of muscle fibers in the arm may actively shorten or it may generate force to limit elongation and thereby support movement of the arm as a whole. In addition, the contraction of muscle fibers of a given orientation may be highly localized or it may be more generalized, with resulting localized versus general deformations or stiffening. Such diversity of movement and support is not possible in more conventional skeletal support systems such as those with rigid skeletal elements where movement is restricted to joints or most hydrostatic skeletons where muscle contraction increases the pressure throughout. The potential limitation of such a system, however, is the complexity of neuromuscular control that is required. In this regard, recent analyses (Gutfreund et al., 1996; Sumbre et al., 2001, 2005, 2006) that have identified mechanisms of simplifying the control are of particular interest and importance for our understanding of these appendages.

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