The Functional Morphology of the Musculature of Squid (Loliginidae) Arms and Tentacles

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ABSTRACT The arms and tentacles of squid (Family Loliginidae: *Sepioteuthis sepioidea* (Blainville), *Loligo pealei* (LeSueur), *Loligo plei* (Blainville), *Lolliguncula brevis* (Blainville)) do not possess the hardened skeletal elements or fluid-filled cavities that typically provide skeletal support in other animals. Instead, these appendages are made up almost entirely of muscle. It is suggested here that the musculature serves as both the effector of movement and as the skeletal support system itself.

High-speed movie recordings were used to observe prey capture by loliginid squid. Extension of the tentacles (1 pair) during prey capture is probably brought about by contraction of transverse muscle fibers and circular muscle fibers. Contraction of longitudinal muscle fibers causes retraction of the tentacles. Torsion of the tentacles during extension may be the result of contraction of muscle fibers arranged in a helical array. The inextensible but manipulative arms (4 pairs) may utilize a transverse muscle mass to resist the longitudinal compression caused by contraction of the longitudinal muscles which bend the arms. A composite connective tissue/muscle helical fiber array may twist the arms.

To exert force, a muscle must be attached to a mechanical structure (Schmidt-Nielsen, '79). Movement, maintenance of posture, and other muscular activities of an organism therefore depend on muscle and a skeletal support system, the mechanical structure to which the musculature is attached. Skeletal support systems in animals can be divided into two general categories. The first is characterized by hardened internal or external skeletal elements as seen in the arthropods, echinoderms, and vertebrates. The second is characterized by hydrostatic skeletons, typically a fiber-reinforced container surrounding a fluid-filled cavity, as seen in polyps and the diverse vermiform animals (Chapman, '58; Alexander, '68; Wainwright et al., '76).

The arms and tentacles of squid lack both hardened skeletal elements and large fluid-filled cavities and thus do not at first appear to fit either of the two general categories of skeletal support. It is suggested here that these appendages actually do possess a type of hydrostatic skeletal support but the system differs from other hydrostatic skeletons because it is made up almost entirely of muscle. The musculature of squid arms and tentacles serves as both the effector of movement and as the skeletal support system itself.

MATERIALS AND METHODS

Experimental animals

I built a lighted float with reflectors and wave baffles to allow underwater observation and tethered it to a dock in 2 m of water at Carrie Bow Cay, Belize. Using a long-handled dipnet, I captured specimens of the squid *Sepioteuthis sepioidea* (Blainville) attracted to the light in the evening and placed them immediately in a large tank of seawater. Tissue for histological examination was obtained from freshly killed animals.

I also observed and histologically examined specimens of the squid *Loligo pealei* (LeSueur), *Loligo plei* (Blainville), and *Lolliguncula brevis* (Blainville) maintained at the Marine Biomedical Institute of the University of Texas Medical Branch at Galveston. The staff of the Marine Biomedical Institute collected and maintained these animals as outlined in Hanlon et al. ('78), and Hulet et al. ('80).

Microscopy

I anesthetized the squid in 1% ETOH in seawater, removed small tissue samples from several locations on the arms and tentacles, and placed the tissue in Bouin's fixative for 24–48 hr. After ethanol dehydration, the tissue was embedded in paraffin (MP 56–58°C) and transverse, frontal, and sagital sections 4–10 μm thick were cut with a rotary microtome. The sections were stained with Mallory's triple stain and studied with bright-field, phase-contrast, and polarized light microscopy. Measurements of fiber angle of the crossed-helical fiber arrays were made on these preparations with a polarizing microscope equipped with a rotating stage with goniometer and ocular cross hairs.

High-speed movie photography

A Redlake Industries HYCAM 16-mm high-speed movie camera was mounted above a large raceway (9.1 m long, 1.8 m wide, 24 cm deep) containing *L. pealei* and *L. plei* at the Marine Biomedical Institute of the University of Texas Medical Branch at Galveston. Lighting was provided by eight 300-W dichroic mirror bulbs (GE-ELH) mounted in two fan-cooled pallets of my own design. Penaeid shrimp were used for prey and were sutured to the end of a fine wire and placed in the center of the camera field. I filmed approximately 40 sequences of prey capture by squid at 750 frames per second. The films were analyzed with a LW International MK-IV 16-mm movie analyzer.

DESCRIPTION OF PREY CAPTURE

Loliginid squid possess five pairs of appendages in a ring encircling the mouth (Fig. 1). Four pairs, termed arms, taper from the base to the tip and bear two rows of suckers on the entire oral surface. The remaining pair of appendages, the tentacles, bear four rows of suckers on an expanded terminal club, whereas the more slender tentacular stalk is cylindrical, only slightly tapered and naked. The tentacles are capable of rapid extension and are used for capture of the squid's diet of fish, crustaceans, and smaller squid. The inextensible arms hold and manipulate the prey once it has been captured and brought within reach by the tentacles.

The capture of prey by loliginid squid and indeed most of the members of the order Teuthoidea has not been well documented. In part this reflects the difficulty of laboratory maintenance of these delicate animals (Bidder, '50), and in part it reflects the fact that the extension and retraction of the tentacles occurs so rapidly it cannot be observed easily by the unaided eye. The staff of the Marine Biomedical Institute of the University of Texas Medical Branch at Galveston has been successful in maintaining loliginid squid in the laboratory. The following is a description of the major events of prey capture taken from approximately 40 high-speed sequences of feeding by specimens of *L. pealei* and *L. plei* maintained in the laboratory at Galveston (temperature, 19°C; salinity, 35 0/00.

In his excellent description of the tentacle strike of the cuttlefish *Sepia officinalis*, Messenger ('68, '77) divided the attack into three phases – attention, positioning, and strike. Owing to the similarity between the attack of *Sepia* and that of the loliginid squid, the same divisions will be employed here.

Attention

If a penaeid shrimp or other suitable prey is introduced into a tank containing squid, the squid respond with rapid movements of the eyes, head, and body. Initially, the head of the squid is rapidly turned so that the arms and tentacles are pointed towards the prey and the eyes are directed forward. Keeping the arms, tentacles, and eyes pointed towards the prey, the animal then uses the funnel and lateral fins to turn so that the long axis of the body is also pointed at the prey. An immediate change to a brown coloration often accompanies the attention movements. This phase of prey capture is brief (approximately 0.5–2 sec) and is followed immediately by the next phase, positioning.

Positioning

Using the funnel and lateral fins, the animal swims directly towards the prey with the arms and tentacles forward. The arms are held together in a tight cone-shaped arrangement with the tips of the tentacles protruding just beyond the arms. During the attention phase and as the squid approaches the prey, both eyes are directed anteriorly towards the prey, resulting in "ocular convergence" (Messenger, '68). After prey capture, the eyes are immediately returned to a laterally directed position. If the prey is moving as the squid approaches, the tips of the tentacles and arms bend in the direction of movement and the animal alters its course, facing the prey and keeping the tentacles aimed directly at it. The duration of the positioning phase is variable (1–4 sec) and depends on the distance the squid must swim to the prey.

Strike

The final phase of the attack occurs as the animal continues to approach the prey. When the tips of the tentacles are approximately 4–6 cm from the prey (squid dorsal mantle length of 13–20 cm), the animal lunges towards the prey, the arms are flared out from their previous tight cone, and the tentacles are extended rapidly. The terminal portions, or dactyli, of the tentacular clubs are attached to one another as the tentacles are extended in a straight trajectory, reaching the prey in approximately 15–35 msec. The tentacles strike the prey with such force that the prey often is pushed further away and the compressive force on the tentacle results in buckling of the tentacular stalk (Fig. 1). The buckling of the tentacles disappears as they are retracted and the prey is drawn back within reach of the arms. The tentacle strike often is accompanied by a rapid color change of the entire animal to clear or white (chromatophores retracted). The arms manipulate the prey into the proper position to be eaten. Once the prey is withdrawn to the arms, the tentacle clubs release their hold and are not involved further in prey manipulation.

In several of the high-speed prey capture sequences, an additional torsional movement of the tentacles was observed. As the tentacles were extended, they twisted along their long axis either in a clockwise or counterclockwise direction. Torsion of the tentacles did not occur when the long axis of the prey was parallel to the long axis of the squid. Torsion may be important in orienting the side of the tentacle equipped with suckers so that the suckered surface strikes the prey.

The tentacle attack of the loliginid squid differed in several respects from that reported for the cuttlefish, *Sepia* (Messenger, '68, '77). During the attention phase, the loliginid squid were not observed to erect the first pair of arms. In addition, a pause at an "attack distance" after positioning typically was not exhibited. Instead, the approach during positioning continued up to the point of tentacle extension.

Movement of the prey appears to affect the nature of the attack. When the prey is stationary, the tentacles are sometimes not used and the squid simply lunge forward and grasp the

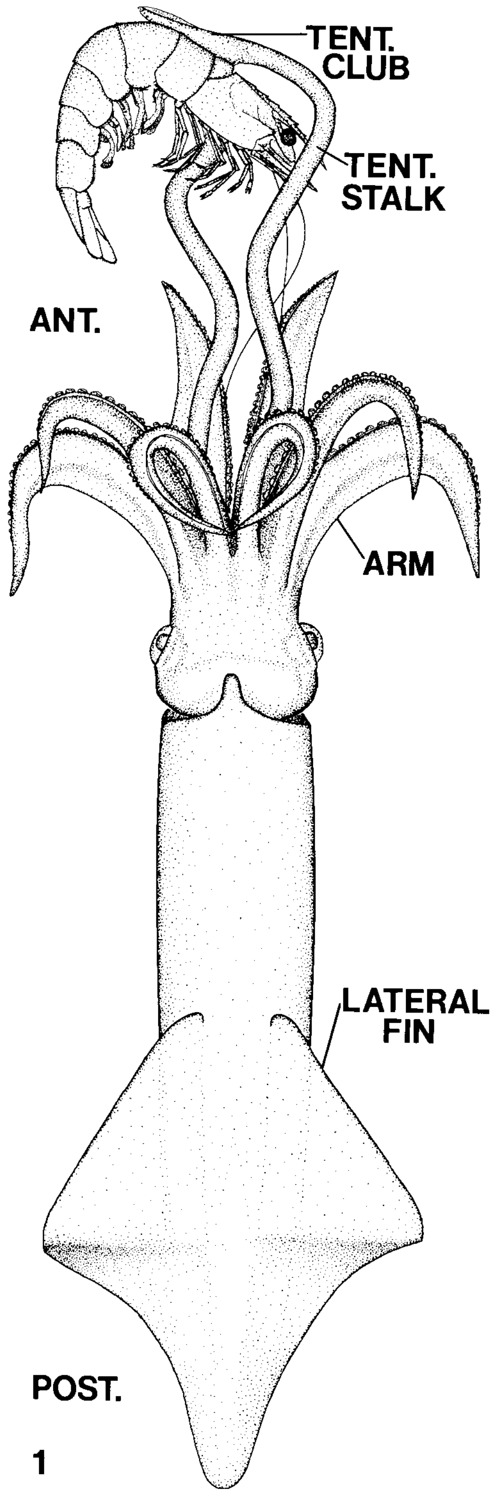

Fig. 1. Tracing from a projected 16-mm frame of a high-speed (750 frames per second) film of the capture of a penaeid shrimp by *Loligo pealei* (19-cm dorsal mantle length). The two tentacles have buckled upon striking the shrimp but will straighten out as the prey is drawn into the eight flared arms.

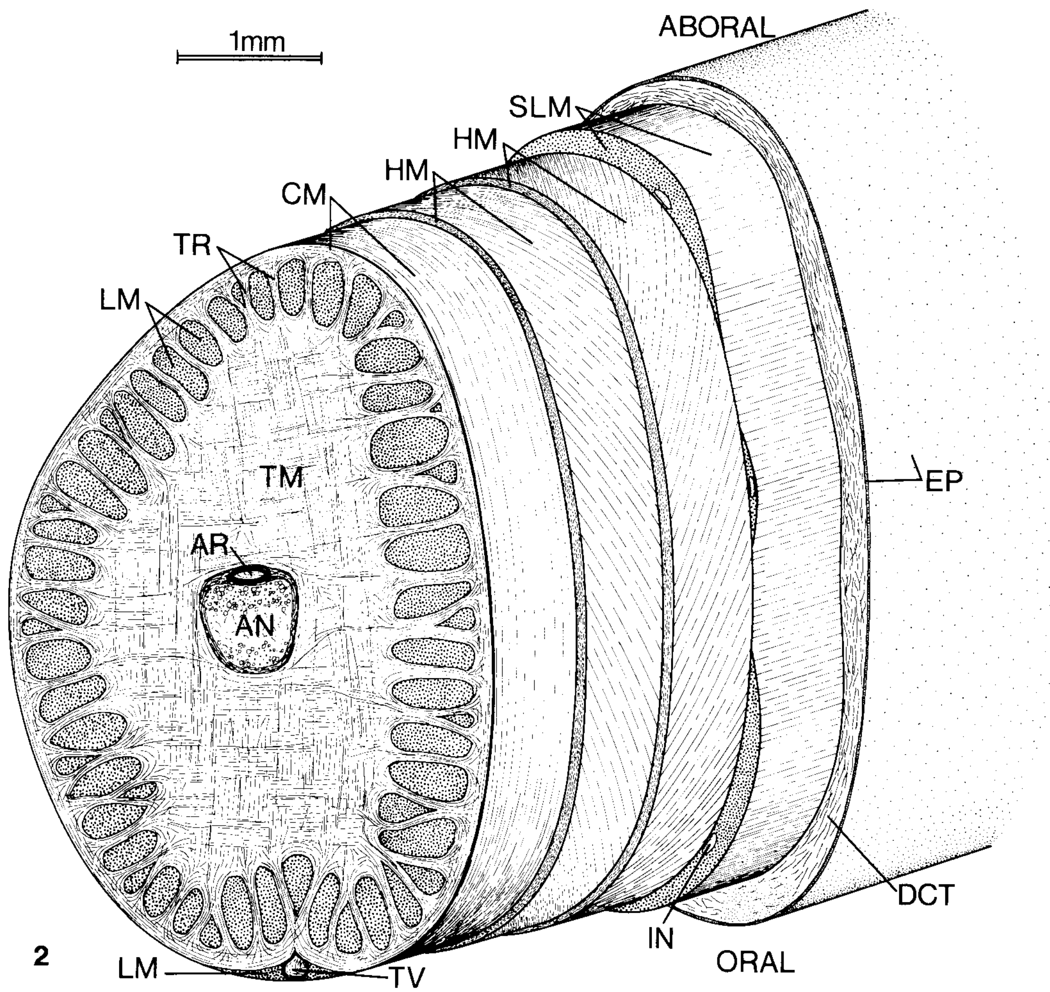

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Fig. 2. Diagram of left tentacular stalk of a loliginid squid. AN, axial nerve cord; AR, artery; CM, circular muscle; DCT, dermal connective tissue; EP, epithelium; HM, helical muscle; IN, intramuscular nerve cord; LM, longitudinal muscle; SLM, superficial longitudinal muscle; TR, trabeculae of transverse muscle; TM, transverse muscle; TV, superficial tentacular vein.

prey with their arms. Bradbury and Aldrich ('69) noted similar behavior in *Illex illecebrosus* (LeSueur) when the animals were feeding on dead capelin (fish).

MORPHOLOGY OF THE TENTACULAR STALK

Figure 2 is a schematic cutaway view of the tentacular stalk of a loliginid squid (*L. pealei, L. plei, Loliguncula brevis, Sepioteuthis sepioidea* are all similar) showing the muscles and associated structures. Figure 3 is a photomicrograph of a transverse section through the left tentacular stalk of *L. pealei.* Running longitudinally down the central axis of the tentacle is a bundle of nerve cell bodies and nerve fibers, the axial nerve cord (AN) (Graziadei, '71). The structure of the nerve cord was described by Colasanti (1876), Guérin ('08), and Graziadei ('71) and will not be considered further here. The axial nerve cord is surrounded by a loose connective tissue sheath containing a large aboral artery (AR) running parallel with the nerve cord. Surrounding the axial nerve cord and its connective tissue sheath is a mass of transverse muscle (TM). Muscle fibers within the transverse muscle lie in planes perpendicular to the long axis of the tentacle. In the periphery of the transverse muscle mass lie

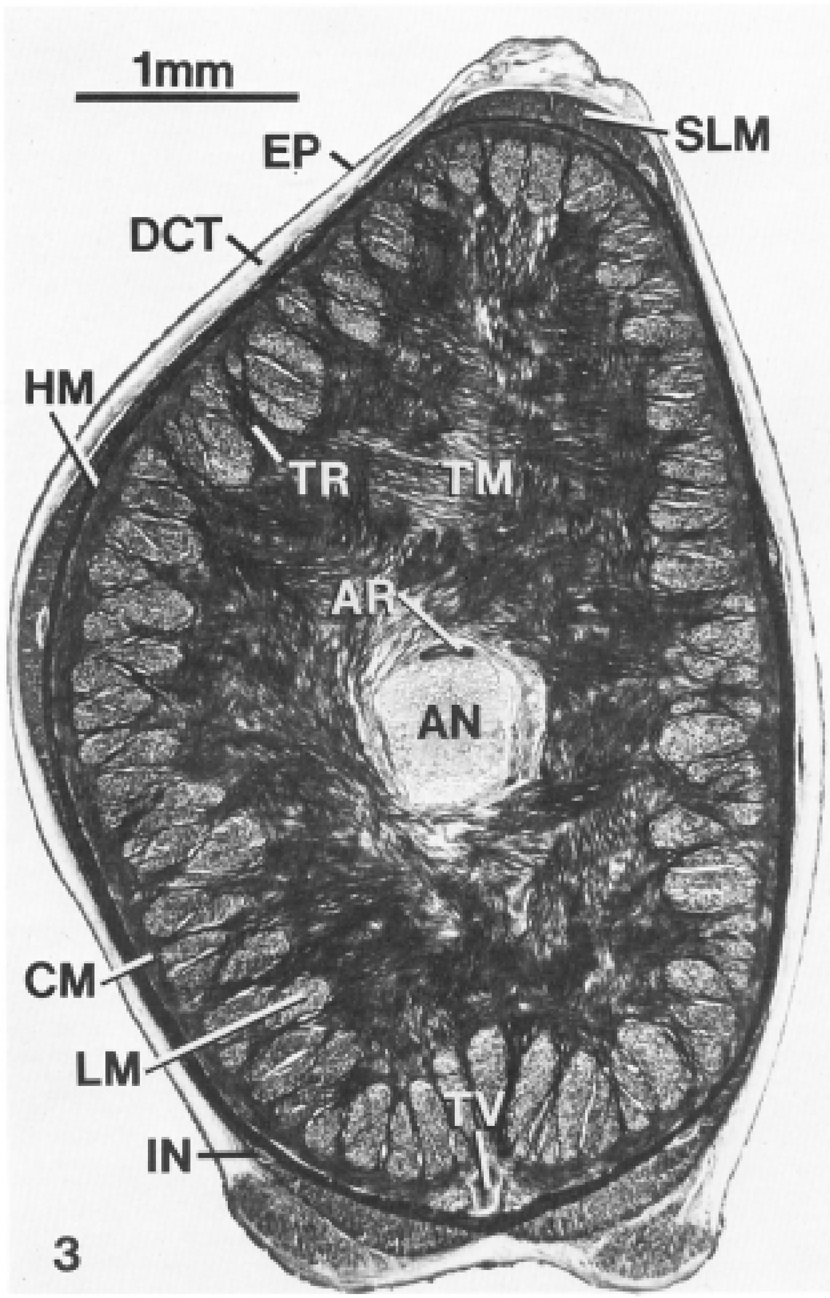


Fig. 3. Micrograph of transverse section of left tentacular stalk of *Loligo pealei*. See Figure 2 for details. Direct microscopy of paraffin section stained with Mallory's triple stain.

bundles of longitudinal muscle fibers (LM). Muscle fibers from the transverse muscle mass extend out in groups in between longitudinal muscle fiber bundles to a layer of circular muscle (CM). Similar extensions of a transverse muscle mass of the arms of *Octopus* were called trabeculae by Graziadei ('65) and the term "trabeculae" (TR) is therefore adopted for similar structures in the squid. Muscle fibers of the trabeculae can be observed to flare out into the circular muscle layer (Fig. 4). The transverse musculature thus does not appear to insert peripherally on a connective tissue sheet or tendon and instead interfingers into the circular muscle layer. A thin epimysial connective tissue layer surrounds the circular muscle layer.

The circular muscle layer is wrapped by two thin muscle layers made up of helically oriented muscle fibers (HM) (Figs. 2, 5). The inner helical layer of the left tentacular stalk consists of a sheet of muscle fibers wrapped in a right-hand helix and the outer layer consists of muscle fibers wrapped in a left-hand helix. The arrangement is reversed in the right tentacular stalk, the inner layer being a left-hand and the outer layer a right hand helix. The fiber angle (angle that a muscle fiber makes with the long axis of the tentacle) varies with the degree of extension of the tentacle from a maximum of approximately 67° in a retracted tentacle to a minimum of approximately 36° in a fully extended tentacle.

The helical muscle layers are, in turn, surrounded by a layer of superficial longitudinal muscle (SLM). Orally and adjacent to the helical muscle layers, the superficial longitudinal muscle layer surrounds a superficial tentacular vein (TV) (Williams, '09). Also within the superficial longitudinal muscle layer and adjacent to the helical muscle layers are six intramuscular nerve cords (IN) containing nerve fibers and nerve cell bodies. For a more complete description and discussion of their function see Guérin ('08) and Graziadei ('65, '71). Surrounding the entire tentacular stalk is a dermal layer of loose connective tissue containing chromatophores, blood vessels, and nerves. This is in turn covered by a simple cuboidal to columnar epithelium.

The morphology of the tentacular club and its functional significance will not be described here because they are similar to those of the sessile arms discussed below.

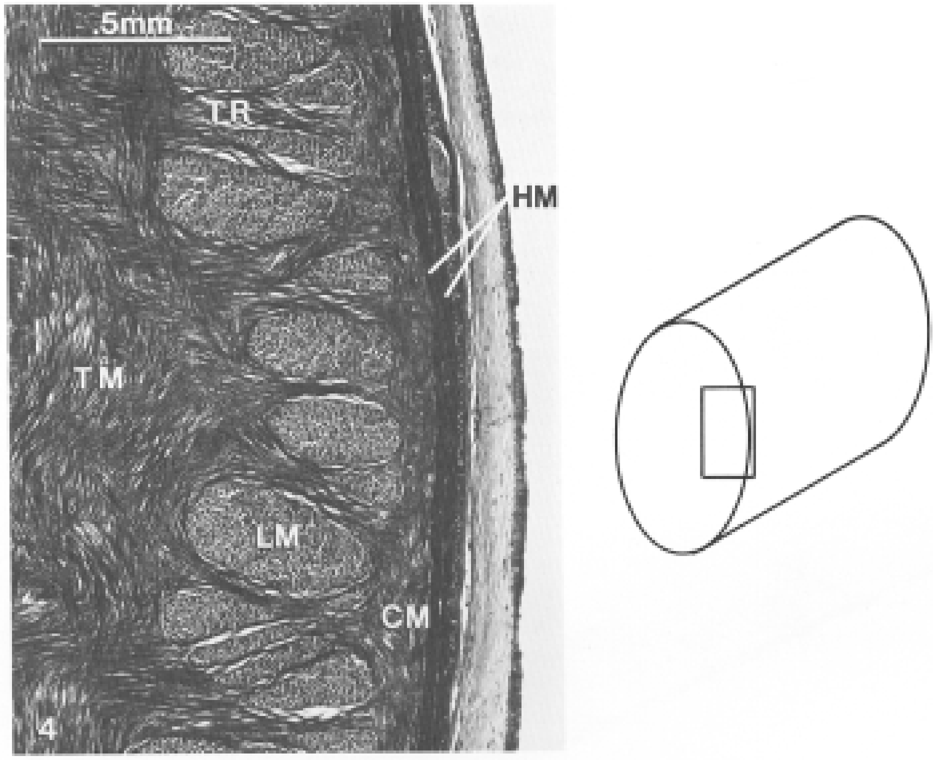
FUNCTIONAL ROLE OF TENTACULAR STALK MORPHOLOGY

In order to understand the possible functional role of tentacular morphology in extension, retraction, and torsion of the tentacle, it is useful to consider the tentacular stalk as a cylinder of constant volume. The primary constituent of muscle tissue is an aqueous fluid, which at physiological pressures, may be considered to be essentially incompressible. This fact, coupled with the lack of gas-filled spaces in the tentacle, makes the assumption of constant volume reasonable.

If the cross section of a constant-volume cylinder is decreased, an increase in length must result. Contraction of the muscle fibers of the transverse muscle mass and circular muscle layer of the tentacular stalk causes a decrease in the cross section of the tentacular stalk. Because the tentacle is constant in volume, any decrease in cross section must result in extension of the tentacle. It is therefore likely that the transverse and circular muscle masses are responsible for tentacle extension. Tentacle retraction after the strike is probably brought about by contraction of the longitudinal muscles, which run the length of the tentacular stalk.

Figure 6 shows the percentage increase in length of a hypothetical constant-volume cylinder of elliptical cross section versus the percentage decrease in the major and minor axes of the cross section (the elliptical cross section and initial length/diameter ratio approximate those of the tentacular stalk). This plot shows that a 70% increase in length (an extension typically exhibited by the tentacular stalk in prey capture) results from only a 23% decrease in cross section. For one of the typical animals filmed, the retracted tentacular stalk length was approximately 5.8 cm and the minor axis width was approximately 0.3 cm. The extended tentacular stalk length was approximately 9.5 cm, but the change in width during extension could not be resolved. A very small change in width would be expected from the relation plotted above. For this 66% extension, Figure 6 predicts a 22% decrease in width, a change of only 0.07 cm. (The width measurements were also complicated by the changing orientation of the elliptical cross section during tentacle torsion.)

The structure of the muscle fibers of the transverse and circular musculature of the tentacular stalk may reflect the role of these muscles in the rapid extension of the tentacle. Guerin ('08) reported transverse striation of the transverse musculature of *L. media* and *Sepia officinalis* (species that rapidly extend their tentacles in prey capture), but he did not report transverse striation in the musculature of other cephalopod appendages. The loliginid species studied here also exhibit striation of



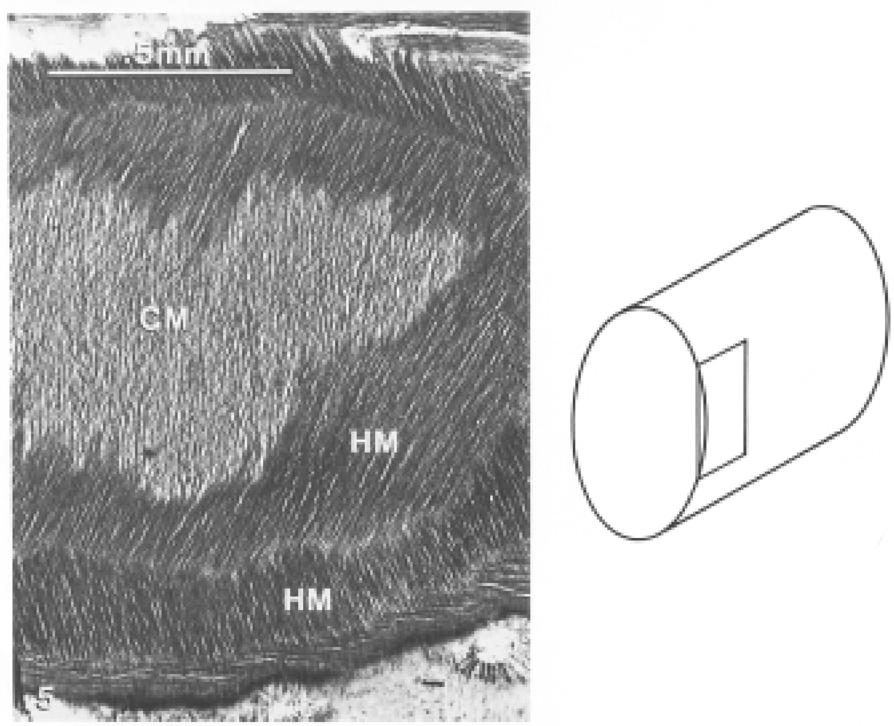


Fig. 4. Micrograph of transverse section of left tentacular stalk of *Loligo pealei*. Muscle fibers of the transverse muscle mass (TM) extend out in trabeculae (TR) in between the longitudinal muscle bundles (LM) and become part of a circular muscle layer (CM). The pair of thin helical muscles (HM) are adjacent to the circular muscle layer. Inset shows orientation of section plane. Direct microscopy of paraffin section stained with Mallory's triple stain.

Fig. 5. Micrograph of parasagital section of right tentacular stalk of *Loligo pealei*. The circular muscle layer (CM) can be observed in the center. The two helical muscle layers (HM) lie outside the circular muscle layer. The long axis of the tentacular stalk runs left to right in this micrograph. Inset shows orientation of section plane. Direct microscopy of paraffin section stained with Mallory's triple stain.

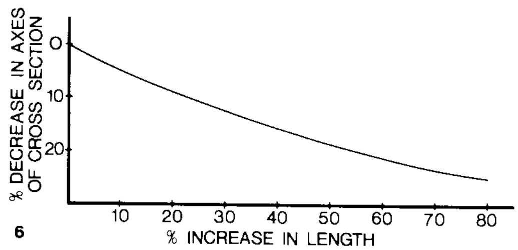


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Fig. 6. Plot of relationship between percentage increase in length of hypothetical cylinder of elliptical cross section and percentage decrease in major and minor axes of the cross section. Major axis/minor axis = 3/2; initial length/initial minor axis width = 20/1. Note that a decrease in cross section results in a large increase in length.

the transverse and circular muscle fibers of the tentacular stalk (light microscopy of paraffin sections only) but do not show similar striation in the other tentacle musculature or in the musculature of the nonextensible arms. The morphology of the transverse and circular muscle fibers of the tentacle may reflect the ability of these muscle fibers to contract quickly and forcefully, extendint the tentacle with the rapidity observed (see, for example, Bone, '81). Further work on the ultrastructural and enzymatic nature of the various muscle groups is planned in order to gain additional insight into the proposed functional role of this musculature.

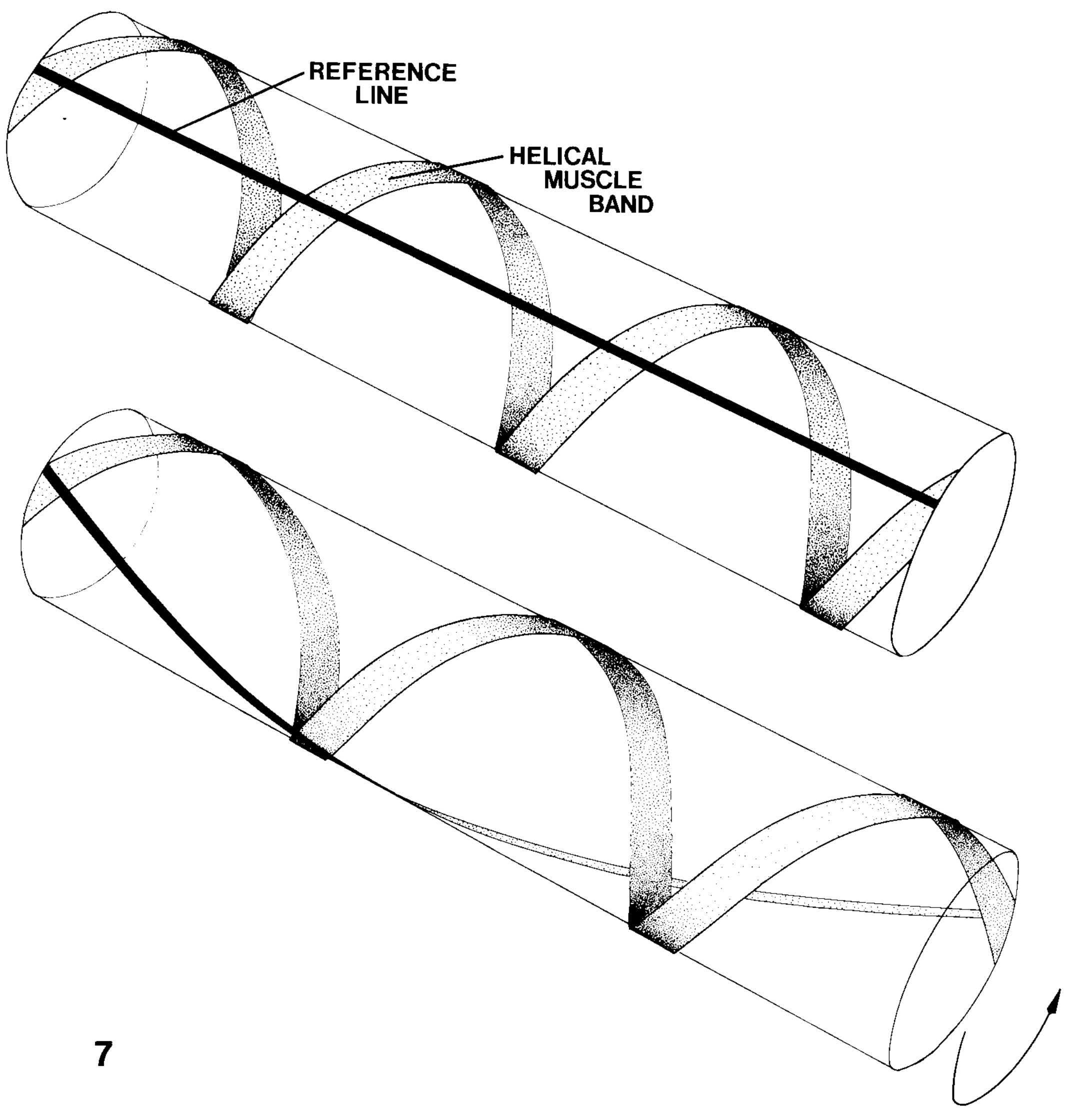

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Fig. 7. Diagram of a single hypothetical helical muscle band (in this case, a left-hand helix). The black line is a reference line. Upon contraction of the muscle band, the cylinder twists.

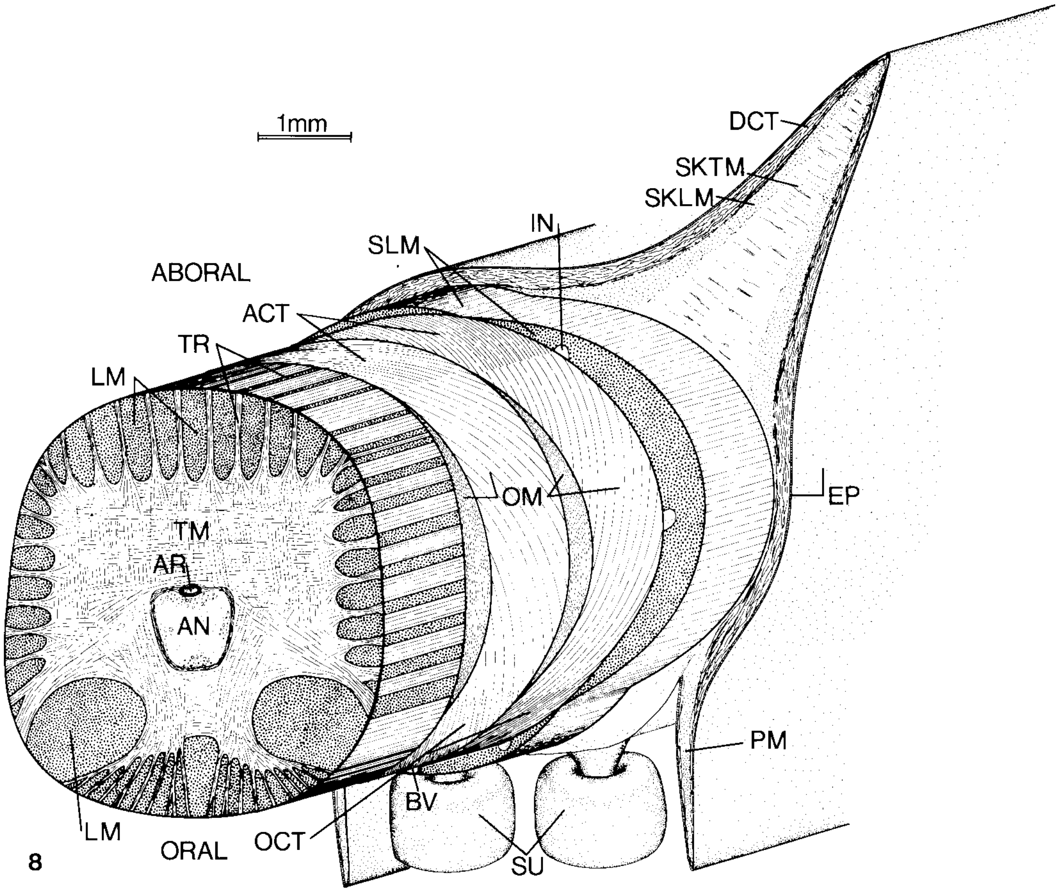

Fig. 8. Diagram of left arm of a loliginid squid. AN, axial nerve cord; ACT, aboral connective tissue (fibrous); AR, artery; BV, superficial brachial vein; DCT, dermal connective tissue; EP, epithelium; IN, intramuscular nerve cord; LM, longitudinal muscle; OCT, oral connective tissue (fibrous); OM, 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.

It will be recalled from the earlier description of the tentacle strike that in some prey capture sequences, the tentacles are twisted along their longitudinal axis. The two helical muscle layers of the tentacular stalk, if separately innervated, could be responsible for this twisting or torsion. To visualize this, it is helpful to consider a hypothetical, single muscle band wrapping around the tentacle from base to club (Fig. 7). The contraction of this muscle band would result in torsion. Contraction of the right-hand helical muscle layer would result in a counterclockwise torsion of the tip of the tentacle relative to the base (when viewed from the base to the tip) and contraction of the left-hand helical muscle layer would result in clockwise torsion. Contractile activity in both muscle layers would result in increased resistance to a torsional force.

MORPHOLOGY OF THE ARM

Figure 8 is a schematic view of the arm of a loliginid squid (*L. pealei, L. plei, Loliguncula brevis, Sepioteuthis sepioidea* are all similar). Figure 9 is a photomicrograph of a transverse section of right arm number 2 of *Sepioteuthis sepioidea.* Running down the center of the arm is an axial nerve cord made up of nerve cell bodies and nerve fibers surrounded by a loose connective tissue sheath. The functional association of ganglionic expansions of this nerve cord with the location of suckers has been discussed by Graziadei ('71). An aboral artery is associated with the connective tissue surrounding the axial nerve cord.

A central core of transverse muscle surrounds the nerve cord. Muscle fibers of this mass lie in planes perpendicular to the long

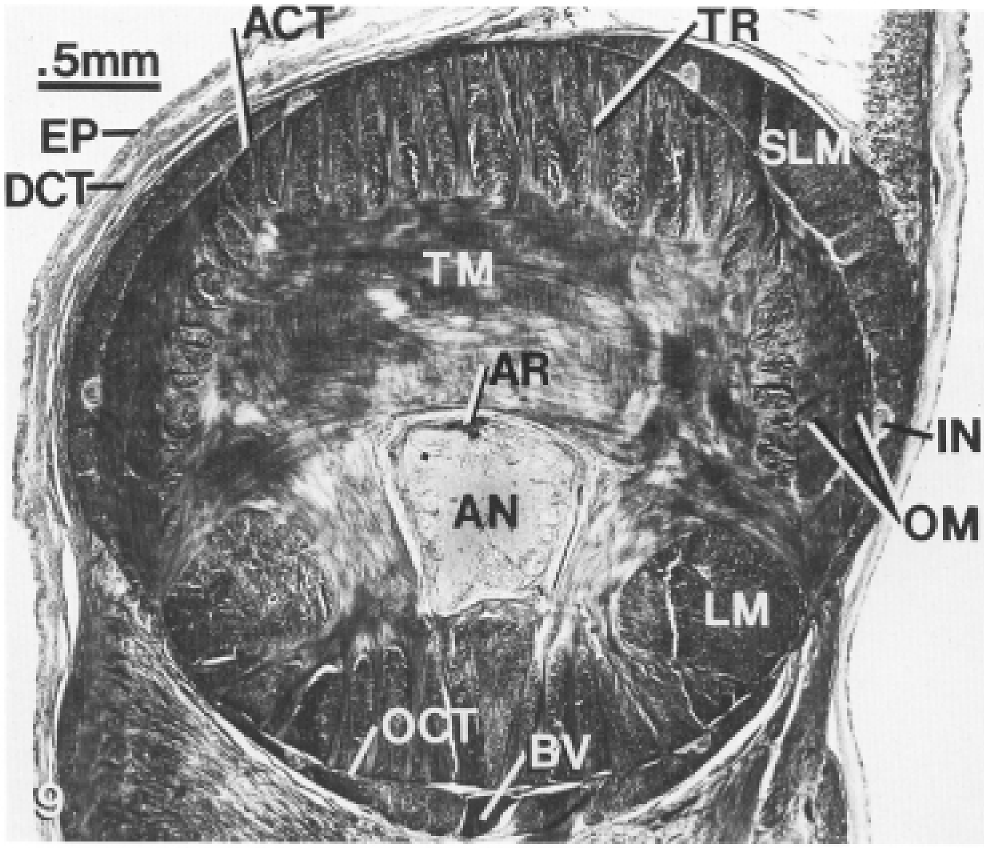

Fig. 9. Micrograph of transverse section of right arm #2 of *Sepioteuthis sepioidea*. See Figure 8 for details. Direct microscopy of paraffin section stained with Mallory's triple stain.

axis of the arm and extend out in trabeculae to insert orally and aborally on fibrous connective tissue sheets (ACT,OCT) (stain blue with Mallory's triple stain) and laterally on the inner member of a pair of oblique muscles on each side of the arm. Longitudinal muscle fiber bundles run between the trabeculae formed by the transverse muscle fibers.

A pair of oblique muscles (OM) on each side of the arm insert on the oral and aboral fibrous connective tissue sheets. Connective tissue fibers in the sheets are in a crossed-fiber arrangement with a fiber angle (angle fiber makes with the long axis of the arm) of approximately 72° (Fig. 10). The pair of oblique muscles is made up 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 connective tissue sheets and oblique muscles are three bundles of superficial longitudinal muscle fibers that are crescentic in cross section, one oral and two lateral. The oral bundle surrounds a superficial brachial vein (BV) lying adjacent to the oral connective tissue sheet (Williams, '09). Six intramuscular nerve cords containing nerve fibers and nerve cell bodies are located adjacent to, and outside of, the perimeter formed by the oblique muscles and fibrous connective tissue upon which the oblique muscles insert. The aboral surfaces of the arms are equipped with tapering swimming keels, the most prominent of which is located on the third pair of arms (counting from dorsal to ventral) and projects aborally. The cores of the swimming keels are made up of nonfibrous connective tissue with scattered muscle bundles (SKTM) arranged transversely across the keel. Longitudinal muscle fibers (SKLM) lie in a sheet over the core.

The oral surface of the arm is equipped with a double row of suckers (SU) lapped on both sides of the arm by thin protective membranes

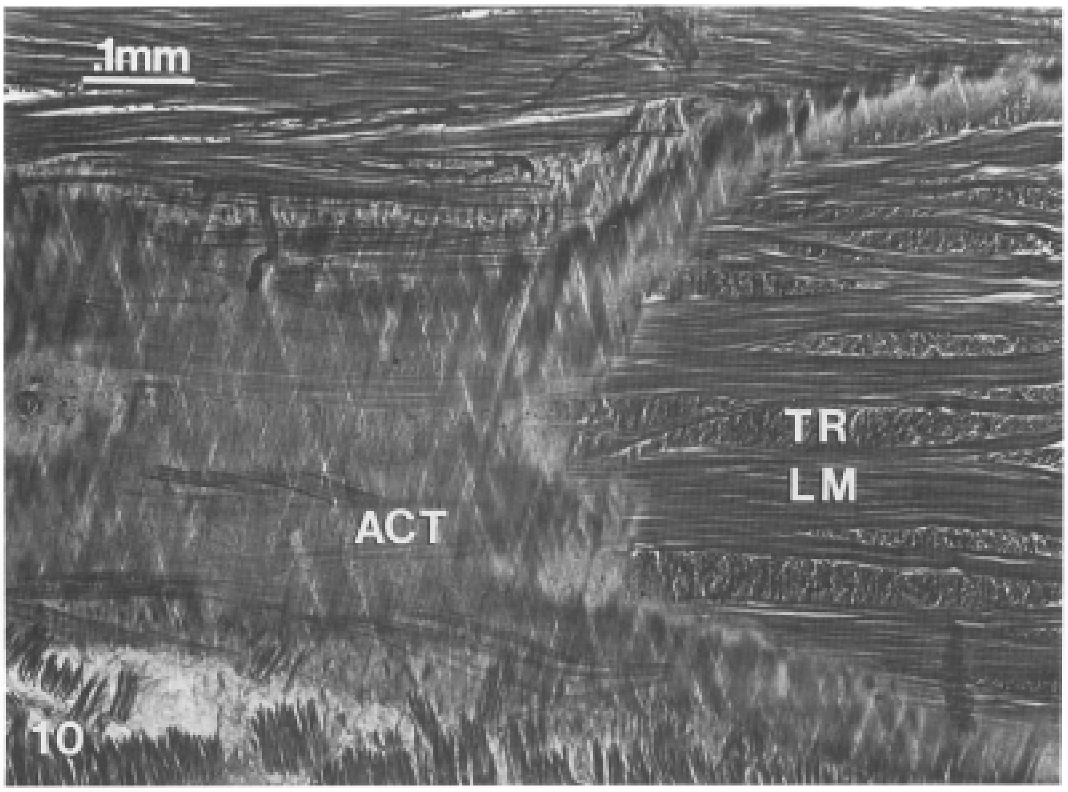

Fig. 10. Micrograph of frontal section of arm of *Sepioteuthis sepioidea*. The right-hand side of the section is deeper than the left. The longitudinal muscle bundles (LM) are cut in long section. The trabeculae (TR) of the transverse muscles are in cross section. The crossed fibers of the aboral connective tissue (ACT) sheet are in long section on the left. Direct microscopy of paraffin section stained with Mallory's triple stain.

(PM). The musculature of the sucker peduncle and protective membranes inserts on the oral connective tissue sheet. The suckers will not be considered further here as they do not appear to be involved in the mechanical functioning of the arms and tentacles and have received attention in the literature previously. Girod (1884), Niemic (1885), Williams ('09) and Naef ('21) described the suckers, but the best accounts of structure and function of decapod suckers are by Guérin ('08) and Nixon and Dilly ('77). The arm is enclosed by a loose connective tissue dermis (DCT) containing chromatophores, iridophores, blood vessels, and nerves. A simple cuboidal-to-columnar epithelium (EP) layer caps the dermis.

FUNCTIONAL ROLE OF ARM MORPHOLOGY

The possible functional morphology of the four pairs of inextensible but manipulative arms may be allied with the previous proposals for the pair of extensible tentacles. In this discussion, it is useful to consider the arm to be a cylinder of constant volume (in a manner similar to that outlined for the tentacles). Bending of the arm presumably is caused by selective contraction of longitudinal muscles on one side of the arm (the side representing the concave radius of the bend). In order for this muscle contraction to bring about bending, some component of the arm must resist longitudinal compression. Without this component, contraction of longitudinal muscles would serve simply to shorten the arm.

What then serves to resist the longitudinal compression that results from the contraction of muscles involved in bending? Any decrease in length of a constant-volume cylinder must result in an increase in diameter. In order to limit longitudinal compression, increase in diameter must be prevented. The transverse muscle mass and associated trabeculae of the arm are oriented in such a way that contractile activity in these muscles would prevent an in-

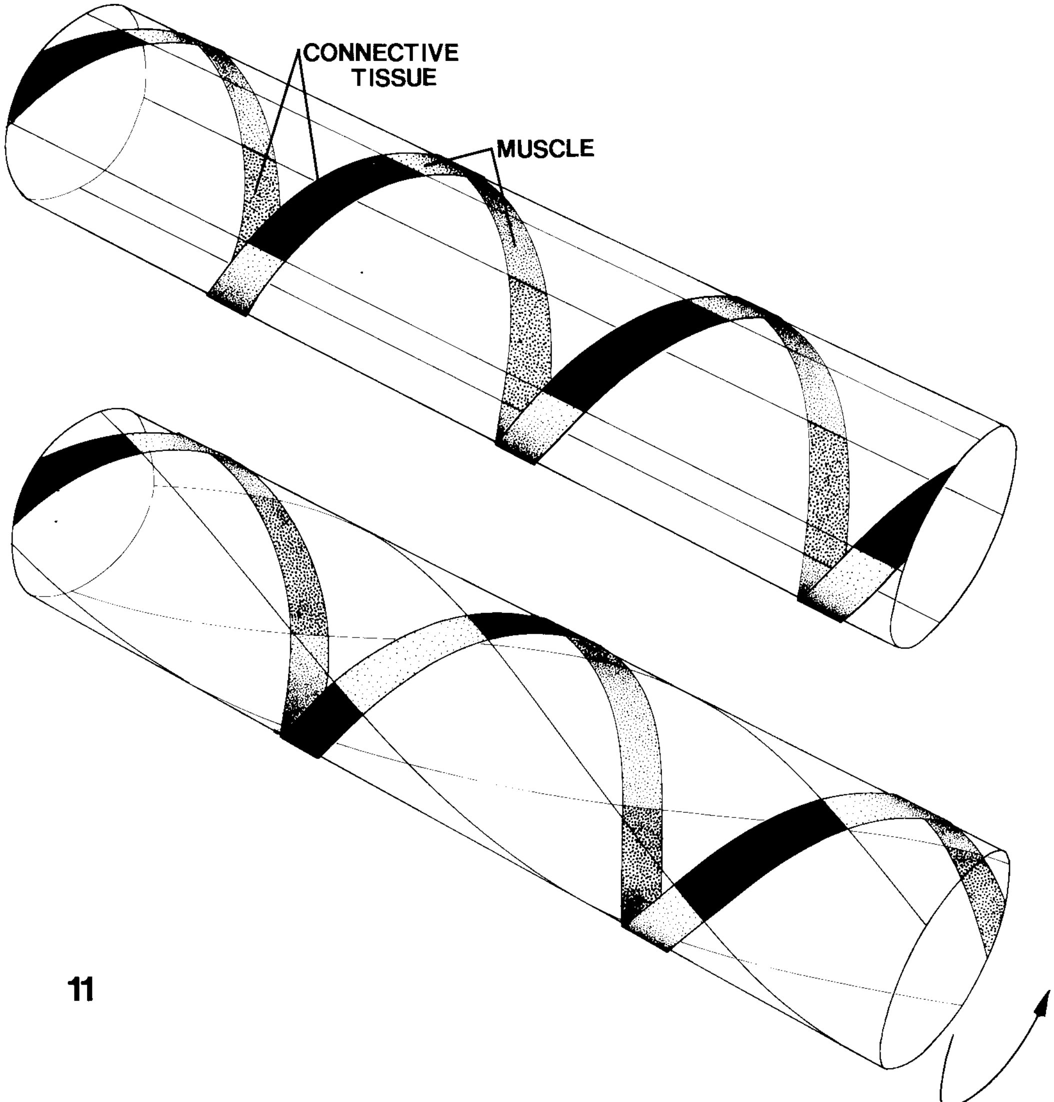

Fig. 11. Diagram of single hypothetical composite muscle/connective tissue band (in this case, a left-hand helix). Upon contraction of the muscles of the composite, the cylinder twists.

crease in diameter. It seems likely therefore that the transverse muscle mass resists longitudinal compression of the arms by resisting increase in arm diameter.

In this context it is interesting to note the location of the large longitudinal muscle masses on the oral side of the arm. The forceful bending of the arms orally is important in handling prey while it is eaten, once the tentacles have retracted to bring the prey within reach of the arms.

The functional role of the oblique muscles and associated connective tissue sheets is less obvious. The fiber angle of the connective tissue fibers is the same as that of the oblique muscle fibers (inner left-hand helix, outer right-hand helix for right arms; opposite for left). Each of the left- and right-hand helical systems can be considered as a composite of muscle fibers alternating with connective tissue fibers. It is helpful to consider a single hypothetical muscle/connective tissue band as it wraps the cylinder of the arm in a helical fashion (Fig. 11). With one end of the cylinder fixed, contraction of the muscles of the composite would result in torsion of the cylinder. The direction of torsion would once again depend on the right- or left-handed nature of the helix.

In the high-speed movie sequences (*L. pealei, L. plei*) torsion of the arms was common during the manipulation of prey immediately after prey capture. In addition to creating torsion, the helical muscle/connective tissue fiber composite systems could be used to resist torsion, thereby preventing struggling prey from freeing itself from the squid's grasp by twisting the arms.

DISCUSSION

The functional difference between the arms and tentacles of squid appears surprising at first because the morphology is so similar. Both the arms and the tentacles possess a large central mass of transverse muscle surrounded by bundles of longitudinal muscle, yet the tentacles undergo rapid extension and retraction, and the arms are inextensible. If the functional proposals outlined here are correct, the transverse muscle mass is actually involved in length change in both sets of appendages. In the tentacles, the transverse muscle mass appears to create length change. In the arms, the transverse muscle prevents length change. The difference in function appears to be reflected in the structure of the muscle fibers of each muscle mass. As mentioned earlier, the muscle fibers of the transverse muscle mass of the rapidly extensible tentacles are transversely striated. The muscle fibers of the transverse muscle mass of the inextensible arms are not transversely striated. The longitudinal muscles are antagonists to the transverse muscles in both cases. In the arms, contractile activity of the transverse and longitudinal muscles presumably occurs simultaneously. In the tentacles, contractile activity occurs at different times (transverse muscle contraction during extension, longitudinal muscle contraction during retraction).

In the preceding discussions, the hydrostatic nature of the supportive system is emphasized. According to Wainwright ('70), a hydrostatic supportive system consists of a fluid under pressure in a container. In squid arms and tentacles, the fluid under pressure and the container are not immediately distinguished because these two constituents are not distinct entities. In fact, the compression-resisting fluid is made up, in part, of elements of the tension-resisting container: muscle fibers of the transverse muscle mass.

Wainwright ('70) also listed a number of observations that apply to hydraulic systems in animals that help to identify the similarities of and differences between other hydrostatic systems and the hydrostatic system of squid arms and tentacles. One of these states that it is possible to distinguish purely tensile components from those that resist compression. As previously noted, the transverse muscle array of squid arms and tentacles serves as both a compression-resisting and a tensile element. This view can be reconciled if one looks at the structure of the muscle fibers and the role played by that structure. The myofilaments of the muscle fiber resist (or in this case, create) tension and it is the sarcoplasm of the muscle fiber in addition to extracellular fluids that resists compression. The sarcoplasm and extracellular fluids of this musculature serve the same role as the coelomic fluid of other hydrostatic skeletons.

Wainwright ('70) noted that, typically, the compression-resisting fluid is concentrated in the central region of the supportive system and the tensile materials are peripheral. Although components of the tension-resisting container (the transverse muscle mass) occur centrally in the squid appendages, their ability to resist or create tension would not be possible without the peripheral systems to which they are attached: the circular muscle layer of the squid tentacle and the connective tissue and oblique muscle layer of the squid arm.

The arms and tentacles of loliginid squid exhibit a dynamic hydrostatic skeleton. Muscle fibers function in roles typically played, in other hydrostatic systems, by connective tissue fibers and aqueous fluid. The degree of flexibility and the range and speed of movements observed in the appendages of these animals may be related to the control of the properties of the system conferred by this dynamic morphology.

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