

## MUSCLE ARRANGEMENT, FUNCTION AND SPECIALIZATION IN RECENT COLEOIDS

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### ABSTRACT

The bodies of coleoid cephalopods are characterized by a dense musculature consisting of tightly packed bundles of muscle fibers arranged in three mutually perpendicular planes. This arrangement of muscle, termed a 'muscular hydrostat', generates force and also provides skeletal support. Muscle function during movement and locomotion thus does not depend on rigid skeletal elements, even though many extant coleoids possess hard parts.

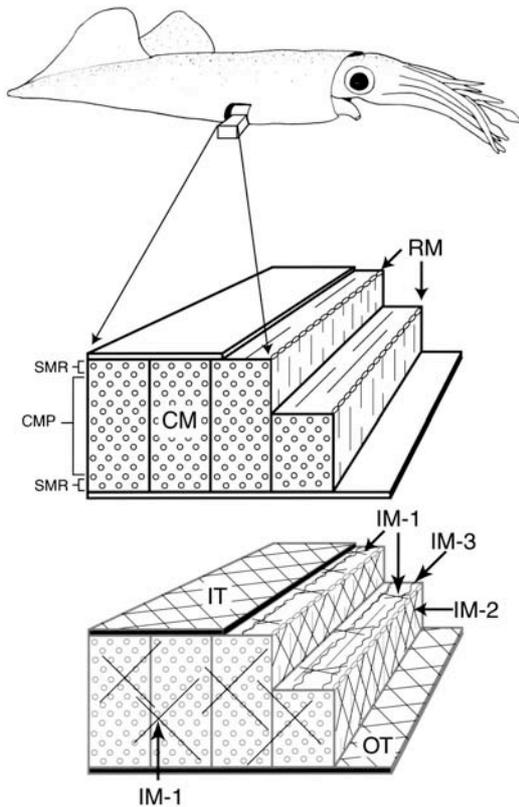
In this review, we describe the arrangement and microanatomy of the musculature and connective tissues from a variety of coleoids and from a range of cephalopod organs and systems including the mantle, funnel, fins, arms, tentacles, and suckers. We analyze the muscle and connective tissues from the standpoint of biomechanics in order to describe their function in movement and locomotion. This analysis demonstrates that the same basic principles of support and movement are shared by all of these structures. In addition, the crucial role played by fibrous collagenous connective tissues in these systems is emphasized. Further work is required, however, to describe the mechanical functions of the musculature of the diverse pelagic cephalopods, to understand neuromuscular control of these complex systems, and to explore the mechanisms of specialization of coleoid cephalopod muscle.

### INTRODUCTION

Although many recent coleoids retain hard parts, they resemble the soft-bodied invertebrates because muscle function during movement and locomotion generally does not depend on hardened skeletal elements. The shell of modern coleoids serves as a buoyancy control device in the sepioids (Denton 1974, Denton & Gilpin-Brown 1959, 1961), is reduced and has an uncertain supportive role in the teuthoids (Donovan & Toll 1988, Nigmatullin *et al.* 1991, Toll 1988), and is greatly reduced and modified in the octopods (Wells 1978). The transmission of force, antagonism of the musculature, and the amplification of force, displacement or velocity of muscle contraction in most cases depend instead on a form of skeletal support that resembles the hydrostatic skeleton of soft-bodied invertebrates.

The coleoid body is characterized throughout by

dense musculature consisting of tightly packed bundles of muscle fibers arranged in three mutually perpendicular directions (see Budelmann *et al.* 1997 for a review of the microanatomy). Such an arrangement of muscle, termed a 'muscular hydrostat', serves both to generate the force and to provide the skeletal support required for movement and locomotion (Kier & Smith 1985, Smith & Kier 1989). The basic principle of such a system of skeletal support is straightforward. At physiological pressures, muscle tissue is essentially incompressible and muscle contraction results in no significant change in volume [measurements suggest that the volume change is only 0.002% (Baskin 1967)]. Since the block of muscle is essentially constant in volume, a decrease in one dimension due to contraction of a given bundle of muscle fibers must result in an increase in another dimension. Since the muscle fibers are typically arranged with bundles that can control each of the three



**Fig. 1** Diagram of the ventral portion of the mantle of a loliginid squid. Each tissue block is oriented with the mantle cavity toward the top and the skin toward the bottom. The upper block of the mantle illustrates the arrangement of the muscle fibers. CM, circular muscle fibers; RM, radial muscle fibers; CMP, central mitochondria-poor zone of circular muscle fibers; SMR, superficial mitochondria-rich zones of circular muscle fibers. The lower block illustrates the organization of the connective tissue fibers (in black; muscle in gray). Note that the collagen fibers in intramuscular fiber system 1 (IM-1) are visible in both sagittal and frontal planes, indicating that an individual IM-1 fiber follows an oblique trajectory through the mantle. IT, inner tunic; IM-1, collagen fibers in intramuscular fiber system 1; IM-2, collagen fibers in intramuscular fiber system 2; IM-3, crimped collagen fibers in intramuscular fiber system 3. OT, outer tunic. [Loliginid sketch modified from a photograph in Norman 2000]

dimensions, a remarkably diverse array of deformations and movements can be produced. In addition to the complex arrangement of muscle fibers, many of the muscular-hydrostatic systems in cephalopods include arrays of collagenous connective tissue fibers. These fibers serve an extremely important role in control of shape change and in elastic energy storage for restoration of shape following muscle contraction.

In this review we will focus on the arrangement and

function of muscle and connective tissues in recent coleoid cephalopods. In keeping with the theme of the symposium for which this publication was prepared, we hope that the insight provided from an understanding of the recent forms will be of use in the interpretation of fossil coleoid structure, function and evolution.

## MANTLE

### *Musculature*

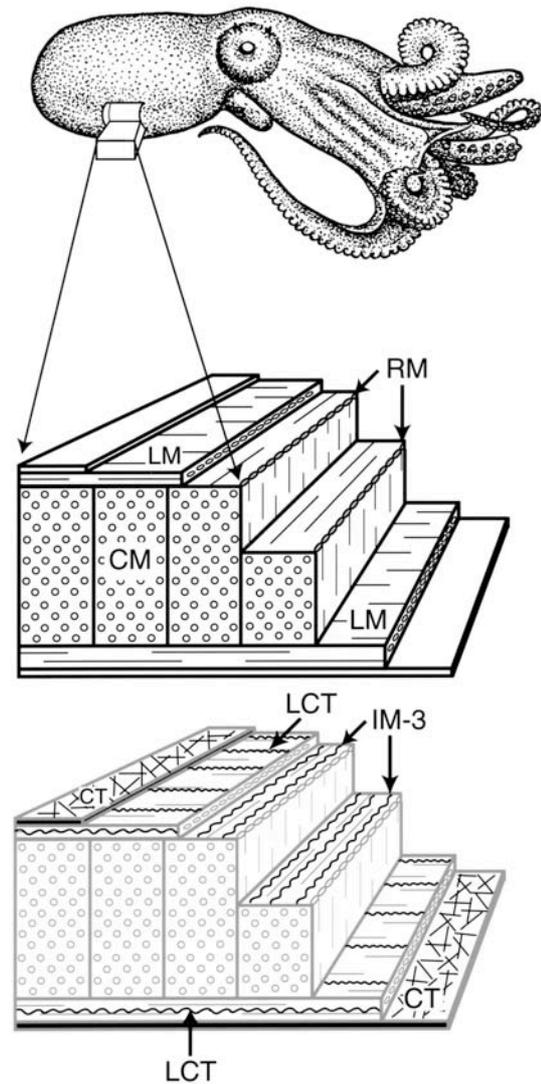
The mantle of coleoids serves important roles in ventilation and locomotion by jet propulsion. The structure and function of the mantle of loliginid and ommastrephid squids has received the greatest attention in the literature and will therefore be the focus of the following description, although descriptions of other coleoids will also be included. The mantle of loliginid and ommastrephid squids includes two predominant muscle orientations: circumferential muscle fibers (known as circular muscles) that constitute the bulk of the mantle wall and radial muscle fibers that extend from the inner to the outer surface of the mantle wall as partitions between the bundles of circular muscle fibers (Fig. 1; Marceau 1905, Williams 1909, Young 1938). Each circular muscle fiber is obliquely striated, uninucleate, 1 to 2 mm in length, up to 10  $\mu$ m in diameter, and is electrically coupled to adjacent circular muscle fibers, presumably by gap junctions (Bone *et al.* 1981, 1995, Milligan *et al.* 1997, Young 1938). The radial muscle fibers are also obliquely striated, uninucleate and may be up to 5  $\mu$ m in diameter (Bone *et al.* 1981, Mommsen *et al.* 1981).

The circular muscle fibers of a number of loliginid and ommastrephid squid species are differentiated into three zones: an outer zone adjacent to the external surface of the mantle, a central zone, and an inner zone adjacent to the inner surface of the mantle (Fig. 1). The circular muscle fibers of the inner and outer zones, known as superficial mitochondria rich (SMR) fibers (Preuss *et al.* 1997), contain large cores occupied by many mitochondria, show high succinic dehydrogenase (SDH) activity and have a large ratio of oxidative to glycolytic enzymes (Bone *et al.* 1981, Mommsen *et al.* 1981). By contrast, the circular muscle fibers of the

central zone, termed central mitochondria poor (CMP) fibers (Preuss *et al.* 1997), have few mitochondria, low SDH activity and a low ratio of oxidative to glycolytic enzymes (Bone *et al.* 1981, Mommsen *et al.* 1981). The blood supply to these zones parallels these differences and includes a dense capillary plexus in the inner and outer zones compared with a sparse capillary plexus in the central zone (Bone *et al.* 1981). The radial muscle fibers are similar in structure and in mitochondrial density to the CMP fibers (Bone *et al.* 1981, Mommsen *et al.* 1981) although Bone *et al.* (1994) suggest that radial muscle fibers may be aerobic given their repetitive activity in respiration. The metabolic differentiation of the circular muscle fibers is thought to be analogous to the subdivisions of red and white muscle observed in the vertebrates (Bone *et al.* 1981, Mommsen *et al.* 1981, Rome *et al.* 1988). The SMR circular muscle fibers, analogous to the red muscles of vertebrates, power the constant ventilatory movements and prolonged slow-speed swimming. The CMP circular muscle fibers, analogous to the white muscles of vertebrates, produce the brief escape jets (Bartol 2001, Bone *et al.* 1981, Gosline *et al.* 1983, Mommsen *et al.* 1981). In several species of loliginids, the relative abundance of SMR circular muscle fibers decreases substantially during growth (Preuss *et al.* 1997, Thompson & Kier 2001a, 2002).

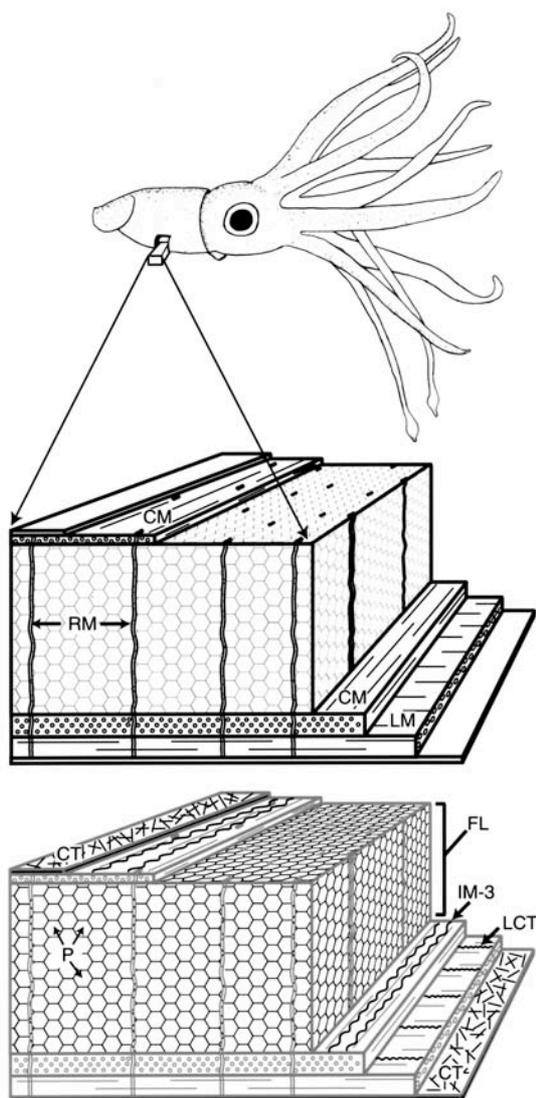
Unlike loliginid and ommastrephid squids, the mantle of many octopodids contains two layers of muscle fibers oriented parallel to the long axis of the mantle, in addition to the circular and radial muscle fibers. In *Octopus vulgaris*, for example, two layers of longitudinal muscle fibers enclose densely packed circular and radial muscles (Fig. 2, Wilson 1960). Neither the longitudinal nor the circular muscle fibers are differentiated into zones based on structural characteristics (unpublished observation). Little has been published about the vascular organization of the octopodid mantle.

The morphology of the mantle musculature of many gelatinous-bodied midwater and deepwater squids and octopods differs from that of the shallow water octopodids or the loliginid and ommastrephid squids described above (unpublished observations). In octopoteuthids, cycloteuthids, and some lepidoteuthids there are three orientations of muscle fibers in the mantle: a thin layer of longitudinal muscle fibers adjacent to the outer surface of the mantle, two



**Fig. 2** Diagram of the ventral region of the mantle of a shallow-water octopus. Each tissue block is oriented with the mantle cavity toward the top and the skin toward the bottom. The upper block illustrates the organization of the muscle fibers. CM, circular muscle fibers; LM, longitudinal muscle fibers; RM, radial muscle fibers. The lower block illustrates the arrangement of the connective tissue fibers (in black; muscle in gray). CT, feltwork of connective tissue fibers; IM-3, connective tissue fibers in intramuscular fiber system 3; LCT, longitudinal connective tissue fibers. [*Octopus* sketch modified from Nesis 1987]

relatively thin layers of circular muscle fibers near the inner and outer surfaces of the mantle, and radial muscle fibers (Fig. 3). In *Cirrothauma murrayi* Chun the arrangement of the muscles is similar but an additional layer of longitudinal muscle fibers is present along the inner surface of the mantle (Aldred *et al.* 1983). In mastigoteuthids, chiroteuthids, histioteuthids, and batoteuthids the arrangement of muscle layers is similar to that described above but longitudinal muscle



**Fig. 3** Diagram of the ventral portion of the mantle of a deep-water squid. Each tissue block is oriented with the mantle cavity toward the top and the skin toward the bottom. The upper block indicates the arrangement of the muscle fibers. CM, circular muscle fibers; LM, longitudinal muscle fibers; RM, radial muscle fibers. The lower block illustrates the organization of the connective tissues (in black; muscle in gray). CT, feltwork of connective tissue fibers; FL, gelatinous, fluid-filled layer; IM-3, connective tissue fibers in intramuscular fiber system 3; LCT, longitudinal connective tissue fibers; P, polyhedral connective tissue capsules. [Sketch of a histioteuthid based on a photograph in Norman 2000]

fibers are absent. In all the families of gelatinous-bodied cephalopods mentioned, the two layers of circular muscle fibers enclose a gelatinous layer. The gelatinous layer may constitute most of the mantle wall, as in octopoteuthids, lepidoteuthids, chiroteuthids, and *Cirrothauma murrayi* or may be a small fraction, as in batoteuthids and histioteuthids. It is unknown if the circular muscle is differentiated into

layers that differ in biochemical and morphological characteristics as observed in the loliginid and ommastrephid squids. Seibel *et al.* (2000) however, demonstrated the presence of enzymes important for both aerobic (citrate synthase) and anaerobic (octopine dehydrogenase) metabolism in the mantle musculature of more than 20 species of mid- and deep-water gelatinous-bodied cephalopods. The blood supply to the mantle muscles in these animals has not been studied in detail.

### Connective Tissue

The radial muscle fibers of loliginids and ommastrephids have their origin and insertion on the inner and outer tunics, robust layers of collagenous connective tissue fibers that lie beneath the skin on the inner and outer surface of the mantle (Fig. 1). The fibers of the tunics are arranged in layers of closely packed parallel fibers that are oriented either as right-handed or left-handed helices. The handedness of each layer in the tunic alternates and the fiber angle, the angle that a fiber makes with the longitudinal axis of the mantle, ranges from about  $17^\circ$  in *Sepioteuthis lessoniana* to  $27^\circ$  in *Loligo pealei* and *Lolliguncula brevis* (Thompson & Kier 2001a, Ward & Wainwright 1972). In *S. lessoniana*, the fiber angle of the tunics decreases during ontogeny from  $33^\circ$  in hatchlings to  $17^\circ$  in subadult animals (Thompson & Kier 2001a).

In addition to the connective tissue fibers of the tunics, the mantle also includes networks of connective tissue fibers, termed "intramuscular connective tissue fibers," that span the mantle wall (Bone *et al.* 1981, Gosline & Shadwick, 1983a, 1983b, Ward & Wainwright 1972). Three groups of intramuscular connective tissue fibers (IM) have been identified in the cuttlefishes and loliginid squids, and are denoted IM-1, IM-2 and IM-3 (Fig. 1). IM-1 fibers originate and insert on the inner and outer tunics and follow straight or slightly curved trajectories through the mantle wall (Ward & Wainwright 1972). Viewed in sagittal section, the IM-1 fibers are arranged at a low angle ( $28^\circ$  in *L. brevis*) relative to the long axis of the mantle (Ward & Wainwright 1972) (Fig. 1). In sections tangential to the surface of the mantle, the collagen fibers in IM-1 are also arranged at low angles ( $10^\circ$  to  $15^\circ$  in *Alloteuthis subulata*,  $32^\circ$  in *S. lessoniana*) relative to the long axis of the mantle (Bone *et al.*

1981, Thompson & Kier 2001a) (Fig. 1). Thus, the IM-1 fibers follow an oblique path through the mantle wall, relative to both tangential and sagittal planes.

IM-2 fibers also originate and insert on the tunics (Fig. 1). They are localized to the radial muscle bands, follow straight trajectories, and are arranged at an angle of about 55° to the mantle surface in *A. subulata*, *Sepia officinalis* and *S. lessoniana* (Bone *et al.* 1981, Curtin *et al.* 2000, Thompson & Kier 2001a).

IM-3 fibers, which are crimped or buckled in histological sections, are arranged parallel to the circular muscle fibers and are not attached to the tunics (Bone *et al.* 1981) (Fig. 1).

Measurements of the birefringence of the connective tissue fibers of IM-1 by Gosline and Shadwick (1983a) suggest that they are collagen. Transmission electron microscopy of IM-1, IM-2, and IM-3 in *L. pealei* by MacGillivray *et al.* (1999) revealed collagen fibers ranging from 1.5 to 4.5  $\mu\text{m}$  in diameter. Bone *et al.* (1981) reported that at least some of the connective tissue fibers of the mantle of *L. vulgaris* and *A. subulata* may be elastic fibers, based on histochemical staining and absence of the characteristic 68-nm repeat pattern typical of collagen fibers observed by transmission electron microscopy. MacGillivray *et al.* (1999), however, did not observe staining of intramuscular connective tissue fibers indicative of elastic fibers in *L. pealei*.

Published descriptions of the connective tissue organization of the mantle of octopodids are limited. The mantle of *Octopus bimaculatus* does not contain well-defined inner and outer tunics (unpublished observation). Instead, the connective tissue layers that enclose the mantle resemble a feltwork, with robust collagen fibers arranged in various orientations. IM-3 connective tissue fibers are present in the mantle of *O. bimaculatus* (Fig. 2). The IM-3 fibers exhibit histochemical staining properties consistent with collagen. Robust connective tissue fibers aligned parallel to the long axis of the mantle are also found in the two longitudinal muscle layers in the mantle (Fig. 2). Connective tissue fibers similar to the IM-1 and IM-2 fibers of squids are not observed in octopodids.

The mantle of many gelatinous-bodied squids and octopods also differs in connective tissue morphology from that described above (unpublished observations). The central gelatinous portion of the mantle wall is

reinforced by a three dimensional meshwork of sheets of robust connective tissue fibers (Fig. 3). These sheets consist of connective tissue fibers that are embedded in a matrix and form numerous small, polyhedral capsules that may be filled with ammoniacal fluids, other low-density fluids, or hemolymph. The fibers exhibit birefringence and histochemical staining properties consistent with collagen. Those gelatinous-bodied squids that have longitudinal muscle fibers (e.g. octopoteuthids, cycloteuthids, and some lepidoteuthids) also lack well-defined tunics; inner and outer tunics are present in gelatinous-bodied animals that lack longitudinal muscle fibers. IM-1 and IM-2 connective tissue fibers are absent in chiroteuthids, cycloteuthids, some lepidoteuthids, mastigoteuthids, and octopoteuthids. IM-3 connective tissue fibers are present in nearly all coleoids that have been examined.

### **Biomechanics**

The basic function of the mantle musculature of loliginids and ommastrephids depends on a muscular hydrostatic mechanism. During ventilation of the mantle cavity and jet locomotion, contraction of the circular muscle fibers decreases the diameter of the mantle, expelling water from the mantle cavity *via* the funnel. Lengthening of the mantle is prevented by the connective tissue fibers of the tunics (Ward & Wainwright 1972). Because the mantle wall is essentially constant in volume, decrease in mantle diameter by circular muscle contraction must also result in an increase in the thickness of the mantle wall, thereby extending the radial muscle fibers and stretching the connective tissue fibers of IM-1 and IM-2. Following circular muscle contraction, elastic recoil of the IM-1 and IM-2 connective tissue fibers and contraction of the radial muscle fibers cause the mantle wall to thin. This thinning results in an increase in the diameter of the mantle and expansion of the mantle cavity, thereby generating subambient pressure that refills the mantle cavity with water (see Curtin *et al.* 2000, Gosline & Shadwick 1983a, 1983b, Gosline *et al.* 1983, MacGillivray *et al.* 1999). Thinning of the mantle wall also stretches the IM-3 connective tissue fibers (Gosline *et al.* 1983).

During a locomotory jet, three phases are observed. The first phase is termed “hyperinflation” and involves

contraction of the radial muscles only, expanding the mantle cavity to a diameter that is larger than the resting mantle diameter (Gosline *et al.* 1983). The second phase, “the jet” occurs as the circular muscles contract. Elastic recoil of the IM-3 connective tissue fibers may aid the early stages of contraction of the circular muscles (Gosline *et al.* 1983). The final phase, “refilling” occurs as the mantle cavity re-expands, primarily due to elastic recoil of the IM-1 and IM-2 connective tissue fiber networks, often with assistance from radial muscle contraction (Gosline & Shadwick 1983a, Gosline *et al.* 1983). Additional assistance in refilling of the mantle may be provided by flow-induced pressure differentials when the animals are swimming at high velocities (Vogel 1987). Respiratory movements of the mantle are smaller than those of the locomotory jet and typically occur in the anterior half of the mantle only (Packard & Trueman 1974). Two patterns of respiratory movement occur in loliginid squids: 1) radial muscle contraction and water intake by mantle expansion (i.e., hyperinflation) followed by elastic recoil of the mantle and water expulsion; 2) mantle contraction due to circular muscle activation expels water from the mantle cavity followed by water intake as the mantle recoils elastically (Gosline *et al.* 1983). In European cuttlefish *Sepia officinalis* and possibly also in loliginid squids, contraction of the radial muscles fills the mantle cavity and inward movements of the muscular collar flaps of the mantle expel water from the mantle cavity (Bone *et al.* 1994).

Coleoids exhibit remarkable control over the mantle, from low amplitude respiratory movements to large amplitude contractions during escape-jet locomotion. In loliginids, the only squids in which neuromuscular anatomy and physiology have been well-studied, this fine control is likely the result of innervation of the circular muscle fibers by both giant and small diameter axons. The giant axons, which may exceed 800  $\mu\text{m}$  in diameter, activate the circular muscles in an all-or-none response during escape-jet locomotion (Young 1938). The small diameter axons range from 0.5 to 50  $\mu\text{m}$  (Bone *et al.* 1981) and produce graded contractions of the mantle when stimulated. They are hypothesized to control respiratory movements of the mantle and low-speed jet locomotion (Wilson 1960, Young 1938), although some of the small diameter axons of the mantle may

also serve as sensory fibers. Otis and Gilly (1990) found that the small diameter axons of *Loligo opalescens* could also initiate delayed escape-jet responses with or without giant axon activity. Interaction of the giant and non-giant axon systems may be important in modulating the magnitude of escape responses (Otis & Gilly 1990). Such interaction, however, may be limited to mature animals because the small diameter axons of newly hatched *L. opalescens* cannot elicit an escape response (Gilly *et al.* 1991).

The skeletal support of the mantle of gelatinous-bodied coleoids does not depend on a muscular hydrostatic mechanism. The gelatinous, fluid-filled chamber in the center of the mantle wall implies that skeletal support is analogous to the closed hydrostatic skeletal support systems of annelids or the foot of gastropod molluscs. Nevertheless, the principles of mechanical function of the mantle are probably conserved among all coleoids: the volume of the mantle wall is essentially constant, circular and radial muscle fibers act antagonistically, and the tunics prevent lengthening of the mantle. In those animals that lack well-defined tunics, longitudinal muscle fibers control mantle length. One important exception to the similarity in mechanical function of the mantle is elastic energy storage. The arrangement of the IM-1 and IM-2 collagen fibers of loliginids, ommastrephids, and cuttlefishes permits a substantial fraction of the energy expended by the circular and radial muscle fibers to be stored as elastic energy. The geometry of IM-1 and IM-2 fibers makes the mantle mechanically anisotropic and allows relatively small changes in the thickness of the mantle wall (e.g. during contraction of the circular muscles) to store significant elastic energy (Curtin *et al.* 2000, Gosline & Shadwick 1983a, MacGillivray *et al.* 1999). In contrast, the polyhedral connective tissue capsules that support the fluid-filled compartments of the mantle wall of gelatinous-bodied coleoids probably make the mantle mechanically isotropic. Although the geometry of the connective tissue capsules are ideal for limiting deformation of the mantle equally in three dimensions, we predict that the collagen fibers within the capsules will store only a minor component of the energy expended by the circular and radial muscle fibers during jet locomotion.

## FUNNEL

The funnel, also known as the siphon, directs the flow of water from the mantle cavity during respiration and jet locomotion. The tip and trunk of the funnel are highly flexible and may be pointed in nearly any direction (Tateno 1992, O'Dor 1988, Zuev 1966). The aperture at the tip of the funnel of squids may be varied during jet locomotion to permit fine modulation of the thrust of the jet (O'Dor 1988, Zuev 1966).

### *Musculature and Connective Tissue*

In loliginid squids, the funnel consists of obliquely striated muscle fibers oriented in three mutually perpendicular planes. Longitudinal muscle fibers are located in bundles along the outer surface of the trunk of the funnel. Circular muscle fibers compose the bulk of the funnel, but thin bands of radial muscle extend through the thickness of the funnel wall in an arrangement analogous to the radial muscles of the mantle (Williams 1909).

Thin layers of connective tissue fibers along the outer and inner surfaces of the funnel enclose the musculature. Other than Young's (1938) observation that connective tissue fibers are present in the musculature of the funnel, information on the connective tissues is limited.

### *Biomechanics*

The organization of the muscle fibers and connective tissue fibers of the funnel implies that its function depends on a muscular hydrostatic mechanism. Protrusion and retraction of the funnel trunk may be accomplished *via* contraction of the circular and longitudinal muscle fibers, respectively. Contraction of the circular muscle fibers will also decrease the diameter of the funnel trunk. An increase in the diameter of the funnel trunk may be accomplished by contraction of the radial muscle fibers and/or the longitudinal muscle fibers of the funnel. Bending of the funnel tip and trunk may be accomplished by contraction of the radial muscle fibers while longitudinal muscle fibers on the side of the bend contract. The tonus of the longitudinal muscle fibers on the side of the funnel opposite the bend may affect the

degree of bending.

## FUNNEL, CEPHALIC, AND NUCHAL RETRACTOR MUSCLES

Many coleoids possess muscles that control the positions of the funnel and head relative to the mantle. In loliginid squids, a pair of funnel retractor muscles inserts on the dorsal portion of the funnel and originates on the chitinous gladius of the mantle (Williams 1909). Activity of the funnel retractor muscles helps to support and position the funnel during jet locomotion.

The cephalic and nuchal retractor muscles are tube- or cone-shaped and enclose portions of the digestive tract. The cephalic muscle originates on both the gladius and nuchal cartilage, and inserts on the posterior portion of the cephalic cartilage that encloses the brain (Williams 1909). The nuchal retractor is a robust muscle that originates on the pen (immediately anterior to the cephalic retractor) and inserts on the dorso-lateral edges and ventral surfaces of the nuchal cartilage (Williams 1909). The functions of the cephalic and nuchal retractor muscles of loliginid squids include movement of the head in and out of the mantle cavity.

### *Musculature*

Longitudinal and transverse muscle fibers compose the funnel retractor muscles of loliginid squids (Young 1938). Circular muscle fibers have not been reported. The longitudinal muscle fibers of the funnel retractor are continuous with the longitudinal muscle fibers of the funnel itself (Williams 1909, Young 1938).

The orientation of muscle fibers in the nuchal and cephalic retractors is similar. In each, a thin layer of circular muscle fibers encloses a thick tube of longitudinal muscle fibers. Transverse muscle fibers whose orientation resembles that of the radial muscles of the mantle are also present (Young 1938).

### *Connective Tissue*

A thin layer of connective tissue fibers encloses the funnel, cephalic, and nuchal retractor muscles. In

addition, sagittal sections of the funnel retractor muscles of the loliginid squid, *Sepioteuthis lessoniana*, reveal connective tissue fibers that span the entire width of the muscle. The connective tissue fibers exhibit staining reactions consistent with collagen, are birefringent, and are arranged at an angle of about 55° to the long axis of the muscle (unpublished observations).

### **Biomechanics**

The organization of the muscle and connective tissue fibers in the funnel, cephalic, and nuchal retractors is consistent with a muscular hydrostatic mechanism. Shortening of the funnel retractors may occur *via* contraction of the longitudinal muscle fibers and relaxation of the transverse muscles. Elongation of the funnel retractor muscles may be accomplished by contraction of the transverse muscle fibers and relaxation of the longitudinal muscles. The orientation (i.e., about 55° to the long axis of the muscle) of the connective tissue fibers spanning the width of each funnel retractor is appropriate to resist elongation and shortening of the muscle nearly equally (see Harris & Crofton 1957). Therefore, the connective tissue fibers may help antagonize both the transverse and longitudinal muscle fibers and may also limit changes in the shape of the muscle.

Shortening of the cephalic and nuchal retractors and withdrawal of the head into the mantle cavity may occur *via* contraction of the longitudinal muscle fibers and relaxation of the circular and transverse muscle fibers. Protrusion of the head out of the mantle cavity may be accomplished by contraction of the circular or the transverse muscle fibers and relaxation of the longitudinal muscle fibers.

Although innervation of the funnel, cephalic, and nuchal retractor muscles is complex, portions of all three muscles are innervated by the same giant axon (Young 1938). This highlights the close functional relationship of the three muscles during jet locomotion. For example, withdrawal of the head into the mantle cavity occurs at the onset of escape-jet locomotion (Thompson & Kier 2001b) as a result of simultaneous activation of the cephalic and nuchal retractor muscles (Young 1938).

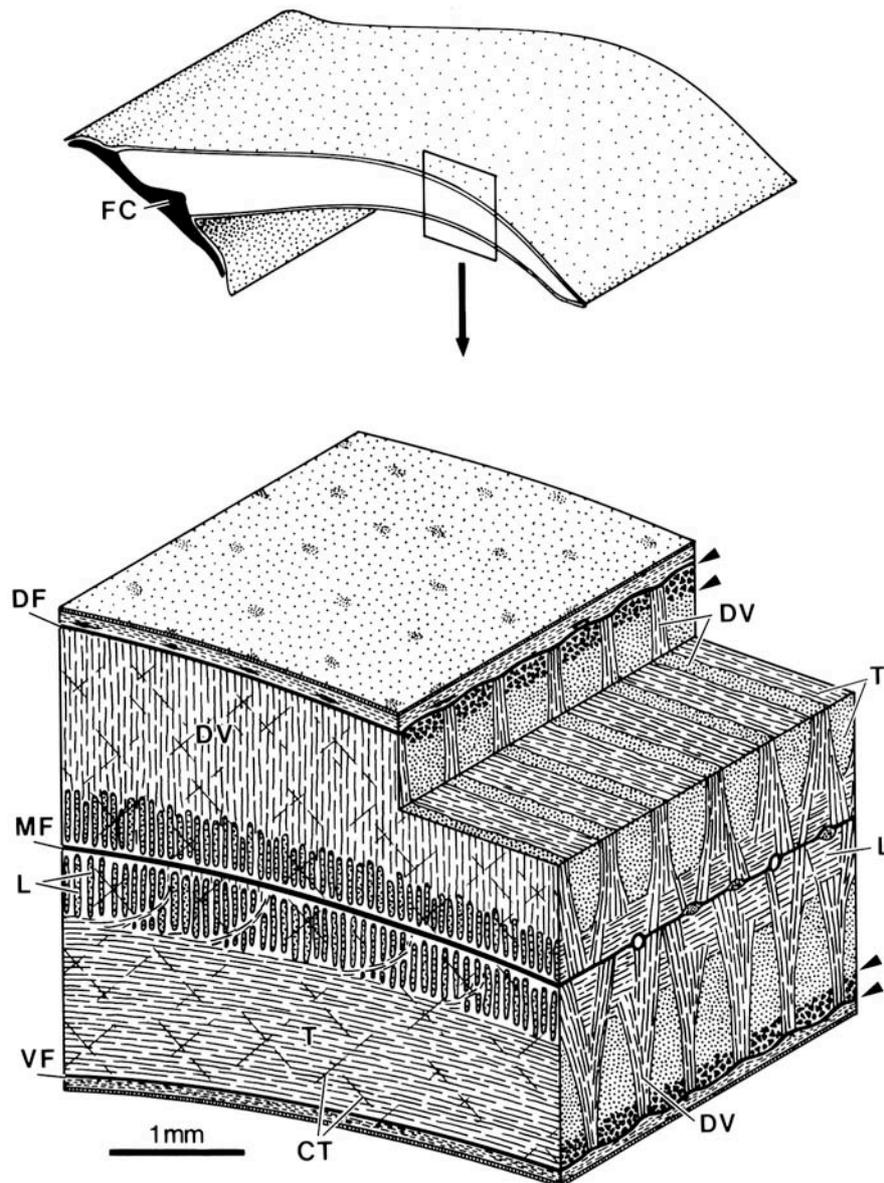
### **FINS**

The fins of cuttlefishes and squids produce rhythmic undulatory waves that are used in locomotion and hovering. Although much of the thrust for locomotion is produced by contraction of the mantle during jet propulsion, the fins aid in producing thrust at low swimming speeds, in providing stability, and in providing lift for hovering (Bidder & Boycott 1956, Boycott 1958, Hoar *et al.* 1994, O'Dor & Webber 1986, Russel & Steven 1930). The fins of cuttlefishes, loliginid and ommastrephid squids lack rigid supportive elements and instead provide yet another example of a three-dimensional array of musculature termed a 'muscular hydrostat'.

The profile and aspect ratio of the fins of coleoids varies widely, and includes examples ranging from the narrow fins of cuttlefishes that extend along the entire length of the mantle to the more wing-like fins of many pelagic squids (Hoar *et al.* 1994, Sweeney *et al.* 1992). The structure and function of the fins of the cuttlefish (*Sepia officinalis*) and of the loliginid squids (*Loligo forbesi* and *Sepioteuthis sepioidea*) have received the most attention previously and will therefore be described here.

### **Musculature**

The general arrangement of the musculature of the fins of cuttlefishes and loliginid squids is similar and includes bundles of obliquely striated muscle fibers oriented in three mutually perpendicular directions (Fig. 4). A dorsal and a ventral division of the musculature is observed, separated by a median connective tissue fascia. In both the dorsal and ventral divisions of the fin, bundles of transverse muscle fibers originate on the fin cartilage at the base of the fin and extend laterally toward the fin margin, sending off small bundles of fibers that insert on the median fascia. The transverse muscle bundles in both the dorsal and ventral portions of the fin are separated from one another by sheets of dorsoventral muscle fibers that originate on the median fascia. In the dorsal portion of the fin these fibers extend to insert on an additional fascia called the dorsal fascia that is located adjacent to the dermis on the dorsal surface of the fin. An analogous ventral fascia serves as the site of insertion



**Fig. 4** Diagram of the fin of *Sepia officinalis* showing the arrangement of the muscle and connective tissue fibres. CT, crossed oblique connective tissue fibres; DF, dorsal connective tissue fascia; DV, dorsoventral muscle; FC, fin cartilage; L, longitudinal muscle; MF, median connective tissue fascia; T, transverse muscle; VF, ventral connective tissue fascia. The arrowheads delimit the dorsal and ventral zones of transverse muscle fibres with more extensive mitochondrial cores (the oxidative fibres). The scale bar indicates the scale for the lower portion of the diagram. [From Kier *et al.* (1989) with permission of the publisher]

of the dorsoventral fibers in the ventral portion of the fin. In addition to the transverse and dorsoventral muscle fibers, a layer of longitudinal muscle is present adjacent to the dorsal and the ventral surface of the median fascia. Examination of the fibers of the transverse muscle bundles using electron microscopy revealed that the mitochondrial content of the fibers was not uniform across the muscle bundles (Kier 1989). Instead, transverse muscle fibers in narrow zones adjacent to the dorsal and ventral fasciae include a significantly larger mitochondrial core than the

remainder of the fibers and resemble the aerobic muscle fibers observed in the mantle musculature (Bone *et al.* 1981, Mommsen *et al.* 1981). The dorsoventral and longitudinal muscle bundles lack muscle fibers with a large mitochondrial core (Kier 1989).

#### **Connective Tissues**

The three fasciae described above include layers of birefringent connective tissue fibres that exhibit

staining reactions typical of collagen. The fibers of the dorsal and ventral fasciae show a slight degree of preferred orientation in the transverse and longitudinal directions, while those of the median fascia are arranged as a feltwork and are embedded in an amorphous matrix. Some of the fibers in the median fascia exhibit staining reactions typical of elastin. In addition to the three fasciae, birefringent connective tissue fibers with staining reactions typical of collagen are embedded in the fin musculature. These fibers form a delicate crossed fiber meshwork of obliquely oriented fibers embedded in the dorsoventral and transverse muscle bundles and extend between the fascia at an angle of approximately 45° (Fig. 4; Kier 1989).

### **Biomechanics**

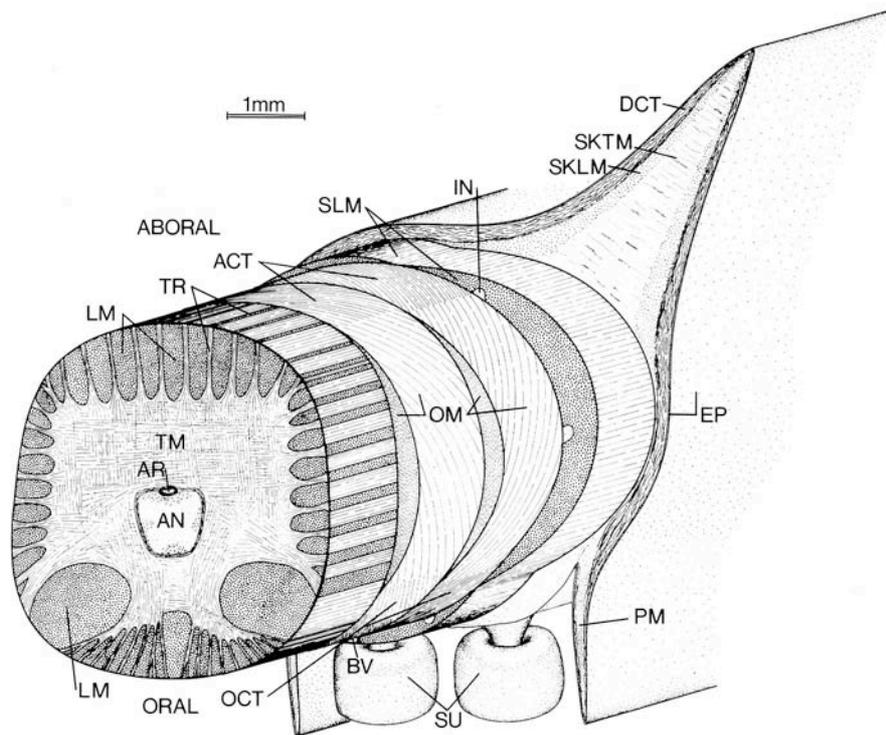
Support and movement of the fin depends on a muscular hydrostatic mechanism. The general form of the movement of a given portion of the fin during the passage of an undulatory wave involves sequential bending dorsally and then ventrally. Dorsal bending requires that the dorsal portion of the fin be reduced in width (laterally compressed) relative to the ventral portion and ventral bending requires an analogous reduction in width of the ventral portion of the fin. The transverse muscle bundles can provide this lateral compression and thus their contraction is required for active bending. This contraction, however, will cause significant bending only if the lateral compressional force on the opposite side of the fin is resisted. Without this resistance, contraction of the transverse muscle bundles will simply reduce the width of the fin by pulling the lateral fin margin medially. Like other muscular hydrostats, the fin is essentially constant in volume and thus any reduction in the width of the fin must result in either an increase in the thickness of the fin or an increase in the length (or both). Increase in length can be resisted by contractile activity of the longitudinal muscles and the fin cartilage at the base of the fin. Increase in thickness can be resisted by contractile activity in the dorsoventral muscles or by the array of crossed connective tissue fibers embedded in the musculature (Johnsen & Kier 1993).

Based on an analysis of muscle activity patterns during fin movement in the cuttlefish using electromyography (Kier *et al.* 1989) and quantitative

modelling of the mechanical role of the crossed connective tissue fibers (Johnsen & Kier 1993) the following interpretation of fin movement has emerged. During the gentle, low amplitude, low frequency fin movements observed during hovering or when the animals rest on the substratum, fin bending is caused by contraction of the thin layer of aerobic fibers of the transverse muscle bundles. Activity of the other muscle orientations is not observed (Kier *et al.* 1989) and the required resistance to lateral compression is provided by the network of connective tissue fibers embedded in the musculature (Johnsen & Kier 1993). During the brief bursts of high amplitude, high frequency fin beating observed during rapid locomotion and maneuvering, the anaerobic transverse muscle fibers are recruited and the required resistance to lateral compression is provided by contractile activity of the dorsoventral muscles on the opposite side of the fin, perhaps with a contribution of the longitudinal muscles for control of overall length of the fin. In addition to providing resistance to lateral compression, the quantitative modelling studies suggest that the crossed connective tissue fibers may store elastic energy during fin bending, allowing the fin to function as a harmonic oscillator and thereby increasing the efficiency of the fins during locomotion (Johnsen & Kier 1993). Although little is known about neuromuscular control mechanisms in the fins, there is evidence for mechanoreceptors that may sense fin deformation and in some way contribute to coordination of fin movements (Kier *et al.* 1989).

### **ARMS AND TENTACLES**

Coleoid cephalopods possess an array of appendages encircling the mouth that serve in a remarkable variety of functions. In the squids and cuttlefishes, five pairs of appendages are present. One pair, termed 'tentacles', is specialized for prey capture by remarkably rapid elongation. For example, in *Loligo pealei* the tentacles elongate by over 80% at peak extension velocities of over 2 m s<sup>-1</sup> and peak accelerations of 250 m s<sup>-2</sup> (Kier & van Leeuwen 1997, van Leeuwen & Kier 1997). During a prey capture strike, the tentacles strike the prey and attach to it with suckers that are present on an expanded terminal portion termed the 'club'. Twisting



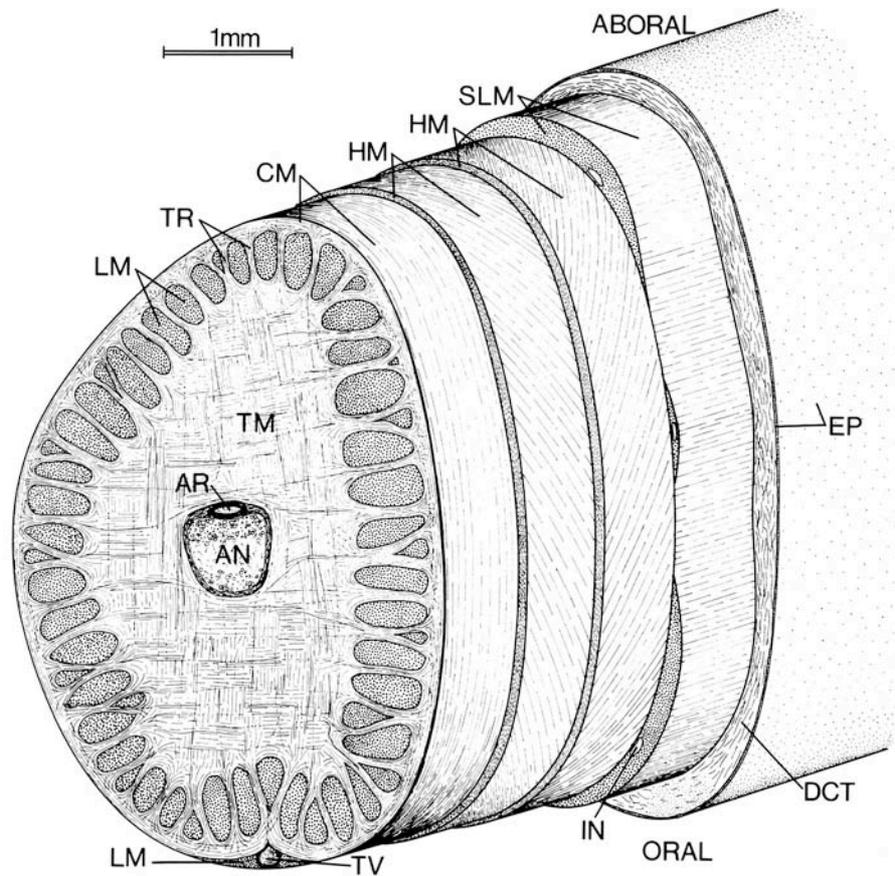
**Fig. 5** Diagram of arm of a loliginid squid. AN, axial nerve cord; ACT, aboral connective tissue (fibrous); AR, artery; BV, superficial brachial vein; DCT, dermal connective tissue; EP, epithelium; IN, intramuscular nerve cord; LM, longitudinal muscle; OCT, oral connective tissue (fibrous); OM, oblique 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. [From Kier, (1982) with permission of the publisher]

of the tentacles about their long axis is frequently observed during elongation. The tentacles then shorten and the prey is withdrawn within reach of the 4 pairs of arms, which subdue and manipulate it for ingestion using primarily bending and twisting movements. The arms of squids and cuttlefishes are also involved in swimming and steering movements, behavioral displays, and reproduction. Octopuses lack the specialized prey capture tentacles observed in squids and instead possess four pairs of arms, which are used for locomotion, prey capture, exploring and manipulating objects, grooming and behavioral displays. The arms of octopuses are capable of a remarkable diversity of movements including elongation, shortening, bending and twisting.

### ***Musculature and Connective Tissues***

Three general groups of muscles are observed in the arms and tentacles of coleoid cephalopods: transverse muscle; longitudinal muscle; and helical or oblique muscle. The arrangement observed in the arms of squids is shown in Fig. 5. The transverse muscle mass

occupies the core of the arm surrounding the central axial nerve cord, and consists of muscle fibers oriented perpendicular to the long axis of the arm. In the tentacles of squids, the transverse muscle fibers are continuous with a thin layer of circular muscle fibers. Groups of fibers termed 'trabeculae' (Graziadei 1965) interdigitate with bundles of longitudinal muscle that are oriented parallel to the long axis of the arm. The transverse muscle fibers have their origin and insertion on crossed fiber connective tissue layers both orally (oral = side of arm facing the mouth) and aborally and on the epimysial connective tissues surrounding a pair of right- and left- handed oblique muscles on each side. The oblique muscles in turn have their origin and insertion on the oral and aboral crossed fiber connective tissue layers. The fiber angle (angle that a fiber makes with the long axis - approximately  $72^\circ$  in *Loligo pealei*) of the connective tissue fibers is the same as that of the associated oblique muscles. Additional superficial layers of longitudinal muscle are present surrounding the core of musculature described above (Kier 1982). All of the muscles of the arms and tentacles consist of obliquely striated fibers with the



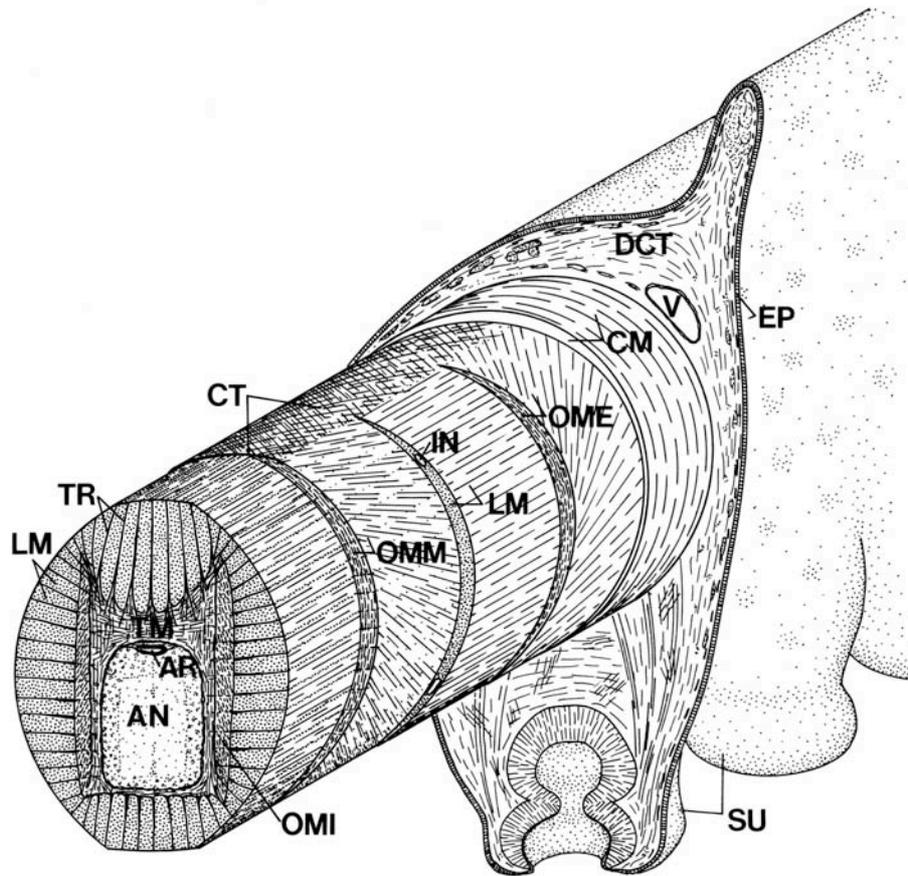
**Fig. 6** Diagram of tentacular stalk of a loliginid squid. AN, axial nerve cord; AR, artery; CM, circular muscle; DCT, dermal connective tissue; EP, epithelium; HM, helical muscle; IN, intramuscular nerve cord; LM, Longitudinal muscle; SLM, superficial longitudinal muscle; TM, transverse muscle; TR, trabeculae of transverse muscle; TV, superficial tentacular vein. [From Kier (1982) with permission of the publisher]

exception of the transverse and circular muscles of the tentacles, which are cross-striated (see below).

The arrangement of the musculature of the tentacles of squids is shown in Fig. 6. As in the arm, the core is occupied by a large mass of transverse muscle surrounding a central axial nerve cord. Groups of transverse muscle fibers extend peripherally and interdigitate with bundles of longitudinal muscle around the perimeter of the tentacle cross-section. After passing between the longitudinal muscle bundles, some of the transverse muscle fibers turn and become part of a circular muscle layer and others extend to insert on a connective tissue layer surrounding the circular muscle layer. The circular muscle layer is in turn wrapped by two thin helical muscle layers, one with fibers arranged as a right-handed helix and the other with fibers arranged as a left-handed helix [the fiber angle is approximately  $36^\circ$  in an extended tentacle and approximately  $67^\circ$  in a retracted tentacle, see Kier (1982)]. Additional longitudinal muscle fibers are

observed in thin layers surrounding the circular muscle layer (Guérin 1908, Kier 1982).

The arrangement of the musculature of the arms of octopuses is shown in Fig. 7. As in the arms and tentacles of squids, the core of the arm is occupied by a mass of transverse muscle fibers. Groups of transverse fibers extend toward the periphery as thin trabeculae that interdigitate between longitudinal muscle bundles and insert on a crossed-fiber connective tissue sheet both orally and aborally and on epimysial connective tissue of a median oblique muscle laterally. As in the arms of squids, right- and left-handed oblique muscles (the median oblique muscles and the external oblique muscles) have their origin and insertion on these crossed-fiber connective tissue sheets, although the two muscles are separated by an additional longitudinal muscle layer on each side. There is also an additional obliquely arranged muscle pair, the internal oblique muscle which is not found in the arms of squids and is located between the transverse muscle and the



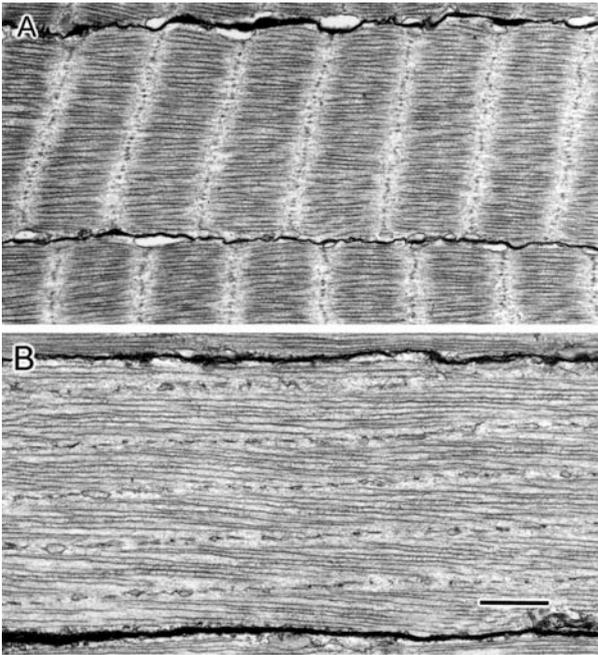
**Fig. 7** Diagram of the arm of *Octopus*. AN, Axial nerve cord; AR, artery; CM, circumferential muscle; CT, connective tissue sheath; DCT, dermal connective tissue; EP, epidermis; IN, intramuscular nerve; LM, longitudinal muscle; OME; external oblique muscle; OMI, internal oblique muscle; OMM, median oblique muscle; SU, sucker; TM, transverse muscle; TR, trabeculae; V, vein. [From Kier (1988) with permission of the publisher]

longitudinal muscle bundles laterally. An additional thin layer of circumferential muscle wraps the outer oblique muscle of the octopus arm (Colasanti 1876, Graziadei 1971, Guérin 1908, Kier 1988, Matzner *et al.* 2000, Sumbre *et al.* 2001, Tittel 1961, 1964, Yekutieli *et al.* 1998).

### **Biomechanics**

Support and movement of the arms and tentacles of coleoids again depends on a muscular hydrostatic mechanism. Since the arms and tentacles consist principally of essentially incompressible muscle, the volume can be considered to be constant. In the case of the tentacles of squids or the arms of octopuses, which both show significant elongation, contraction of the transverse muscle (and associated circular muscle in the tentacles) decreases the cross-section, and because the appendage is constant in volume, the length must increase. The transverse muscle is antagonized by the

bundles of longitudinal muscle, which shorten the appendage and reextend the transverse muscle fibers. Because transverse muscle contraction decreases an area ( $L^2$ ) and this results in an increase in length ( $L^1$ ) the displacement is amplified. For instance, a 70% elongation of the tentacles is produced by only a 23% decrease in tentacle diameter (see Kier 1982, Kier & Smith 1985, van Leeuwen & Kier 1997). In the arms of squids and octopuses, the transverse and longitudinal muscles also play a role in bending movements. Bending results from selective contraction of longitudinal muscle on one side of the arm. In order for bending to occur, however, the longitudinal compressional force must be resisted, otherwise longitudinal muscle contraction will simply shorten the arm. The transverse muscle fibers are arranged to resist this compressional force because any shortening of the essentially constant volume arm must result in an increase in cross-section. Thus, bending movements require simultaneous contraction of longitudinal



**Fig. 8** Transmission electron micrographs of longitudinal sections of the transverse muscle fibres of the tentacle (A) and arm (B) of *Loligo pealei*. The extensive sarcoplasmic reticulum (SR) of the cross-striated tentacle fibres is visible in A. Note the short sarcomeres and short thick filaments of the tentacle fibres in A compared with the much longer thick filaments apparent in the obliquely striated arm fibres in B. The scale bar length equals 1  $\mu\text{m}$ . [From Kier & Curtin (2002) with permission of the publisher]

muscle and transverse muscle (see Kier 1982, Kier & Smith 1985, Smith & Kier 1989). As can be seen in Figs 5, 6 and 7 the longitudinal muscles are typically situated around the perimeter of the cross-section of the arm or tentacle. Such a location away from the neutral axis has mechanical significance since it results in a greater bending moment than a more central location.

Torsion or twisting movements of the arms and tentacles of coleoids are produced by contraction of the helical or oblique muscle layers. The direction of torsion (i.e., clockwise vs. counter clockwise) depends on the handedness of the contracting helical or oblique muscle layer. Torsion in both directions is observed in the arms and tentacles of coleoids and both right- and left-handed helical muscle layers are present in all appendages examined thus far. The torsional moment is greatest if the helical or oblique muscle layers are located peripherally in the arm or tentacle, away from the neutral axis and this is indeed where they are typically located. In this regard the functional role of the internal oblique muscle of the arms of octopuses is

perplexing, since it occupies a more central location than the other two sets of oblique muscles.

### *Muscle Specialization in the Tentacles of Squids*

The overall arrangement of the musculature of the arms and tentacles of squids is quite similar (compare Figs 5 and 6), yet as described above, the functional role of the musculature is dramatically different. In the arms, the transverse muscle provides the support required for the relatively slow bending movements while in the tentacles, the transverse muscle is responsible for the extremely rapid elongation that occurs during prey capture.

What specializations of the tentacle muscle allow for this dramatic difference in behavior? The most significant difference in the transverse muscle of the tentacles is the ultrastructure. Unlike the obliquely striated muscle that characterizes virtually all of the musculature of coleoids, the muscle fibers of the transverse muscle of the tentacles are cross-striated with unusually short sarcomeres and myofilaments (Kier 1985, 1996, Kier & Curtin 2002) (Fig. 8). For instance, in *Loligo pealei*, the thick myofilaments of the obliquely striated muscle fibers of the arms are approximately 7.4  $\mu\text{m}$  while those in the cross striated tentacle fibers are approximately 0.8  $\mu\text{m}$  (Kier & Curtin 2002). The remarkably short myofilaments and sarcomeres of the tentacle fibers result in more elements in series per unit length of fiber. Since shortening velocities of elements in series are additive (Huxley & Simmons 1972, Josephson 1975, van Leeuwen 1991), this ultrastructural specialization results in a dramatic increase in the shortening velocity of the tentacle fibers. Indeed, recent measurements (Kier & Curtin 2002) show the shortening velocity of the tentacle fibers to be an order of magnitude higher (approximately  $15 L_0 \text{ s}^{-1}$  for the tentacle transverse muscle *versus*  $1.5 L_0 \text{ s}^{-1}$  for the arm transverse muscle at  $19^\circ\text{C}$ ).

Although significant ultrastructural differences are observed between the tentacle and arm transverse muscle, comparison of samples of myofilament preparations of the two muscle fiber types using sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE) showed little evidence of differences in contractile protein isoforms (Kier 1991,

Kier & Schachat 1992). In addition, peptide mapping of myosin heavy chains from the two muscle fiber types failed to demonstrate a difference between the tentacle and arm fibers (Kier & Schachat 1992). These biochemical studies, in conjunction with the ultrastructural analyses provide an interesting contrast to the situation observed in vertebrate skeletal muscle fiber types, where the ultrastructural arrangement is relatively invariant (Eisenberg 1983) but significant biochemical heterogeneity is observed (see for example Bandman 1985, Reiser *et al.* 1985, 1988, 1996, Schiaffino *et al.* 1988, Sweeney *et al.* 1988). In the squids, specialization for high shortening speed appears to have occurred primarily through changes in the dimensions and arrangement of the myofilament lattice, rather than through changes in biochemistry.

An analysis of ultrastructural differentiation of the transverse muscle of the arms and the tentacles in the loliginid squid *Sepioteuthis lessoniana* showed that for the first two weeks after hatching, the tentacle transverse muscle fibers do not show the adult ultrastructure and are indistinguishable from the obliquely striated fibers of the transverse muscle of the arms. Transverse striation of the tentacle fibers appears at approximately 3 weeks and the adult ultrastructure is finally present by 4-5 weeks after hatching. High-speed video recordings of prey capture show correlated behavioural changes. During the first 2-3 weeks after hatching, the animals do not employ the rapid tentacular strike; instead, they jet forward and capture the prey with splayed arms and tentacles (Kier 1996). This pattern of development is of interest in the context of the presumed evolutionary history of the arms and tentacles. Based on developmental and comparative data, the ancestral coleoid is thought to have possessed ten similar arm-like appendages (Naef 1921-1923, Boletzky 1993). In the decapods (sepioids and teuthoids) arm pair IV was modified and elaborated to form the tentacles while in the octopods arm pair II is believed to have been lost. The similarity in gross arrangement between the arms and tentacles of squids is thus not surprising in this light. In addition, the most parsimonious hypothesis is that the ancestral muscle striation pattern in cephalopods was obliquely striated and the ontogenetic transition from obliquely striated to cross-striated may reflect phylogeny (Kier 1996).

## SUCKERS

The suckers of coleoid cephalopods are used for a remarkable variety of tasks including locomotion, anchoring the animal to the substratum, holding prey, cleaning maneuvers, chemotactile recognition, behavioural displays, and manipulating, sampling and collecting objects (Packard 1988). The structure and function of the suckers of octopuses has received the most attention previously and so will be the focus of the description that follows. Two major divisions of the suckers of octopus are recognized. The exposed, disc-like portion of the sucker, termed the infundibulum (Girod 1884), is flattened against the surface of the object when the sucker is attached. It is covered by a chitinous cuticle or sucker lining and bears a series of radial grooves and ridges (Naef 1921-1923, Nixon & Dilly 1977, Packard 1988). A rim of loose and folded dermis and epithelium encircles the infundibulum and is separated from it by a circumferential groove. At the center of the infundibulum is an orifice that opens into a spherical cavity called the acetabulum, the second major division of the sucker. The inner surface of the acetabulum is covered by a continuation of the chitinous cuticle (Hunt & Nixon 1981) that covers the infundibulum. The radial grooves, in combination with tiny denticles or pegs that cover the surface of the chitinous lining of the infundibulum, may be important in transmitting the reduced pressure in the acetabulum underneath the infundibulum, establishing a pressure differential over the entire area of the infundibulum and pressing it against the substratum. This may be of considerable importance in increasing the resistance to shearing forces (for details see Kier & Smith 1990, 2002).

### *Musculature and Connective Tissues*

As in the other coleoid cephalopod organs and structures described above, a tightly packed three-dimensional array of musculature characterizes the suckers of octopuses (Girod 1884, Guérin 1908, Kier & Smith 1990, Nachtigall 1974, Niemiec 1885, Tittel 1961, 1964). Three major obliquely striated muscle fiber orientations are observed: 1) radial muscles that traverse the wall; 2) circular muscles arranged



in the acetabular cavity resists significant expansion and a decrease in pressure in the cavity balances the expansive force of the radial muscle of the acetabular wall. Because of the high bulk modulus of water in the acetabular cavity, it behaves mechanically like a solid in tension. The radial muscles of the acetabulum are antagonized by the meridional and circumferential muscle bundles which, upon contraction, decrease the circumference and thereby increase the thickness of the acetabular wall (Kier & Smith 1990, 2002).

The infundibulum of the sucker is responsible for formation of a watertight seal and must therefore be flexible and dexterous in order to conform to the wide variety of shapes and textures of objects to which the suckers attach. As in the acetabulum, the movements and deformations depend on a muscular-hydrostatic mechanism. Radial muscle contraction thins the infundibular wall and increases the diameter of the infundibulum. The radial muscles are antagonized by the meridional muscles, which upon contraction decrease the diameter of the infundibulum. Contraction of the circumferential muscle bundles constricts the infundibulum to a conical shape. It is likely that simultaneous contraction of the meridional and radial muscles flattens the infundibulum and bends its rim towards the acetabulum. A muscular-hydrostatic mechanism may be particularly advantageous because highly localized and complicated bends and deformations may be produced at any location in the infundibulum (Graziadei 1962, Graziadei & Gagne 1976a, b, Kier & Smith 1990, 2002). The infundibulum can thus be deformed to closely match the contours of the surface and provide a watertight seal.

The muscular-hydrostatic mechanism can generate large pressure differentials between the ambient pressure and pressure inside the sucker, but it appears to require constant muscle contraction. It is common, however, to observe an octopus remain attached for many hours to an object or to the wall of an aquarium. This may imply that the suckers possess a mechanism of elastic energy storage that could be used to maintain sub-ambient pressures without significant muscle activity. Such a mechanism is suggested by the presence of intramuscular crossed connective tissue fibers in the roof of the acetabulum. As described above for the mantle, the intramuscular connective tissue fibers will be strained if force is applied to the sucker roof that increases its thickness. The connective

tissue fibers are collagenous and thus they have high resilience and can store significant strain energy. Once the force that thickens the acetabular wall is removed, the strain energy stored in the fibers exerts a force that thins the roof and tends to expand the acetabular cavity. Long-term attachment may therefore be provided if the acetabular roof is first thickened by contraction of the meridional and circular muscles, storing elastic energy in the intramuscular fibers, followed by sealing of the sucker to an object. When the meridional and circular muscles relax, the energy stored in intramuscular fibers will then exert a force tending to thin the wall, reducing the pressure in the acetabular cavity. Since the water filling the sucker has a high bulk modulus, the volume change in the acetabular cavity during this process is likely to be very small. Indeed, the tensile properties of water have important general implications for the attachment forces of the suckers (see Smith 1991, 1996).

#### *Decapod Suckers*

The suckers of decapod coleoids differ from those of the octopodids described above because they are attached to the arms or tentacles by a muscular stalk or pedicle. The stalk includes connective tissue and longitudinal and transverse muscle fibers that allow elongation, shortening and bending motions similar to that described above for the arms (Guérin 1908). In addition, the acetabulum is lined with a stiff inner cylinder of chitin that is often equipped with tooth-like projections that may aid attachment and prevent shear (Hunt & Nixon 1981, Nixon & Dilly 1977). The wall and roof of the acetabulum and infundibulum includes radial, meridional and circular muscles (Guérin 1908) that presumably operate in a manner analogous to that proposed above for the octopodid suckers (Nixon & Dilly 1977). In addition, the muscular roof of the acetabulum is often arranged as “piston” within the stiff cylinder such that tension on the stalk pulls the piston back against the resistance of the water (Naef 1921-1923, Smith 1996). Thus, the greater the tension on the stalk, the greater the pressure differential and the greater the attachment force (Smith 1996). There is considerable variation in the form of decapod suckers including forms that show both radial and bilateral symmetry, and in some groups (e.g. enoploteuthids and onychoteuthids) the suckers may be replaced by

proteinaceous claws or teeth (Nixon & Dilly 1977).

## SUMMARY AND PERSPECTIVES

A remarkable diversity of coleoid cephalopod structures and organs are characterized by dense musculature that includes tightly packed bundles and sheets of muscle fibers arranged in three mutually perpendicular directions. This arrangement of muscle, termed a “muscular hydrostat” resembles the hydrostatic skeleton of soft-bodied invertebrates and provides both the force and the skeletal support that is required for movement and locomotion. The overview provided above also emphasizes the crucial role played by fibrous collagenous connective tissues in these systems. The connective tissues transmit the force of muscular contraction, control shape change, and in several cases store elastic energy in a manner that may reduce the costs of locomotion, movement, or adhesion.

Although we have a basic understanding of the arrangement and function of the musculature of the coleoid body in common near-shore forms such as the loliginid and ommastrephid squids, some sepioids, and some octopodids, we have relatively little detailed information on the diverse pelagic cephalopods that are less easily sampled. The range of mantle structure in the pelagic forms summarized above serves to emphasize the importance of future comparative studies in providing us with an accurate picture of the diversity of muscle structure and function in coleoids.

The complexity of the arrangement of the musculature and the lack of rigid elements and joints provides these structures with the potential to produce more complicated and varied movements than observed in animal structures that rely on more conventional skeletal support systems. A more highly subdivided and complicated neuromuscular control system is required for a muscular-hydrostat that has the potential to bend with multiple degrees of freedom at a number of locations. We know relatively little, however, about neural control of movement in these structures, and this therefore also remains as an important area for future research (see Matzner *et al.* 2000, Sumbre *et al.* 2001, Yekutieli *et al.* 1998).

Finally, the lack of rigid elements and joints implies that different mechanisms must be used for mechanical

amplification of the force, displacement, and velocity of muscle contraction. This may require different mechanisms of muscle fiber specialization from that observed previously in animals with rigid skeletons. Indeed, muscle fiber specialization in the tentacles of decapods (described above) is unusual because it primarily involved changes in the dimensions and arrangement of the myofilaments, rather than in their biochemistry. It is unclear, however, whether this represents a general mechanism of muscle specialization for cephalopods and additional studies on the ultrastructure, biochemistry and molecular biology of cephalopod muscle are thus needed as well.

## ACKNOWLEDGEMENTS

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