SQUID CROSS-STRIATED MUSCLE: THE EVOLUTION OF A SPECIALIZED MUSCLE FIBER TYPE

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ABSTRACT

The musculature of the arms and tentacles of squid provides an opportunity to examine the specialization of muscle because these two appendage types are specialized for different types of movement and the relation between structure and function has been examined at behavioral, morphological, mechanical, ultrastructural and biochemical levels. In morphological and biomechanical studies it was shown that a specific muscle mass of the tentacles, the transverse muscle, produces the extremely rapid extension of the tentacles that occurs during prey capture. Although the gross arrangement and fiber architecture of this tentacle muscle is remarkably similar to the homologous muscle in the arms, the ultrastructure of the muscle cells of the tentacle muscle differs from that of all other cephalopod musculature. The ultrastructural characteristics of the tentacle muscle cells include transverse striation and short sarcomeres, which are indicative of specialization for fast contraction. Biochemical analysis of the myofilament proteins of the musculature of the arms and tentacles suggests little accompanying alteration of the biochemical composition of these fast contracting cells. Thus, the specialization of the muscle cells for fast contraction appears to have occurred primarily through changes in the arrangement and dimensions of the components within the muscle cells rather than through changes in their gross arrangement or biochemical composition.

Muscle may evolve in response to functional demands at a number of levels. For example, a muscle or a muscular system may show specialization of the pattern of activity of individual muscles or groups of muscles (Cundall, 1983; Herring et al., 1979; Wainwright and Lauder, 1986; Weeks and English, 1985). Evolution can also occur at the level of the gross arrangement of the muscle or its fibers through variation in fiber architecture (Gans, 1982; Gans and Bock, 1965; Gans and DeVree, 1987; McClearn, 1985; Sacks and Roy, 1982; Woittiez et al., 1984). The mechanics of a muscle may change through modifications of the interactions between muscle, connective tissues and skeletal elements. At the level of individual muscle fibers, the arrangement and dimensions or amount of ultrastructural components such as the myofilaments, sarcoplasmic reticulum or mitochondria may be modified (Josephson, 1975). Finally, the biochemical composition of the contractile proteins of the fiber may also show specific patterns that relate to functional demands (Bárány, 1967; Edgerton, 1978; Schachat et al., 1987; Sweeney et al., 1988).

Our general conception of the patterns of specialization, i.e., the fit between structure, physiology, function and adaptation has in general been dominated by patterns observed in vertebrate muscular systems. Authors such as Hoyle (1983), Josephson (1975) and Prosser (1979, 1982) have suggested that different patterns exist in invertebrates, but the ways in which invertebrate muscle has evolved on these various levels have received relatively little attention.

In this paper, I will analyze the specializations of squid arm and tentacle musculature at a variety of levels. This case provides a virtually unique opportunity because homologous muscles with radically different functions can be identified and in these muscles the relation between structure and function has been examined at behavioral, morphological, mechanical, ultrastructural and biochemical levels in a single system. This study is important because, as I will show, the pattern of specialization at various levels differs from that generally observed in

vertebrates and provides new insight into the ways in which muscle and muscle systems may evolve.

USE OF THE ARMS AND TENTACLES IN PREY CAPTURE

Squid possess ten appendages that encircle the mouth (Fig. 1). Two of these appendages are specialized for prey capture and are called tentacles. The other eight appendages, termed arms, are used for prey manipulation, behavioral displays and are also involved in reproduction (Kier, 1982). The proximal portion of a tentacle, the stalk, is capable of extremely rapid elongation. High speed cine films (Kier, 1982) show that elongations of 70% of resting length can occur in as little as 15 msec. During a successful strike, the suckers, which are located on the distal portion of the tentacle, attach to the prey. The tentacular stalk then retracts to its original length, bringing the prey within reach of the arms. The arms possess suckers along their entire length and use the suckers in conjunction with bending and twisting movements to subdue and orient the prey for ingestion. Once the prey has been transferred to the arms, the tentacles are no longer involved in prey manipulation.

Thus, in squid, two classes of appendages exist that differ in behavior, function and biological role. The two tentacles are specialized for prey capture by rapid elongation and the eight arms serve a more general role in the slower movements required for prey manipulation, displays and reproduction.

MORPHOLOGY AND MECHANICS OF THE MUSCULATURE OF THE ARMS AND TENTACLES

Both the arms and tentacles, like the general musculoskeletal system of cephalopods, are characterized by a tightly packed three-dimensional array of muscle (Kier, 1982, 1988). A large mass of transverse muscle fibers occupies the core of both the tentacles and arms along their entire length (Figs. 2, 3). The transverse muscle fibers extend across the diameter in planes perpendicular to the long axis. In the tentacular stalk, the transverse muscle fibers extend into a narrow layer of circular muscle that wraps the core of musculature (Fig. 2). A circular muscle layer is not present in the arms. Bundles of longitudinal muscle fibers are situated around the circumference of both the arms and tentacles and interdigitate with the transverse muscle cells. In addition, helical or oblique muscle fiber orientations are present in the arms and tentacles but the specifics of their arrangement and function will not be discussed here. For details see Kier (1982).

How does this tightly packed, three-dimensional array of musculature produce the movements of the tentacles and the arms? Squid arms and tentacles are members of a class of animal structures that lack hardened internal or external skeletal elements and also lack the large fluid filled cavities that characterize hydrostatic skeletal support. These structures, termed muscular-hydrostats (Kier and Smith, 1985; Smith and Kier, 1989), rely on a form of hydrostatic skeletal support in which the musculature itself serves as the hydrostatic fluid. Because muscle is essentially incompressible at physiological pressures, the arms and tentacles are constant in volume. A decrease in one dimension will result therefore in an increase in another. The three-dimensional arrangement of muscle described above for the arms and tentacles provides a means to control all dimensions and therefore to produce a variety of movements.

During the strike, the muscle cells of the transverse muscle mass of the tentacular stalk contract, thereby reducing its diameter. Because the stalk is constant in volume, a decrease in diameter results in elongation. Shortening of the stalk after

TENT.
CLUB

TENT.
STALK
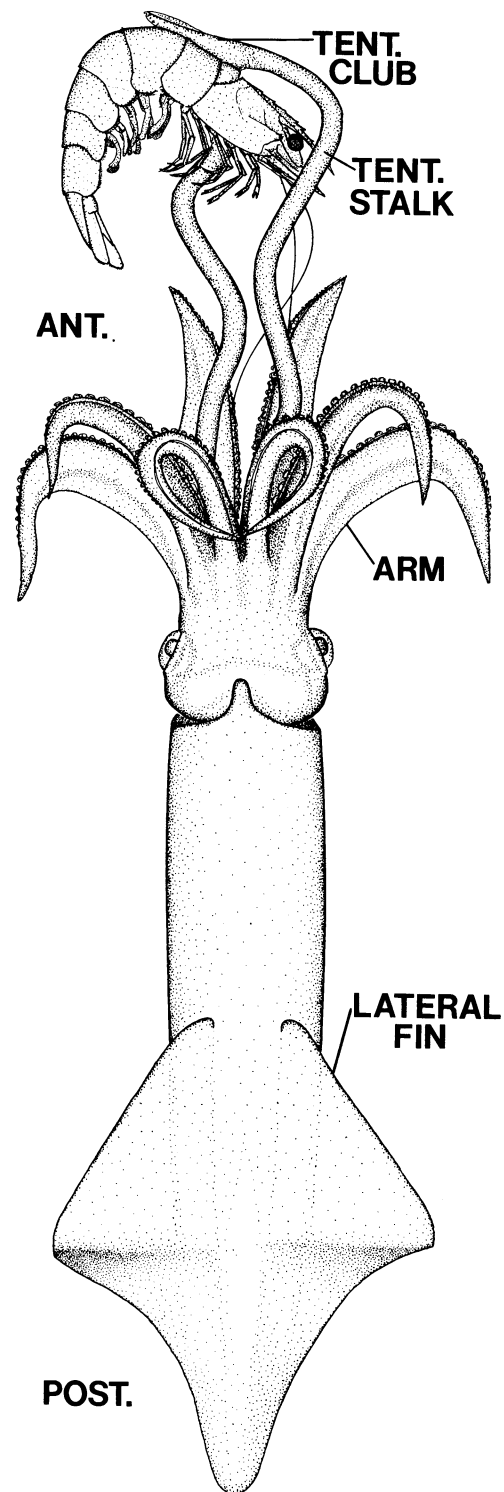
ANT.

ARM

LATERAL
FIN

POST.

Figure 1. Tracing from a single frame of a 16 mm 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 prey but will straighten as the prey is drawn within reach of the eight arms. (From Kier, 1982 with permission of the publisher.)
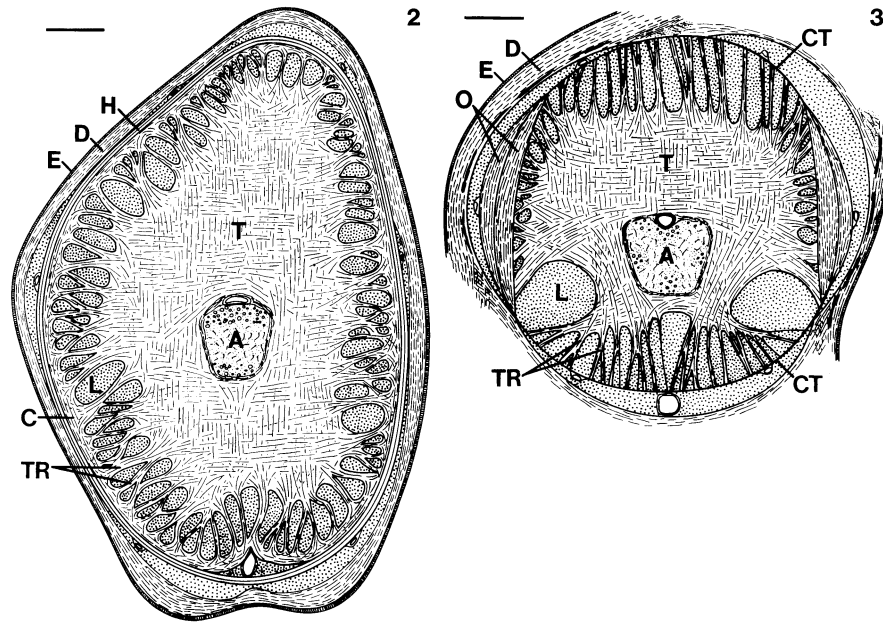
Figure 2. Schematic transverse section of the tentacular stalk of *Loligo pealei*. A, axial nerve cord; C, circular muscle; D, dermis; E, epithelium; H, helical muscle; L, longitudinal muscle; T, transverse muscle; TR, trabeculae of transverse muscle. The scale bar length equals 1 mm. (From Kier, 1985 with permission of the publisher.)

Figure 3. Schematic transverse section of the arm of squid. A, axial nerve cord; CT, connective tissue sheet; D, dermis; E, epithelium; L, longitudinal muscle; O, oblique muscle; T, transverse muscle; TR, trabeculae of transverse muscle. The scale bar length equals 1 mm. (From Kier, 1985 with permission of the publisher.)

the strike is caused by contraction of the longitudinal muscle bundles and results in extension of the transverse muscle cells.

The musculoskeletal system of the arms also involves a muscular-hydrostatic mechanism. The transverse muscle mass of the arm, however, serves a different role from the transverse muscle mass of the tentacle. In the arm, the transverse muscle mass generates the force required for support of bending movements (Kier, 1982). Bending of the arms involves contraction of longitudinal bundles on one side of the arm. This longitudinal muscle contraction will create bending of the arm only if the longitudinal compressional force exerted on the entire arm is resisted. Without resistance to longitudinal compression, unilateral longitudinal muscle contraction merely shortens the arm. Because the arm is constant in volume, shortening due to a longitudinal compressional force would result in an increase in diameter. The transverse muscle cells of the arm are oriented such that they resist increase in diameter and thus they resist longitudinal compression and allow bending. [For further details on bending in muscular-hydrostats, see Kier (1987, 1989), Kier and Smith (1985), Kier et al. (1989), Smith and Kier (1989)].

The transverse muscle mass of the specialized tentacles creates the rapid elongation observed during prey capture and the transverse muscle mass of the arms provides the support required for the slower bending movements. The longitudinal muscle bundles of the tentacle are responsible for retraction after the strike and

Table 1. Comparison of squid arm and tentacle musculature

	Tentacle	Arm
Use:	prey capture	prey manipulation
Function of long. musc:	retraction after strike	bending movements
Function of trans. musc:	rapid elongation	support for bending
Ultrastructure of transverse muscle:		
Striation type:	cross-striated	obliquely striated
Cell diameter:	2 μm	3 μm
Thick fil. length	0.5–0.9 μm	2.8 μm or greater
Thick fil. diameter	24–31 nm	31–36 nm

the longitudinal muscle bundles of the arm are involved in creating bending movements. Thus, although the gross arrangement of the transverse muscle masses of the arms and tentacles is similar, their function is radically different (Table 1).

ULTRASTRUCTURE OF THE TRANSVERSE MUSCLE MASS OF THE ARMS AND TENTACLES

If there is little to differentiate the musculature of the arms and tentacles on the gross level despite the behavioral and functional differences, what adaptations of the musculature reflect the specialization observed? Virtually all cephalopod "skeletal" muscle consists of obliquely striated muscle cells (Amsellem and Nicaise, 1980; Chantler, 1983; Hanson and Lowy, 1960; Hoyle, 1964; Nicaise and Amsellem, 1983). In obliquely striated muscle, the myofilaments, although parallel to the longitudinal axis of the cell, are not transversely aligned in register across the fiber. Instead, the myofilaments are staggered, forming an oblique pattern of Z elements, A Bands, and I Bands (Fig. 4). Ultrastructural examinations demonstrate that the transverse musculature of the tentacle, rather than being obliquely striated, instead consists of cross-striated muscle cells. Thus, specialization of the transverse muscle mass of the tentacles for rapid elongation is reflected in the ultrastructure of the muscle cells.

The ultrastructural characteristics of the arm and tentacle musculature in squid (*Loligo pealei* and *Illex illecebrosus*) are summarized below (Kier, 1985). The transverse muscle mass of the arms consists of typical cephalopod obliquely striated cells (Fig. 5). The cells are fusiform in shape and average approximately 3 μm in diameter. The myofilaments surround a central longitudinally oriented core that includes the mitochondria and the single cell nucleus. An oblique alignment of dense bodies forms the Z elements of the cells. The sarcoplasmic reticulum of the cells includes tubules in the subsarcolemmal cytoplasm, in the plane of the Z elements and in a zone surrounding the mitochondrial core. The outer portion of the tubule membranes of the subsarcolemmal sarcoplasmic reticulum form specialized contacts with the sarcolemma called peripheral couplings. Regularly spaced electron-dense junctional feet are observed between the sarcolemma and the sarcoplasmic reticulum of the peripheral couplings. The thick filaments of the obliquely striated cells taper toward their ends. Their diameter at the center averages approximately 31–36 nm and their length is 2.8 μm or greater in the species studied (Kier, 1985).

The transverse muscle mass of the tentacles consists of cross-striated muscle cells that average approximately 2 μm in diameter (Fig. 6). A central core of mitochondria, seen in the obliquely striated cells, is not present. Instead, mito-
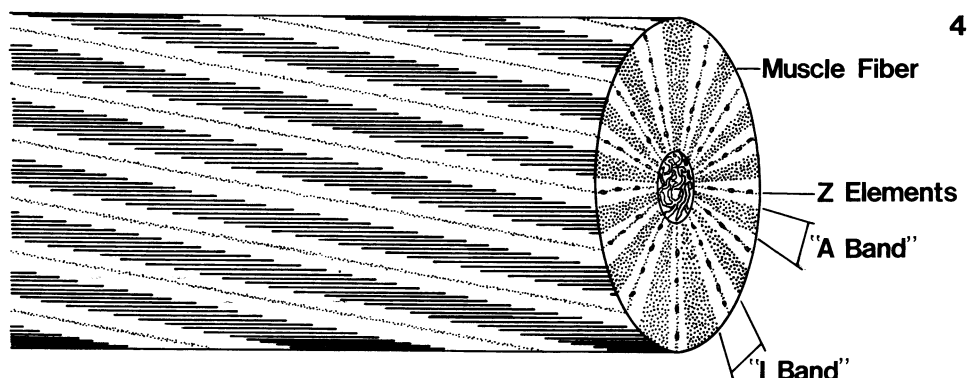
Figure 4. Schematic diagram illustrating the organization of a cephalopod obliquely striated muscle fiber. Note that a cross-section of an obliquely striated muscle cell shows an analogous sequence of bands to those seen in a longitudinal section of a cross-striated cell. The thin filaments have been omitted from the diagram for clarity. (After Kier, 1985.)

chondria are observed only in the subsarcolemmal cytoplasm. Tubules of the sarcoplasmic reticulum are also observed in the subsarcolemmal cytoplasm where they form peripheral couplings similar in morphology to those described above for the obliquely striated cells. Tubules of the sarcoplasmic reticulum were not observed in the myofilament lattice. No invaginated tubules of the sarcolemma are present and thus the cells are not subdivided into myofibrils. The thick filaments of the cross-striated cells are short, measuring only 0.5–0.9 μm in the squid species studied. The average diameter of the thick filaments ranged from 24–31 nm in the species studied. Transverse sections that graze the Z disc show it to be a loosely organized alignment of electron dense material. An M line is not present. The sarcomeres appear to be susceptible to shearing with the result that the Z discs are often not perpendicular to the longitudinal axes of the cells and instead follow an angled or curved course across the cells (Kier, 1985).
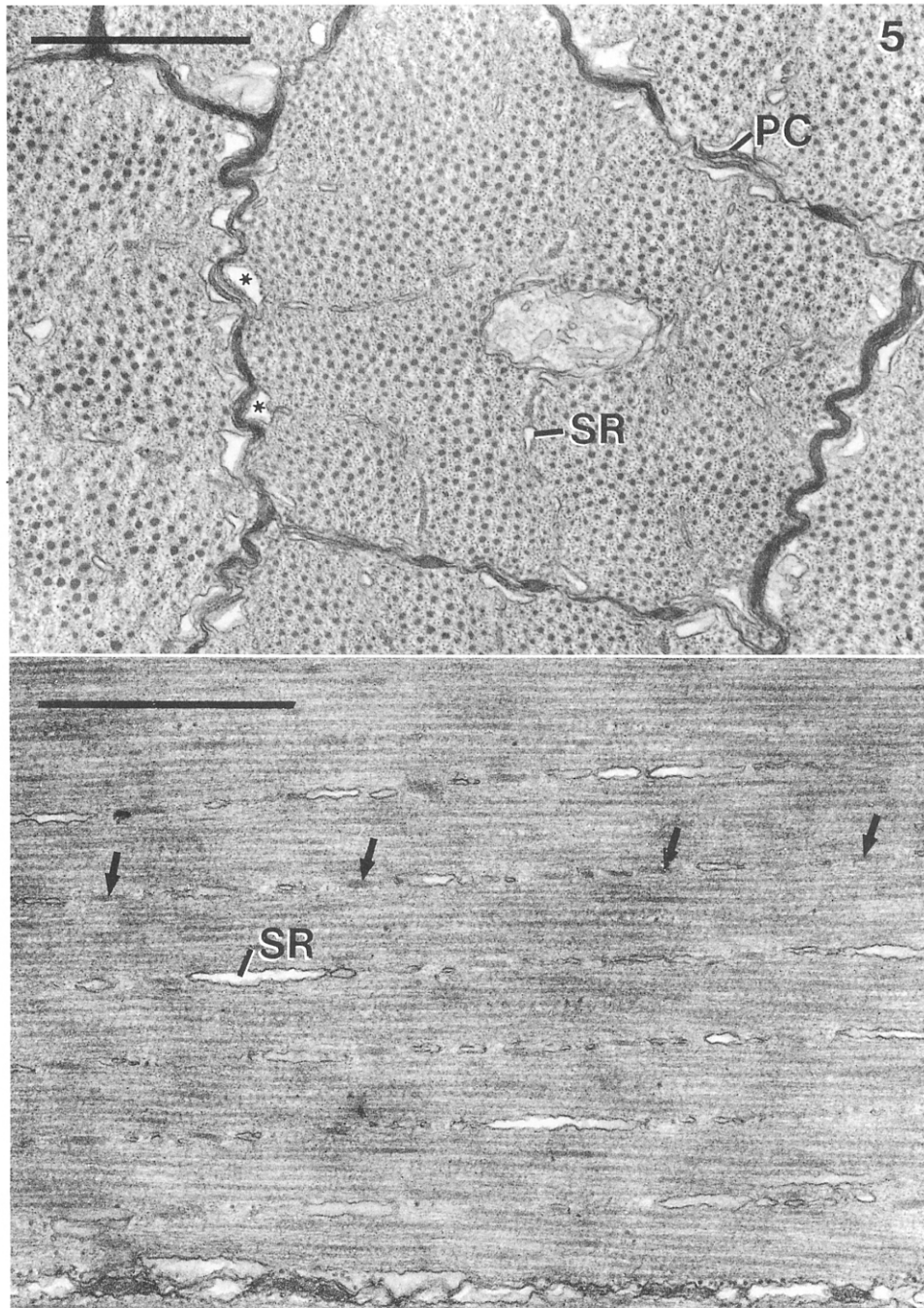
Thus, although the gross morphology and arrangement of the musculature of the arms and tentacles are similar, the ultrastructure reflects the specialization in function. Unlike the rest of the musculature of the tentacle and that of the arm musculature and other cephalopod skeletal musculature, the muscle cells of the transverse muscle mass of the tentacles are cross-striated fibers with short sarcomeres (Table 1).

BIOCHEMICAL COMPARISON OF THE CROSS-STRIATED AND OBLIQUELY STRIATED CELLS

The protein composition of the myofilaments of the cross-striated tentacle cells and the obliquely striated cells of the arm are remarkably similar when compared by sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE) (Kier

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Figure 5. (Top): Electron micrograph of transverse section of obliquely striated cells of the arm of *Loligo pealei*. The outer membranes of the terminal cisternae (*) make specialized contacts, or peripheral couplings (PC) with the sarcolemma. The sarcoplasmic reticulum (SR) and the central core with mitochondria are also visible in the micrograph. The scale bar length equals 1 μm. (Bottom): Electron micrograph of longitudinal section of obliquely striated cells of the transverse musculature of the arm of *Illex illecebrosus*. The long axis of the muscle fiber is oriented horizontally. The sar-

coplasmic reticulum (SR) and dense bodies (arrows) are oriented at a small angle with respect to the horizontally oriented thick filaments. The scale bar length equals 1 μm. The tissue was fixed in 3.0% glutaraldehyde, 0.065% phosphate buffer, 0.5% tannic acid and 6.0% sucrose for 10 h at 4°C. After a buffer wash, the blocks were post-fixed for 40 min in a 1:1 mixture of 2% potassium ferrocyanide in 0.13 M cacodylate buffer and 2% osmium tetroxide. The blocks were dehydrated in ethanol and embedded in Epon. Thin sections were stained with saturated uranyl acetate and lead citrate. For further detail on procedures, see Kier (1985). (From Kier, 1985 with permission of the publisher.)
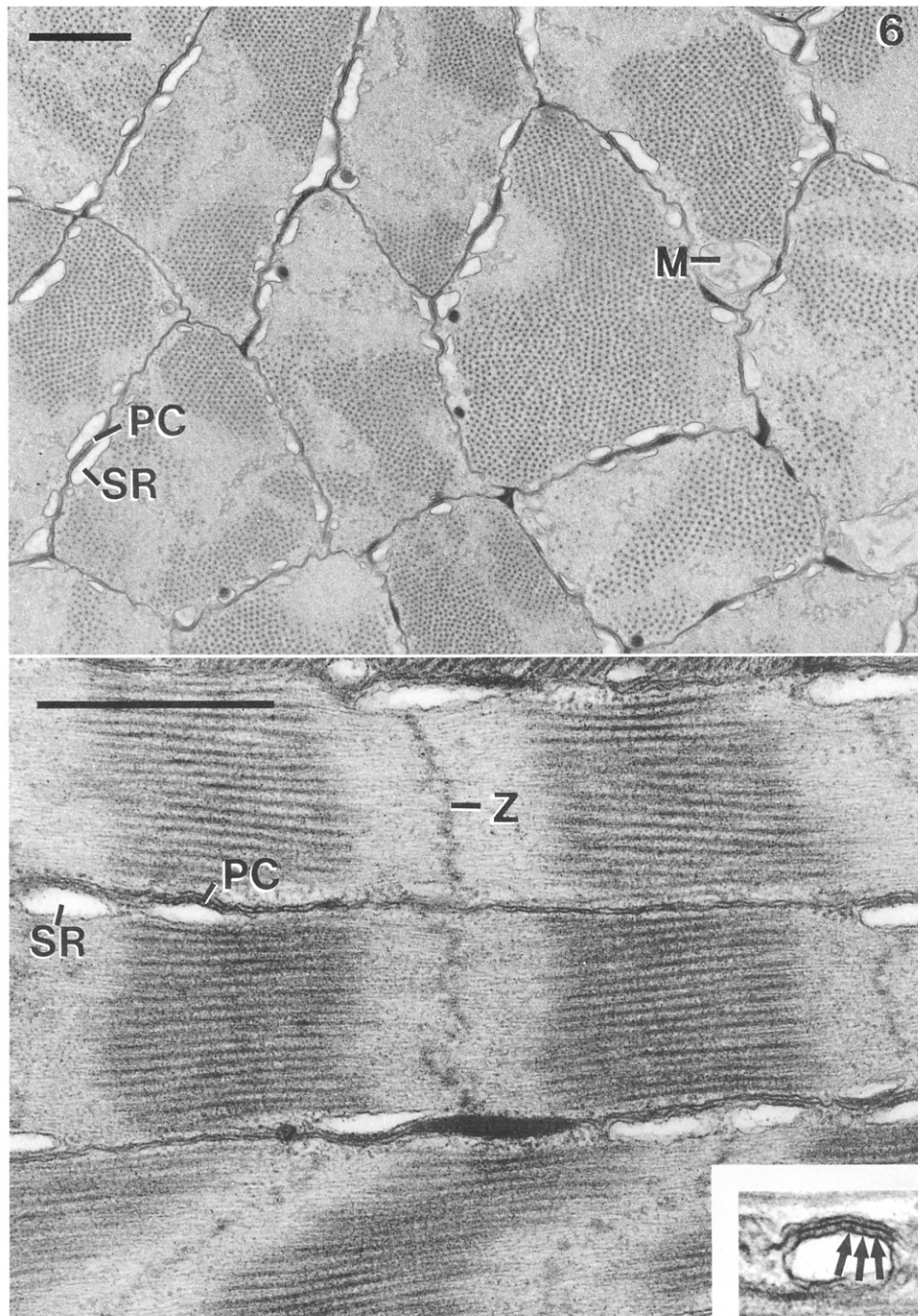
Figure 6. (Top): Electron micrograph of transverse section of cross-striated muscle fibers of the transverse muscle of the tentacle of *Loligo pealei*. Mitochondria (M) are located immediately beneath the sarcolemma. The outer membrane of the sarcoplasmic reticulum (SR) makes specialized contacts or peripheral couplings (PC) with the sarcolemma. The scale bar length equals 1 μm. (Bottom): Electron micrograph of longitudinal section of cross-striated muscle fibers of the transverse musculature of the tentacle of *Loligo pealei*. Peripheral couplings (PC) and the sarcoplasmic reticulum (SR) are visible.

and Schachat, in press). The methods employed are procedures that have revealed biochemical variation between different fiber types in vertebrate cross-striated skeletal muscles and between different nematode (*Caenorhabditis elegans*) obliquely striated muscle fiber types (Bejsovec and Andersen, 1988; Briggs et al., 1987; Schiaffino et al., 1988). In particular, the techniques allow the resolution of differences in myosin light and heavy chains, troponins, and tropomyosins which have, in other muscles, been correlated with differences in physiological performance. When used to study squid muscle, these same techniques reveal no significant differences in protein composition between the cross-striated tentacle cells and the obliquely striated arm cells (Fig. 7). In addition, a cyanogen bromide peptide mapping procedure failed to resolve any differences between the myosin heavy chains of the two muscle types (Kier and Schachat, in press). The only difference observed thus far is in the amount of the thick filament core protein paramyosin. Paramyosin was identified in these muscle cells using established purification procedures (Kier and Schachat, in press). The paramyosin content is reduced significantly in the cross-striated tentacle cells compared to the obliquely striated cells. Previous research has elucidated a correlation between paramyosin content and thick filament length (Chantler, 1983; Levine et al., 1976; Mackenzie and Epstein, 1980; Szent-Györgyi et al., 1971; Winkelman, 1976) and it is likely, therefore, that the reduction in paramyosin is related to a decrease in thick filament length in the cross-striated cells.

DISCUSSION

Evolutionary History of the Arms and Tentacles. — What is the most likely evolutionary history of the musculature of the arms and tentacles? In his discussion of the evolution of the cephalopod order "Decapoda" (an obsolete systematic grouping that included squids, cuttlefish and various fossil cephalopods), Naef (1921/1923) considered the tentacles to be "homonomous" (=serially homologous) to the arms, based on gross structure and development. He describes the arms as being more "primitive" than the tentacles because they are closest to the typical condition in the subclass "Dibranchiata." The tentacles most likely evolved through a modification of the fourth pair of arms (see also Donovan, 1977). If the tentacles are modified arms, it is parsimonious to hypothesize that the cross-striated muscle cells of the tentacles evolved through a modification of obliquely striated muscle cells. If true, a comparison of the two fiber types allows an examination of the evolution of a specific muscle fiber type in a single animal. It appears likely that, during the evolution of the tentacles, selection favored specialization for fast triggering and high shortening speed. By comparing the cross-striated tentacle cells with the obliquely striated arm cells, we can document the specific alterations that occurred in response to such specialization. Many otherwise perplexing aspects of the structure of the cross-striated cells can be understood in light of their derivation from obliquely striated muscle.

Specializations for Fast Contraction in Squid Muscle. — Several design features are characteristic of fast-contracting muscle. These include rapid excitation-contrac-

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The inset shows a higher magnification view of a peripheral coupling in which junctional feet (arrows) are visible. The Z disc (Z) is diffuse. The scale bar length equals 1 μm and the inset is 0.5 μm wide. Preparation procedures were the same as those described for Figure 5. (From Kier, 1985 with permission of the publisher.)
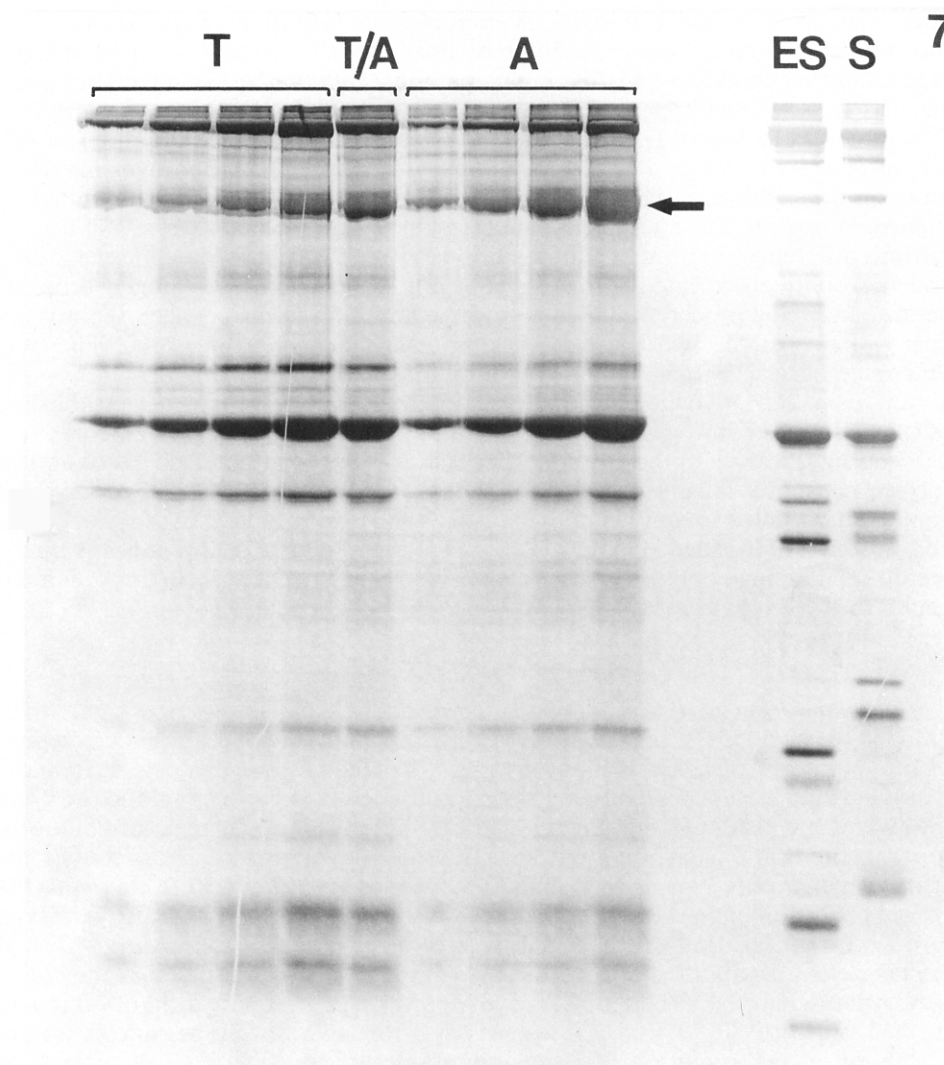
Figure 7. Photograph of silver-stained sodium dodecyl sulfate polyacrylamide gel (10.5% polyacryl-amide) of myofilament extracts of the transverse muscle cells of the tentacle (T) and arm (A) of *Sepioteuthis lessoniana*. The multiple lanes under "T" and "A" show increasing sample loadings from left to right. The lane labelled T/A was loaded with 50% tentacle and 50% arm extract. Note that the protein composition of the arm and tentacle is remarkably similar. For comparison, identically pre-pared myofilament extracts of an Erector Spinae muscle (ES) and Soleus muscle (S) from a New Zealand White rabbit were run in adjacent lanes. Note the greater amount of protein, $M_r = 95,000$–$100,000$ (arrow) in the arm muscle versus the tentacle muscle. Using established purification proce-dures, this protein has been tentatively identified to be paramyosin. For further detail on the procedures, see Kier and Schachat (in press).

tion coupling, allowing rapid development of tension and rapid relaxation, and high shortening velocity. How are these features obtained in the squid muscula-ture? Selection for rapid excitation-contraction coupling may have been an im-portant aspect of the evolution of the cross-striated tentacle cells. Invaginated tubules (transverse tubules) are not present in the ancestral obliquely striated cells. Invaginated tubules are found in many large diameter cross-striated cells in other

animals and are inward projections of the sarcolemma that serve to transmit the depolarization of the sarcolemma internally in the cell to the sarcoplasmic reticulum surrounding individual myofibrils. Without invaginated tubules, the sarcoplasmic reticulum must be associated with the sarcolemma at the surface of the cell, and calcium ions must diffuse from the sarcoplasmic reticulum at the surface to the myofilaments in the core of the cell. In large cells, the time required for such diffusion might be limiting. In order to limit calcium diffusion distances from the sarcoplasmic reticulum to the myofilaments, evolution of the rapidly triggered cross-striated cells requires either a decrease in cell diameter or evolution of a transverse tubular system that would allow division of the cell into myofibrils, each surrounded by sarcoplasmic reticulum (Bone and Ryan, 1973; Hill, 1948; Kidokoro et al., 1974; Kier, 1985; Sanger, 1971). It appears that the simplest transition, that of reducing cell diameter and elaborating the sarcoplasmic reticulum around the periphery of the cells, was adopted in the case of the squid tentacle muscle. Interestingly, single cross-striated muscle *cells* from the tentacle have similar dimensions to single *myofibrils* of vertebrate skeletal muscle. Thus, the dyads (specialized contacts between the sarcoplasmic reticulum and sarcolemma) of the cross-striated squid tentacle cells probably serve an analogous function to that of the triads (specialized contacts between the sarcoplasmic reticulum and the transverse tubules) of vertebrate skeletal muscle fibers. In squid and vertebrate striated muscle, similar functional demands have produced similar design features with different specific morphological components.

Selection for high shortening velocity was also an important aspect of the evolution of the cross-striated tentacle cells. The evolution of the cross-striated cells in squid illustrates an interesting contrast to that observed in vertebrate skeletal muscle fiber types because the specialization appears to have involved changes in the arrangement and dimensions of the myofilament lattice rather than changes in the biochemistry of the components.

Most skeletal muscles in vertebrates contain a mixture of different muscle fiber types. In general, the dimensions of the components of the myofilament lattice remain relatively constant between different mammalian skeletal muscle fibers and in vertebrate skeletal muscle fibers in general (Eisenberg, 1983). The biochemical composition, however, is highly variable. In fact, recent analyses (Moore and Schachat, 1985; Sweeney et al., 1988) have found variation in biochemical composition within single muscle fiber types classified by classical histochemical methods. An extensive literature exists concerning this variation in myosin light chains, myosin heavy chains, troponins and tropomyosins that occurs in different vertebrate muscle fibers. These variations have been correlated, in some studies, with differences in physiological performance. Of most importance for this discussion is the correlation between various myosin isoforms and the shortening speed. Differences in shortening speeds between different vertebrate skeletal muscle fiber types appear to be primarily a function of differences in the myosin isoforms because these differences are reflected in differences in myosin ATPase activity, and hence rate of cross bridge cycling (Bandman, 1985; Bárány, 1967; Close, 1972; Reiser et al., 1985; Schiaffino et al., 1988; Sweeney et al., 1988).

In the cross-striated muscles of the tentacle, however, no differences have yet been detected between it and the obliquely striated muscle in the either the light or heavy myosin chains. Although it is possible that there are differences in myosin isoforms that simply have not been resolved, it must be emphasized that the techniques applied thus far are the same as those used to analyze myosin isoform heterogeneity in both vertebrate muscle and other invertebrate muscle types (Kier and Schachat, in press).

It appears instead that the most important factor in the evolution of high

shortening speed in the cross-striated tentacle muscle was a change in the dimensions and arrangement of the myofilaments, rather than a change in biochemistry. The critical factors are sarcomere length and thick filament length. There is an inverse correlation between thick filament length and shortening speed in molluscan muscle cells (Millman, 1967) and in muscle cells in general (Josephson, 1975). Muscles with short thick filaments and hence short sarcomeres have more sarcomeres in series, per unit length. Because shortening velocities of elements in series are additive, muscles with shorter sarcomeres show higher unloaded shortening speeds, assuming that other factors are constant (Huxley and Simmons, 1972; Josephson, 1975). It is important to note that the decrease in thick filament length that occurred during the evolution of the cross-striated tentacle cells was dramatic. The thick filament length of the obliquely striated cells is 2.8 μm or greater. The 0.5–0.9 μm thick filaments of the cross-striated cells thus represent a large decrease in length.

In summary, rapid excitation-contraction coupling in the cross-striated tentacle muscle was achieved by reducing cell diameter and thereby minimizing calcium diffusion distance. Perhaps as a consequence of the evolutionary history of these cells, the option of transverse tubules such as is seen in vertebrate skeletal muscle, was not readily available. Similar design features were achieved with different morphological components. The specialization for high shortening velocity followed a markedly different pathway in the squid cells when compared to vertebrate skeletal muscle. High shortening speed is achieved in vertebrate skeletal muscle through alterations in biochemical composition with little ultrastructural change. In contrast, in the cross-striated squid cells, radical ultrastructural change occurred, but the molecular components appear relatively unaltered.

Other Features and Consequences. — While the evolution of short sarcomere, cross-striated cells greatly increases shortening speed, it carries with it a potential limit to the range of elongation and contraction possible. Obliquely striated muscle fibers are capable of long range elongation and contraction and have a flattened length-tension relationship (Hidaka et al., 1969; Miller, 1975). As an example, leech obliquely striated muscle fibers can reversibly elongate by up to 300% of their fully contracted state. The mechanisms that allow this range of elongation and contraction may involve both a change in stagger of the thick filaments and thin filaments "changing partners" when pulled beyond overlap with a thick filament (Lanzavecchia and Arcidiacono, 1981). Most cross-striated muscle cells, however, are not capable of such extreme ranges of elongation and contraction. Typically, cross-striated muscle fibers cannot contract by more than 30–40% of their fully extended length (Gans and Bock, 1965; Rice, 1973). Special "supercontracting" striated muscles have evolved in several instances including insects (Rice, 1970; Osborne, 1967), giant barnacles (Hoyle et al., 1965) and the chameleon (Rice, 1973).

Because of the relationship between the diameter and length of the constant volume tentacle, the cross-striated cells of the transverse muscle mass of the tentacle operate over a much smaller range of elongation and contraction than the cells of the longitudinal muscle bundles. The longitudinal muscle bundles are present along the entire length of the tentacle and are parallel to its longitudinal axis. If the tentacle is elongated by 70%, a typical elongation observed during the strike (Kier, 1982), the longitudinal muscle cells are elongated by the same amount, assuming that no shearing occurs between fibers. Due to the geometrical relationship of the diameter and length of a constant volume cylinder such as the tentacle, however, the transverse muscle cells do not operate over as great of a

range of elongation. Calculations predict that a 70% elongation of a constant volume elliptic cylinder with the dimensions of a *Loligo pealei* tentacle results from only a 23% decrease in diameter (Kier, 1982). This relation between the diameter and length provides a means whereby the displacement and velocity created by transverse muscle contraction is amplified and is analogous to the amplification seen in skeletal support systems with rigid levers (Kier and Smith, 1985; Smith and Kier, 1989). Since the transverse muscle fibers that create this 23% decrease extend across the diameter of the tentacle, they shorten by this amount during the strike, assuming that no shearing occurs between them. Thus, the limited range of elongation and contraction typical of cross-striated muscle fibers is not a constraint. As described above, the muscle cells of the longitudinal muscle bundles of the tentacles are subjected to a large range of elongation. Even though they are surrounded by the cross-striated cells of the transverse and circular muscle of the tentacle, examination of their ultrastructure (Kier, 1985) reveals them to be obliquely striated. The large range of elongation can therefore be accommodated.

. We do not yet have information on the aerobic capacity of the cross-striated tentacle muscle compared to the obliquely striated arm muscle. Previous work on squid and cuttlefish mantle (Bone et al., 1981; Mommsen et al., 1981) and fin muscle (Kier, 1989; Kier et al., 1989) has shown the mantle and fins to consist of two populations of obliquely striated muscle fibers that differ in aerobic capacity. Further work on this aspect of the physiology of the tentacle and arm muscle cells is needed.

Prosser (1979, 1982) has emphasized that cross-striated muscle has evolved many times in parallel. Although the transverse alignment of myofilaments is observed in many muscles from diverse organisms, the details of the ultrastructure reflect evolutionary convergence. The achievement of similar functional ends with different morphological details in the membrane systems in squid and vertebrate cross-striated muscle has been emphasized above. In addition, although a Z disc can be identified in the cross-striated tentacle cells, it is not the organized, precise network that has been described for many vertebrate and insect cross-striated cells (see for example, Hoyle, 1983; Rowe, 1971; Smith, 1972). The Z disc of the cross-striated cells may simply be a transverse alignment of dense bodies. Further research on the structure and biochemistry of the Z disc would be interesting in this regard.

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