JOURNAL OF MORPHOLOGY 185:223–239 (1985)

The Musculature of Squid Arms and Tentacles: Ultrastructural Evidence for Functional Differences

WILLIAM M. KIER
Department of Zoology, Duke University, Durham, NC 27706, and Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543

ABSTRACT The transverse muscle mass of the arm and the transverse and circular muscle masses of the tentacle of squid (*Loligo pealei* and *Illex illecebrosus)* were examined by transmission electron microscopy. Previous work had indicated that although similar in gross arrangement, the transverse muscle mass of the tentacle creates rapid elongation during prey capture while the transverse muscle mass of the arm is involved in creating bending movements. The difference in function between the transverse muscle masses of the arms and tentacles is reflected in differences in ultrastructure. The transverse muscle mass of the arm is made up of regular, obliquely striated muscle fibers 1–6 μm in diameter. The transverse and associated circular muscle masses of the tentacle are made up of cross-striated muscle fibers 1–3 μm in diameter. The cross-striated muscle fibers have A bands approximately 0.5 μm *(I. illecebrosus)* and 0.9 μm *(L. pealei)* in length and a resting sarcomere length of 0.9 μm *(I. illecebrosus)* and 1.6 μm *(L. pealei),* suggesting a relatively high shortening speed for this muscle type. The cross-striated cells are not divided up into myofibrils, and the sarcoplasmic reticulum is located beneath the sarcolemma. Vernier displacements of the sarcomeres were observed. The myofilaments of the obliquely striated muscle fibers of the arm surround a central core containing mitochondria and the cell nucleus. The sarcoplasmic reticulum of the obliquely striated cells is located beneath the sarcolemma, in the plane of the Z elements, and surrounding the mitochondrial core.

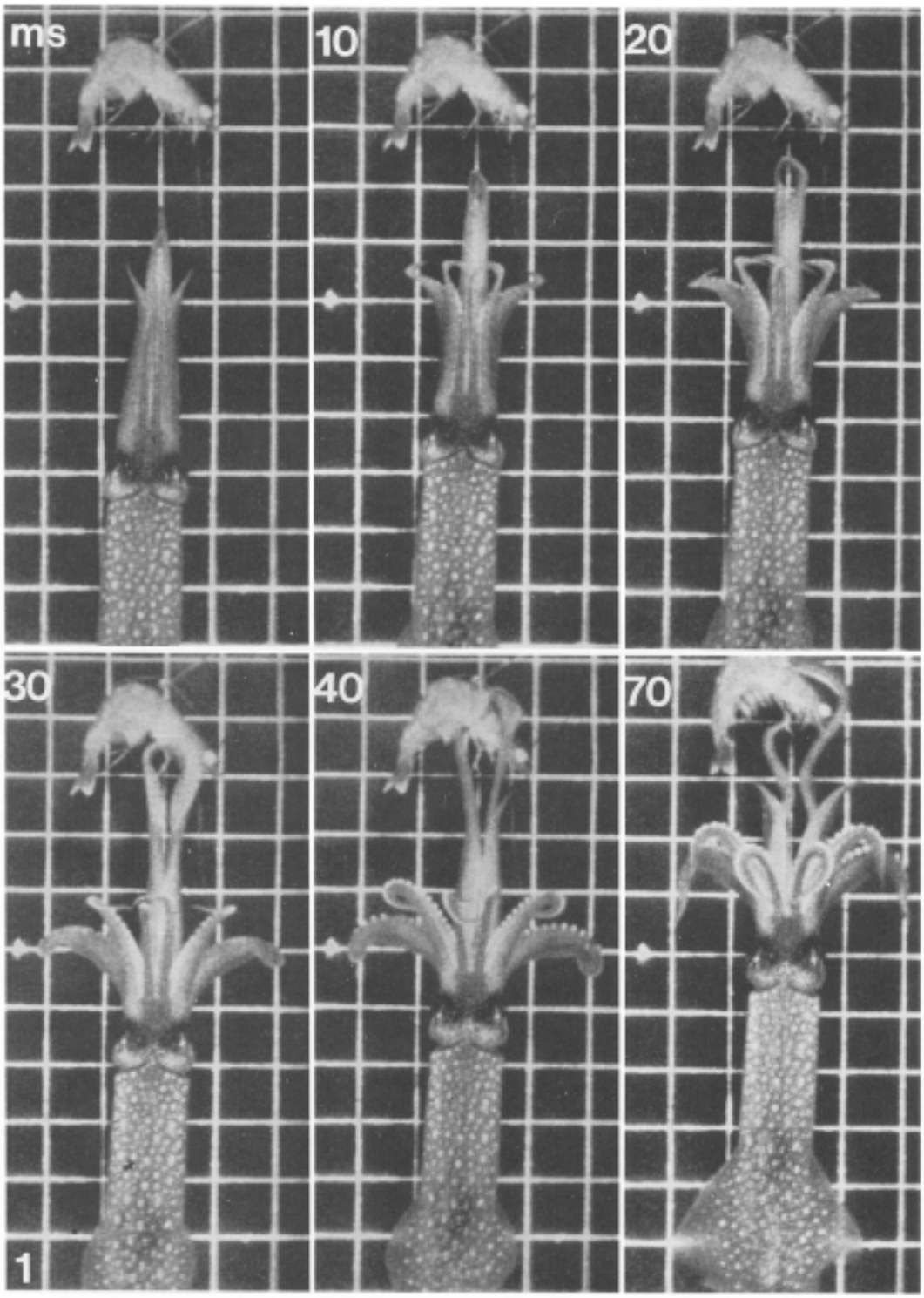
Squid capture and subdue their prey with an array of ten muscular appendages. One pair of appendages, termed tentacles, is used to capture prey by rapid elongation; the remaining four pairs of appendages, termed arms, subdue and orient the captured prey with bending and grasping movements. In spite of the difference in function between the arms and tentacles, the gross arrangement of musculature of these two appendage types is similar (Kier, '82). It has been proposed that the differences in function between the musculature of the arms and tentacles might be reflected in differences in ultrastructure of the muscle itself rather than its gross arrangement (Kier, '82), and this hypothesis is tested here.

The movements of the arms and tentacles, the gross morphology of the musculature, and the proposed functional significance of the muscular arrangement are reviewed briefly. The paper then reports on the types of muscle fibers found in cephalopods as well as on the ultrastructure of the musculature of squid arms and tentacles. The discussion relates these observations to previous descriptions of cephalopod muscle, to vertebrate skeletal muscle, and to the possible physiological parameters of the musculature.

Arm and tentacle movements and prey capture

The arms and tentacles of squid are arranged in a ring that encircles the mouth. The four pairs of arms taper from base to tip and bear suckers on their oral surface (sur-

Address reprint requests to Dr. William M. Kier, Department of Biology, University of North Carolina, Chapel Hill, NC 27514.


ms
10
20
30
40
70
1

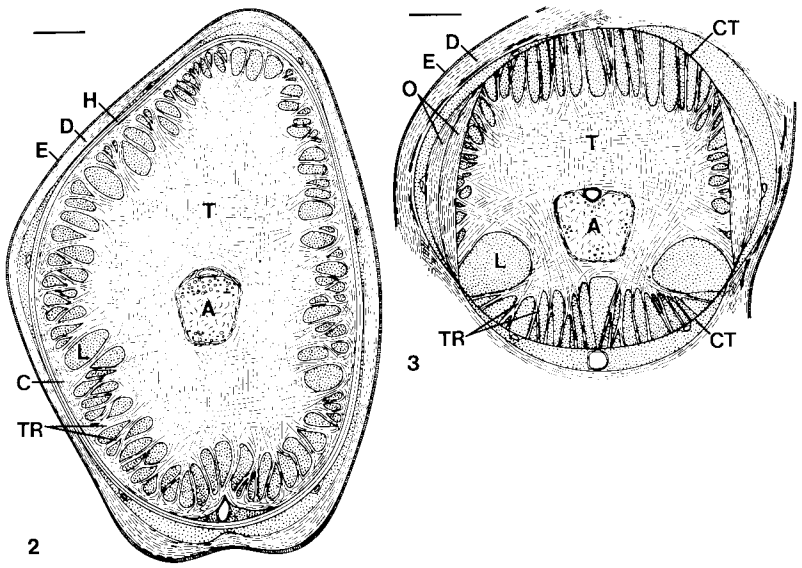


Fig. 1. Composite of photographs of single frames of high-speed cine film (750 frames per second) of dorsal view of strike of *Loligo pealei* during capture of a penaeid shrimp. The cumulative time in milliseconds is indicated. The four pairs of arms flare as the pair of tentacles is elongated. The impact of the tentacular clubs on the prey (last frame) causes compressive buckling of the tentacular stalks and pushes the shrimp further away. The grid spacing is 2 cm.

Fig. 2. Schematic transverse section of the tentacular stalk of squid (ommastrephid and loliginid squid similar). 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.

Fig. 3. Schematic transverse section of the arm of squid (ommastrephid and loliginid squids similar). 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.

face facing the mouth). The pair of tentacles bears suckers on an expanded terminal club, whereas the slender, cylindrical tentacular stalks are naked. The tentacles are used almost exclusively for prey capture (described below), whereas the arms are used both for prey handling and steering during swimming.

Squid pursue and capture live prey–typically fish, crustaceans, and smaller squid. The attack can be divided into three phases–attention, positioning, and strike (Kier, '82; Messenger, '68; '77). During the attention phase, the squid rapidly orients so that the arms, tentacles, and long axis of the body are pointed toward the prey and the eyes are directed forward at the prey. During positioning, the squid swims directly toward the prey with the arms held together in a tight cone-shaped arrangement enclosing the tentacles, the tips of which protrude just beyond the arms. The final phase, the strike, occurs as the squid continues to approach the prey (Fig. 1). During the strike, the arms flare out from their previous tight cone and the tentacular stalks are extended rapidly in a straight trajectory. The tentacular clubs reach the prey in approximately 15–35 msecs, striking the prey and attaching to it with the suckers. The tentacles then shorten, pulling the prey within reach of the arms. The arms converge around the prey from their previous flared arrangement and subdue and orient the prey for ingestion with bending and grasping movements (Kier, '82).

Arm and tentacle microanatomy and function

Diagrammatic cross-sections of the tentacular stalk and the arm are shown in Figures 2 and 3, respectively. A centrally located axial nerve cord (A) lies parallel to the long axes of the tentacle and arm, surrounded by an extensive mass of transverse muscle (T). Muscle fibers of the transverse muscle mass are oriented perpendicularly to the long axes of the tentacle and arm. The transverse mus-

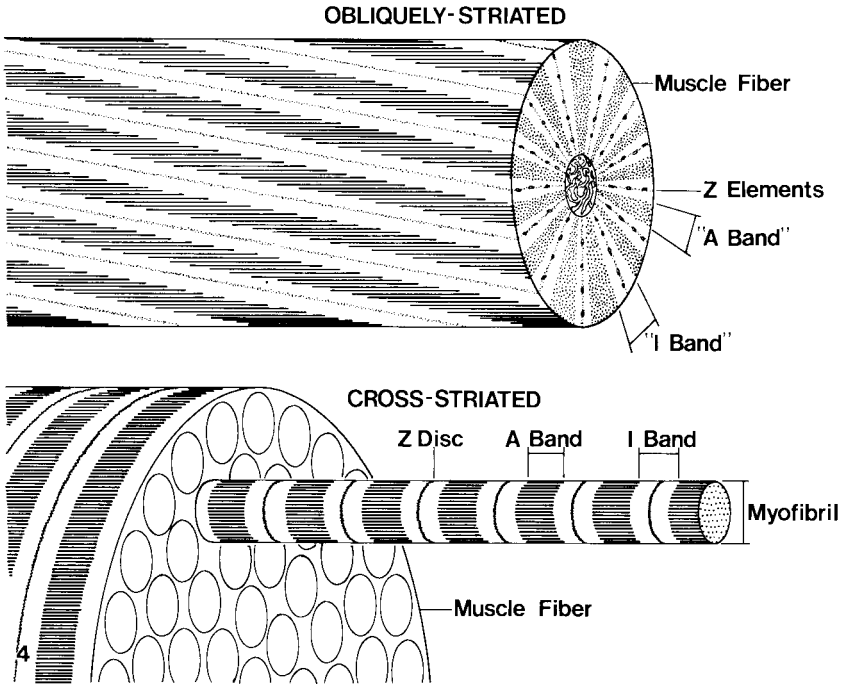


Fig. 4. Schematic diagram illustrating the similarities and differences of obliquely striated and cross-striated muscle fibers. Note that a cross-section of an obliquely striated muscle cell shows an analogous sequence of bands to those seen in a longitudinal section of cross-striated muscle. The thin filaments have been omitted from the diagram for clarity.

cle fibers extend toward the surface, forming groups of fibers called trabeculae (TR) which interdigitate with bundles of longitudinal muscle fibers (L). The trabeculae of the tentacles (Fig. 2) merge into a layer of circular muscle (C). The trabeculae of the arm (Fig. 3) insert on a connective tissue sheet (CT) orally and aborally and on a pair of oblique muscles (O) laterally. The circular muscle layer of the tentacle (Fig. 2) is wrapped by two helical muscle layers (H). The perimeter formed by the oblique muscles and connective tissue sheets of the arm and the helical muscle layers of the tentacle is enclosed by a connective tissue dermis (D) and a simple cuboidal epithelium (E). (See Kier, '82, for a more complete description.)

The arrangement and gross morphology of the transverse muscle masses of the arms and tentacles are similar (Figs. 2,3); however, they probably serve different functional roles (Kier, '82). Upon contraction, the transverse muscle mass of the tentacles decreases the cross-section of the tentacles; because the tentacle is constant in volume, the decrease in cross-section results in tentacular elongation. Shortening of the tentacular stalk after the strike is likely caused by longitudinal muscle contraction. The transverse muscle mass of the arms presumably serves a different function. Bending of the arms requires coordinated contraction of the transverse muscle mass and longitudinal muscle on one side of the arm. The transverse muscle mass of the arms resists the longitudinal compressional force created by longitudinal muscle contraction and allows arm bending (see Kier, '82; Kier and Smith, '85).

Muscle types in cephalopods

Typical cross-striated muscle has a characteristic banded pattern in longitudinal section due to alignment of the sarcomeres between adjacent fibrils (Fig. 4). The sarcomeres are defined by the Z discs. The thin filaments attach to the Z discs. On either side of the Z disc are the I bands, zones containing thin filaments but no thick filaments. The transverse alignment of thick filaments is referred to as the A band.

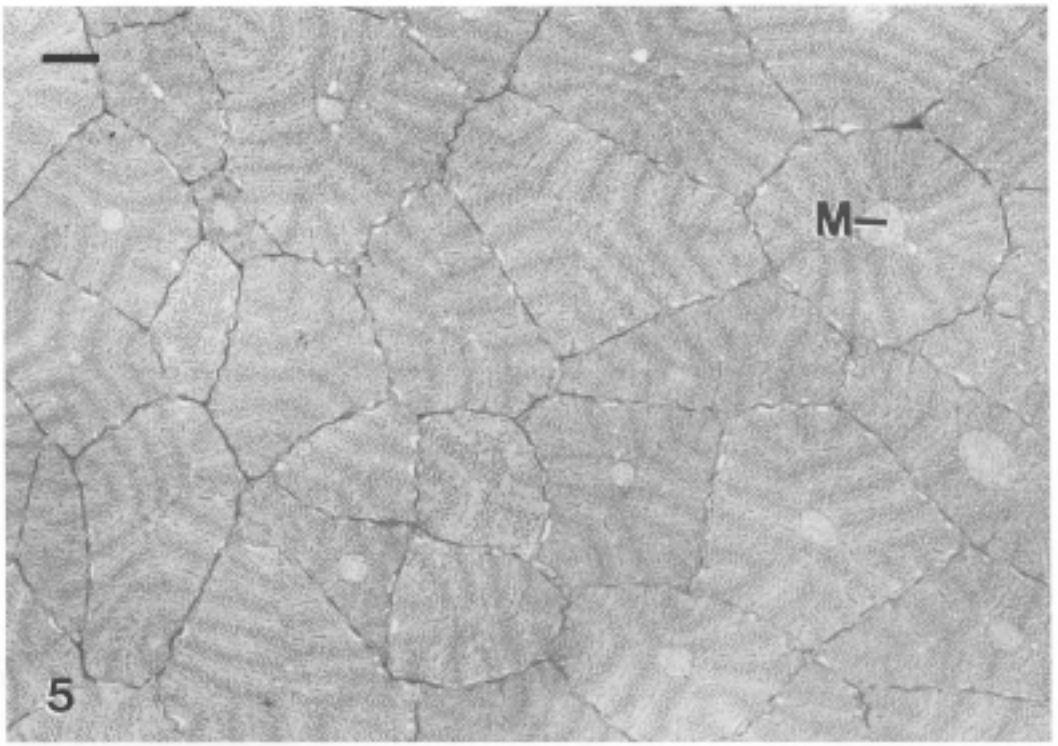
Cross-striated muscle is rare in cephalopods. The cardiac muscle of cephalopods exhibits cross-striation (Dykens and Mangum, '79; Jensen and Tjønneland, '77; Kawaguti, '63; Marceau, '05a; Schipp and Schäfer, '69; but see Amsellem and Nicaise, '80). Alexandrowicz ('27) reports small cross-striated muscles associated with the retina of the cuttlefish. Guérin ('08) and Plenk ('24) report cross-striated muscle in the transverse muscle mass of the tentacle of squid and cuttlefish. Guérin ('08) did not observe cross-striated muscle fibers in the other muscle groups of the tentacle or any of the muscle groups in the arms.

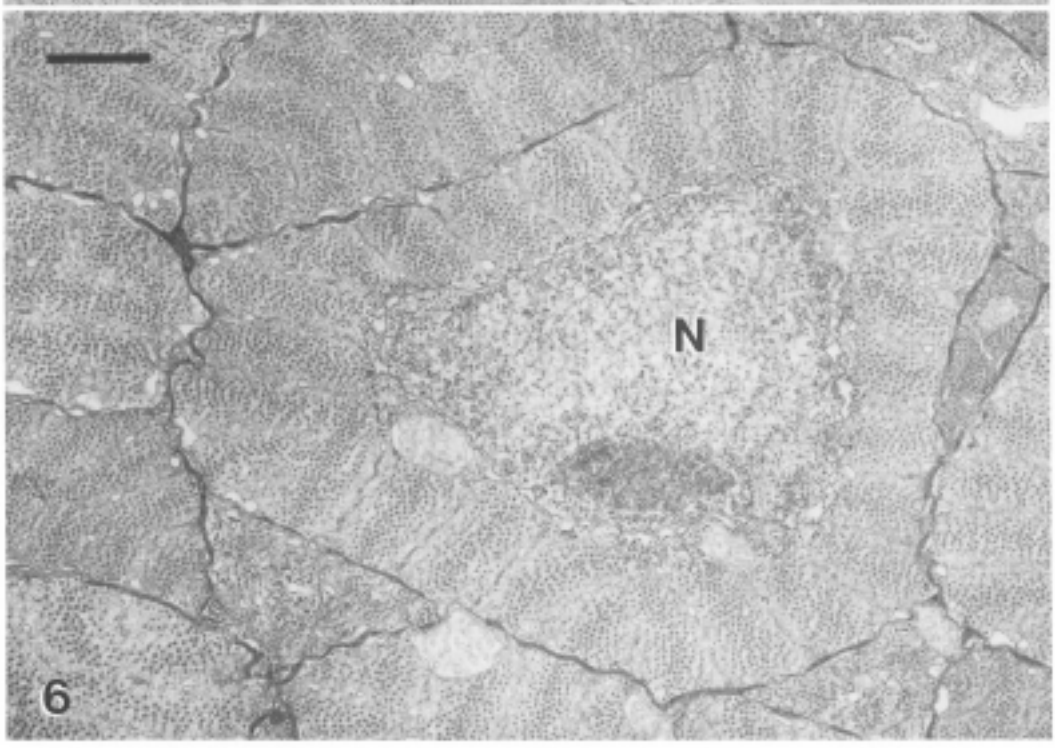
Most cephalopod muscle is obliquely striated (Amsellem and Nicaise, '80; Chantler, '83; Hanson and Lowy, '60; Hoyle, '64; Nicaise and Amsellem, '83). Its myofilaments, although parallel to the long axis of the cell, are not lined up in register across the cell as in cross-striated muscle fibers. In contrast to cross-striated muscle, obliquely striated muscle has its myofilaments staggered so that the Z elements lie in an oblique pattern encircling a central core of mitochondria and a single cell nucleus (Fig. 4). (Obliquely striated muscle containing a mitochondrial core is classified as regular. Irregular, obliquely striated muscle lacks a mitochondrial core (Millman, '67)). Thus obliquely striated muscles lack transverse banding. However, transverse sections of regular, obliquely striated muscle cells show a characteristic appearance with a similar sequence of banding to that in longitudinal section of cross-striated muscle: line of Z elements; an I band, an A band, an I band; and the next line of Z elements (Fig. 4). Of course these bands differ in the angle of section across the filaments. The striation angle (angle of alignment of Z elements relative to the long axis of the muscle cell) depends on the degree of extension and contraction of the muscle. In squid (species not identified) mantle and funnel retractor muscle the striation angle at rest has been reported as 6–12°, and to increase to 60° if the glycerol-extracted muscle was treated with adenosine triphosphate (Hanson and Lowy, '57).

MATERIALS AND METHODS

The transverse and circular musculature of the tentacle and the transverse musculature of the arms of the ommastrephid squid *Illex illecebrosus* (LeSueur, 1821), and the loliginid squid *Loligo pealei* LeSueur, 1821 were examined with the transmission electron microscope. Many sections included portions of the longitudinal muscle masses, but no systematic study of the longitudinal muscle masses was made. Specimens of *I. illecebrosus* were maintained in a 685 m^3 tank at the Aquatron Laboratory, Institute of Oceanography, Dalhousie University, Halifax, Nova Scotia, Canada, as described in O'Dor ('78) and Balch ('78). Specimens of *L. pealei* were obtained from the Marine Biological Laboratories, Woods Hole, Massachusetts. The investigation was begun with specimens of *I. illecebrosus* fixed in five fixative types: 1) 2.8% glutaraldehyde and 4.0% paraformaldehyde in 0.08% M phosphate buffer at pH 7.2; 2) 1.25% glutaraldehyde and 2.0% paraformaldehyde in 0.2 M phosphate buffer at pH 7.2; 3) 1.25% glutaraldehyde and 2.0% paraformaldehyde in 0.15 M phosphate buffer at pH 7.2; 4) 1.25% glutaraldehyde and 2.0% paraformaldehyde in 0.10 M phosphate buffer at pH 7.2; 5) 1.25% glutaraldehyde and 2.0% paraformaldehyde in 0.05 M phosphate buffer at pH 7.2. The best fixation was achieved with fixative type 1, but the condition of the sarcoplasmic reticulum in this material suggested that a fixative of higher osmolarity would have been more suitable. Cross-sectional slabs 2–3 mm thick of the arms and tentacles were obtained from freshly killed animals and fixed for 30 minutes at 40°C. The slabs were then cut into smaller blocks, approximately 1 mm^3, and fixed for an additional four hours at 4°C, followed by a 12-h buffer wash. The tissue was then postfixed in 1% osmium tetroxide for 1 h and dehydrated through a graded series of acetones. The tissue was infiltrated and embedded in epoxy resin (Epon) under reduced pressure.

Specimens of *Loligo pealei* were also examined using a fixative with 3.0% glutaraldehyde, 0.065% phosphate buffer, and 0.5% tannic acid with and without the addition of 6.0% sucrose. An attempt was made to examine tissue close to the surface of the block, as earlier work had indicated that infiltration of the tissue with fixative was difficult to achieve. The fixation obtained in the *L. pealei* material, in particular after 6.0% sucrose was added, was superior to that of the earlier work. Slabs cut from the arms and tentacles of *L. pealei* were fixed for 10 h at 4°C. Portions of the slabs adjacent to the fixation surface were then cut into smaller blocks approximately 1 × 1 × 4 mm and


M
5


N
6

washed overnight in buffer. The blocks were rinsed for 20 min in chilled 0.065% phosphate buffer and postfixed 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.

For light microscopy, sections were cut at 0.5 μm and stained with toluidine blue. Thin sections for electron microscopy were stained with saturated aqueous uranyl acetate and with Reynolds' lead citrate ('63) and were examined with Zeiss EM 10A and Zeiss EM 10CA electron microscopes. The magnification stops were calibrated with a grid replica before each measurement series (Ernest F. Fullam, Inc., No. 1002, 2160 lines/mm).

Glycol methacrylate sections of the musculature of the arms and tentacles of the squids *Loligo opalescens* Berry, 1911 and *Lolliguncula brevis* (Blainville, 1823) were examined with the light microscope. The squid were anesthetized in 1% ETOH in seawater, and 2–3 mm cross-sectional slabs of the arms and tentacles were cut and placed in phosphate buffered 2.5% glutaraldehyde and 4.0% paraformaldehyde for 24–48 hours. The tissue was dehydrated through ethanols to 70% ETOH and infiltrated and embedded in JB-4 embedding medium (Polysciences, Inc.). Sections were cut at 1.5 μm and stained with Lee's methylene-blue basic fuchsin stain (Bennett et al., '76). The sections were studied under phase-contrast and direct microscopy.

RESULTS

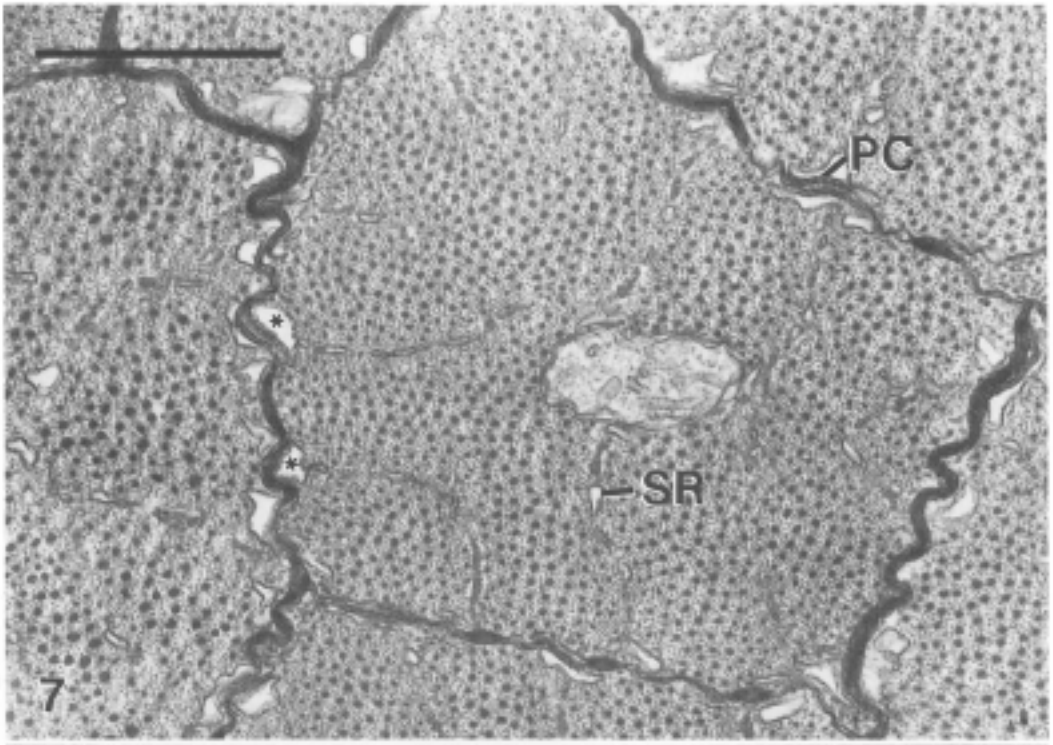
The muscle cells of the transverse muscle mass of the arms

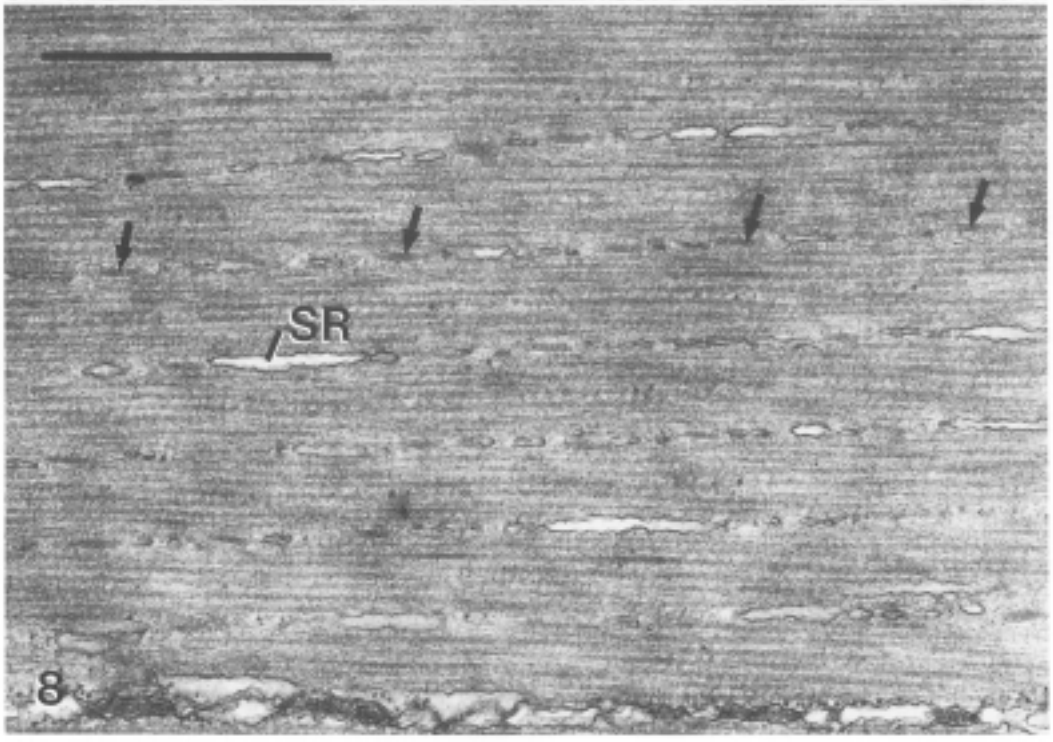
The transverse muscle mass of the arms is made up of closely packed regular, obliquely striated muscle cells (Fig. 5). The cells are circular to polygonal in cross-section, and their diameter ranges from approximately 1–6 μm (*I. illecebrosus*—mean = 3.4 μm, S.D. = 1.1 μm; *L. pealei*—mean = 2.8 μm, S.D. = 0.9 μm). The range of fiber diameters observed in transverse section (Fig. 5) may be a function of the plane of section cutting through different locations along the lengths of fusiform cells. Authors of several previous investigations of obliquely striated cephalopod muscle cells have reported this fusiform shape (Amsellem and Nicaise, '80; Bone et al., '81; Gonzalez-Santander and Socastro Garcia-Blanco, '72). The myofilaments of the cell surround a central longitudinally oriented core containing the cell nucleus and mitochondria (M). Transverse sections that pass through the cell nucleus (N) show the cell diameter to be greatest at that point (Fig. 6). An amorphous, electron-dense extracellular material is located among the cells.

Amsellem and Nicaise ('80) recognized three zones of sarcoplasmic reticulum in obliquely striated muscles of the buccal mass of the cuttlefish *Sepia officinalis*. I have observed a similar arrangement in the squid arm musculature and will therefore employ the same subdivisions here. The first, a peripheral zone of sarcoplasmic reticulum, is present in the subsarcolemmal cytoplasm. The outer portion of the membranes of the terminal cisternae of the sarcoplasmic reticulum in this zone are arranged in parallel to the sarcolemma forming specialized contacts termed "dyads" by Amsellem and Nicaise ('80) and "peripheral couplings" by Nunzi and Franzini-Armstrong ('81) (PC, Fig. 7). Hoyle ('83) defines a "dyad" as a form of close contact between a single sarcoplasmic reticulum element and an invaginated tubule of the sarcolemma. The obliquely striated muscle cells of the transverse muscle mass of squid lack invaginated tubules; I therefore adopt the term "peripheral coupling" for the specialized contacts between the sarcolemma and the sarcoplasmic reticulum. Regularly spaced, electron-dense "junctional feet" are present in the space between the sarcolemma and cisternal membrane of the peripheral coupling. The junctional feet were more easily identified in the tissue processed with potassium ferrocyanide in the secondary fixative (see Nunzi and Franzini-Armstrong, '81). The terminal cisternae are most frequently seen at points where the Z elements approach the sarcolemma. The terminal cisterna of one muscle cell is often located adjacent to the terminal cisterna of another muscle cell. Where the terminal cisternae of

Fig. 5. Low-power electron micrograph of transverse section of regular, obliquely striated muscle cells of the transverse musculature of the arm of *Illex illecebrosus*. The myofilaments surround a central core of mitochondria (M). An electron-dense extracellular material lies in between the closely packed cells. The scale bar length equals 1 μm.

Fig. 6. Electron micrograph of transverse section of regular, obliquely striated muscle cells of the transverse musculature of the arm of *Illex illecebrosus* showing greater cell diameter at the location of the nucleus (N). The scale bar length equals 1 μm.


PC
SR
7


SR
8

two cells are opposed, the amorphous, extracellular electron-dense material normally located between the sarcolemmal membranes is absent (Fig. 7).

The second zone of sarcoplasmic reticulum (SR) is the intramyoplasmic zone which lies in the plane of the Z elements (Fig. 7). Comparison of transverse and longitudinal sections (compare Figs. 7 and 8) suggests that the sarcoplasmic reticulum in this zone is made up of an anastomosing network of units that are elongated parallel to the longitudinal axis of the cell. The Z elements are not organized in a regular pattern such as that seen in the Z disc of many cross-striated muscle cells. Although arranged in a plane and associated with the intramyoplasmic zone of the sarcoplasmic reticulum, the Z areas of these obliquely striated cells are made up of irregularly spaced dense bodies (Fig. 8). In transverse sections, the sarcoplasmic reticulum and associated Z elements divide each cell cross-section into a number of roughly trapezoidal areas of myofilaments. The third zone of sarcoplasmic reticulum is a central zone surrounding the mitochondrial core (Figs. 6, 7).

In transverse sections it can be seen that the thick filament diameters vary and are arranged in an orderly array within each trapezoidal area of myofilaments between the rows of Z elements (Fig. 7). The smallest-diameter thick filaments are located along the two sides of the band of thick filaments nearest to the rows of Z elements, whereas the largest-diameter thick filaments are located down the center of the band. This is interpreted to be the result both of tapering of the thick filaments and their stagger relative to one another due to the oblique striation of the muscle cell (Amsellem and Nicaise, '80; Hoyle, '83). In Figure 9 this is demonstrated by a schematic cross-section through an obliquely arrayed band of fusiform thick filaments. A section passes through the tapered end of the filaments at the edges of the band and through the thickest middle portion of the filaments in the center of the band. The thick filament diameter at the center is approximately 310 Å (mean = 311 Å, S.D. = 19 Å) for *I. illecebrosus* and approximately 360 Å (mean = 358 Å, S.D. = 30 Å) for *L. pealei*. I was unable to obtain accurate measurements of thick filament length due to the difficulty of obtaining exactly longitudinal sections. In some sections, I was able to trace thick filaments for 2.8 μm, but this may not represent their total length.

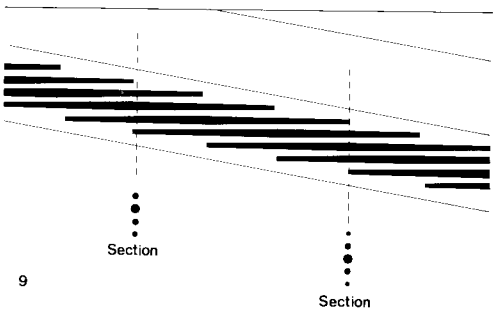


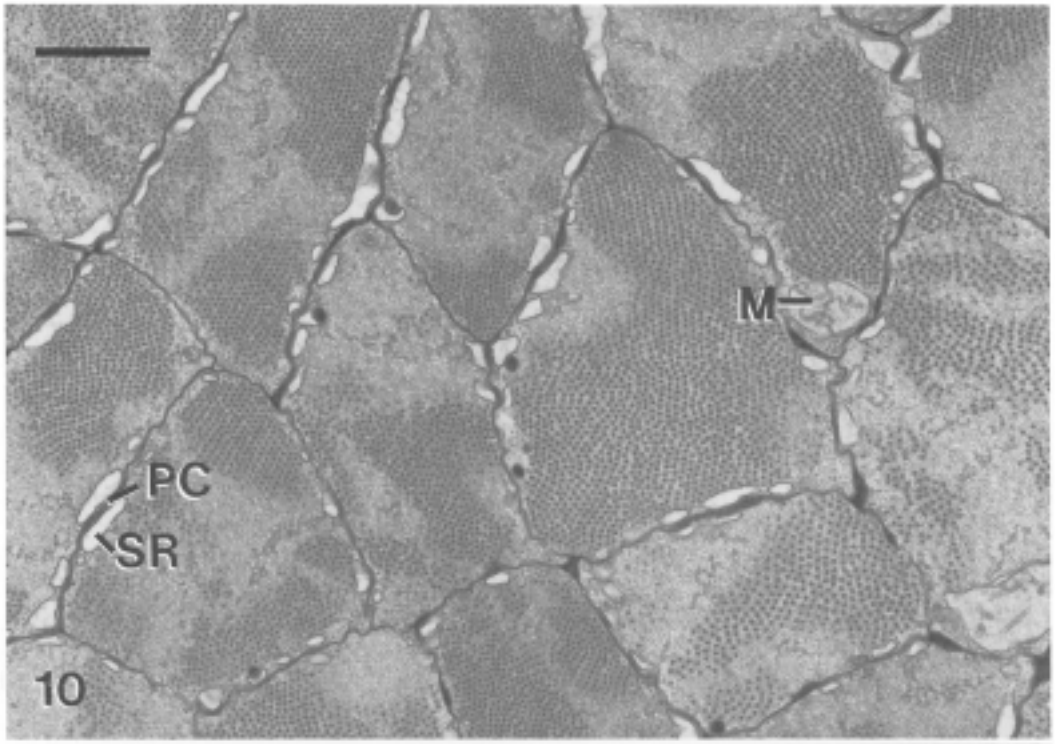
Fig. 9. Schematic diagram of the effect of staggering and tapering of thick filaments on their appearance in cross-section. A single band of staggered thick filaments is illustrated. Note that a transverse section through any point along the band will show larger-diameter thick filaments at the center of the band.

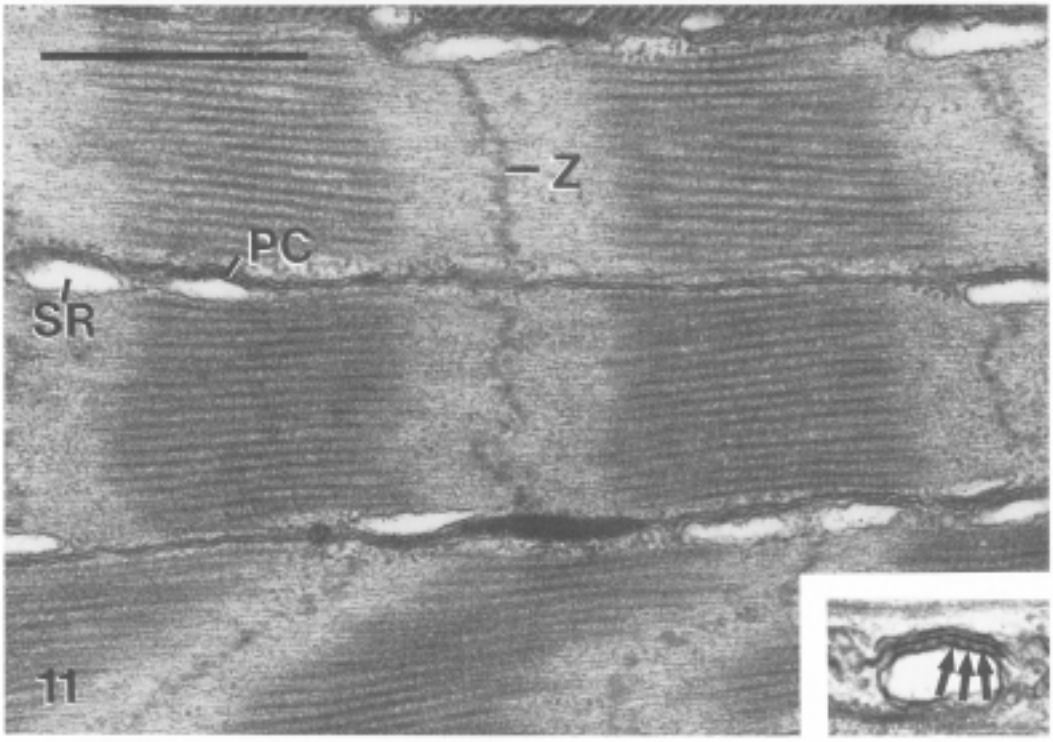
The muscle cells of the transverse and circular muscle mass of the tentacle

The transverse muscle mass of the tentacle is made up of closely packed, cross-striated muscle cells (Figs. 10 and 11). Occasionally, I observed a small bundle of obliquely striated muscle cells (similar in morphology to those of the transverse muscle mass of the arms) within the mass of cross-striated muscle. The diameter of the cross-striated muscle cells is small, ranging from 1–3 μm (*I. illecebrosus*—mean = 2.1 μm, S.D. = 0.5 μm; *L. pealei*—mean- 2.4 μm, S.D. = 0.7 μm). Mitochondria

Fig. 7. Electron micrograph of transverse section of regular, obliquely striated muscle cells of the transverse musculature of the arm of *Loligo pealei*. The outer membranes of the terminal cisternae (*) make specialized contacts or peripheral couplings (PC) with the sarcolemma. Regularly spaced junctional feet are visible in the peripheral coupling labeled PC. The terminal cisternae occur where the Z elements and associated sarcoplasmic reticulum (SR) approach the sarcolemma. Note that within each trapezoidal area of myofilaments delimited by the rows of Z elements and sarcoplasmic reticulum, the thick filament diameters are greatest in the center of the band of thick filaments. The scale bar length equals 1 μm.

Fig. 8. Electron micrograph of longitudinal section of regular, obliquely striated muscle cells of the transverse musculature of the arm of *Illex illecebrosus*. The long axis of the muscle fiber is oriented horizontally on the page. The intramyoplasmic zones of sarcoplasmic 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.


M
PC
SR
10


Z
PC
SR
11

(M) are located peripherally in the cell, immediately beneath the sarcolemma (Fig. 10).

Tubules of the sarcoplasmic reticulum (SR) were never observed in the center of the cells within the myofilaments. Instead, the sarcoplasmic reticulum is located peripherally in the cell immediately beneath the sarcolemma (Figs. 10 and 11). Thus, the cells are not divided into myofibrils and lack invaginated tubules. The sarcoplasmic reticulum forms peripheral couplings (PC) with the sarcolemma similar in morphology to those observed in the obliquely striated muscle described earlier. Regularly spaced, electron-dense junctional feet are present in the space between the outer sarcoplasmic reticulum membrane and the sarcolemma of the peripheral couplings (Fig. 11). As in the obliquely striated cells, the addition of potassium ferrocyanide in the secondary fixative enhanced the contrast of the junctional feet. The peripheral couplings of a cell are often aligned with the peripheral couplings of adjacent cells (Fig. 10).

The A band (thick filament length) is short, approximately 0.5 μm (mean = 0.52 μm, S.D. = 0.03 μm) for *I. illecebrosus* and approximately 0.9 μm (mean = 0.94 μm, S.D. = 0.08 μm) for *L. pealei*. The thick filament diameter was measured to be approximately 240 Å (mean = 237 Å, S.D. = 10 Å) in *I. illecebrosus* and approximately 310 Å (mean = 314 Å, S.D. = 22 Å) in *L pealei*. In transverse sections at high power, the thick filaments appear hollow due to the presence of an electron-lucent core (Fig. 12). The resting sarcomere length was measured to be approximately 0.9 μm (mean = .86 μm, S.D. = 0.6 μm) for *I. illecebrosus* and 1.6 μm (mean = 1.64 μm, S.D. = 0.2 μm) for *L. pealei*. An M band (a band in the exact center of the sarcomere where thick filaments are bound to one another by cross-links) is not present and the sarcomeres appear to be susceptible to shearing, with the result that the Z discs (and A and I bands) often are not perpendicular to the long axis of the fiber and instead follow a curved or angled course across the fiber (Fig. 11). The shearing or lack of alignment is also apparent in transverse sections where it can be seen that the section plane passes in and out of the A band in a single fiber (Fig. 10). The edges of the H region are indistinct (Fig. 11).

The Z disc is more diffuse and less regularly arranged than the Z disc of the cross-striated muscles of vertebrates (Smith, '72; Hoyle, '83). Transverse sections that graze the Z disc (Z, Fig. 13) show a loosely arranged grouping of electron-dense material rather than the organized network seen in vertebrate Z discs (cf. Rowe, '71).

A number of instances of vernier displacements of the cross-striation of the cells were noted (Fig. 14). A vernier displacement results from the insertion of one or more additional sarcomeres in a portion of the muscle fiber (Nunzi and Franzini-Armstrong, '81). This is discussed further below.

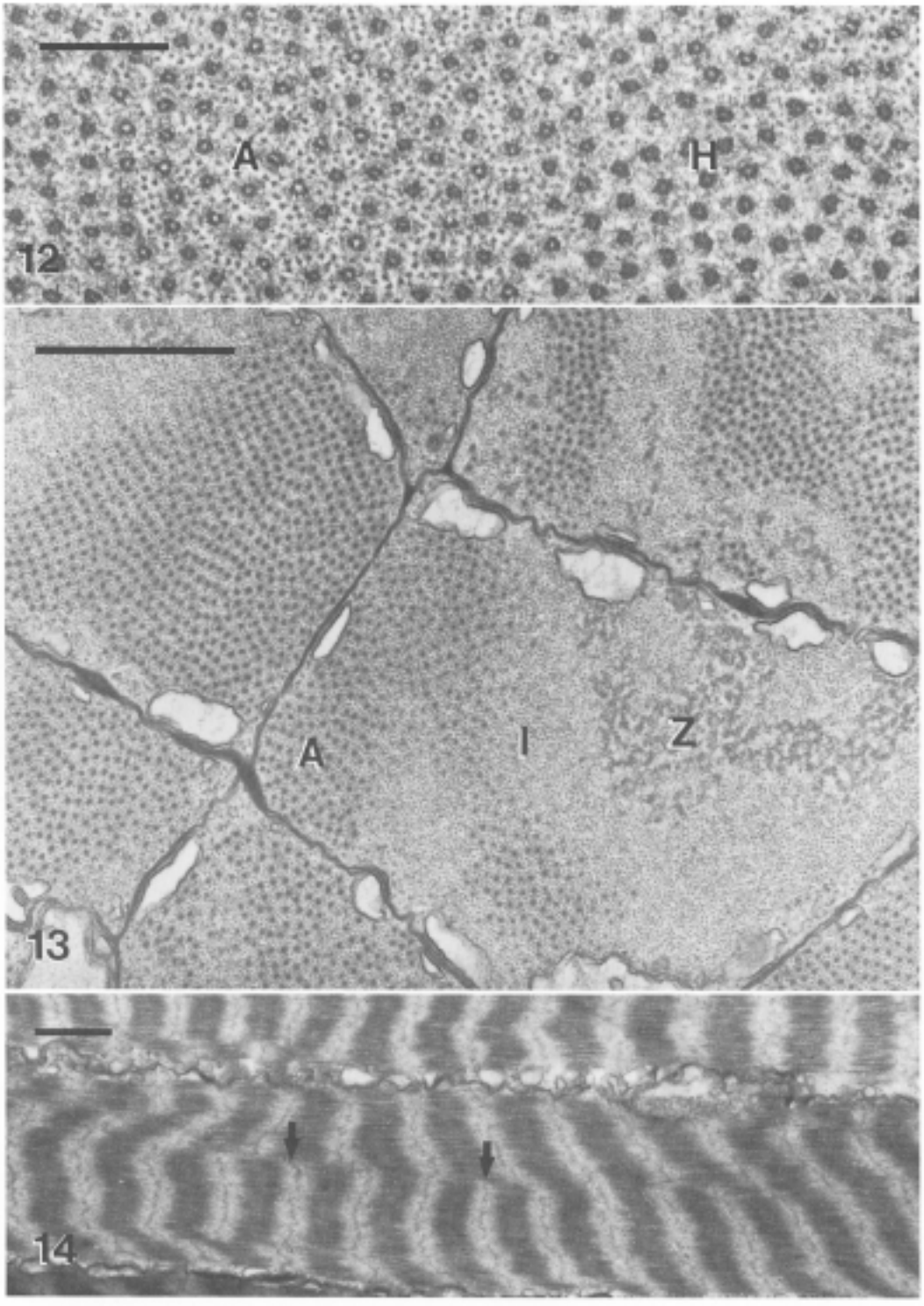
In the squid species studied, the transverse muscle mass of the tentacles of both male and female animals was made up of cross-striated muscle fibers. This contradicts the report of Hanson and Lowy ('60) that "the radial [=transverse] muscles of the long arms [=tentacles] of female decapods are striated while in the shorter arms and in the male they are of the smooth (helical) type" (Hanson and Lowy, '60, p. 275). This would be surprising indeed, because male and female animals use the tentacles in an identical manner.

The muscle cells of the longitudinal muscles of the arms and tentacles

Although the longitudinal muscle bundles of the arms and tentacles were not studied in detail, many sections included parts of these cells. Observations from these sections suggest that the muscle cells of the longitudinal muscle masses of both the arm and the tentacle are the regular, obliquely striated type, similar in ultrastructure to those of the transverse muscle mass of the arms.

Fig. 10. Electron micrograph of transverse section of closely packed, cross-striated muscle fibers of the transverse muscle mass 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. Note that the A band (thick filaments seen in cross-section) passes in and out of the section in a single muscle fiber. The scale bar length equals 1 μm.

Fig. 11. Electron micrograph of longitudinal section of cross-striated muscle fibers of the transverse musculature of the tentacle of *Loligo pealei*. The outer membrane of the sarcoplasmic reticulum (SR) forms peripheral couplings (PC) with the sarcolemma. The inset shows a higher magnification view of a peripheral coupling in which junctional feet (arrows) are visible. Note that the Z disc (Z) is diffuse and sometimes (lower fiber) follows an angled course across the muscle fiber. The scale bar length equals 1 μm and the inset is 0.5 μm wide.


A
H
12
A
I
Z
13
14

DISCUSSION

Ultrastructure of the regular obliquely striated muscle cells

The ultrastructure of the muscle cells of the arms of *Illex illecebrosus* and *Loligo pealei* is similar to that reported in a variety of muscles of other cephalopods: the mantle musculature of squid and cuttlefish (Bone et al., '81; Kawaguti and Ikemoto, '57; Kawaguti, '62; Mommsen et al., '81; Moon and Hulbert, '75; Ward and Wainwright, '72); the arms of cuttlefish and the tentacles of octopus (Gonzalez-Santander and Socastro Garcia-Blanco, '72; Socastro, '69); the digestive tract of the cuttlefish (Amsellem and Nicaise, '80); the chromatophore muscle of squid (Cloney and Florey '68; Florey, '69) and a variety of muscles of the chambered nautilus (Hochachka et al., '78).

There has been confusion historically concerning the classification of obliquely striated muscle. The oblique striation of cephalopod muscle fibers was reported as early as 1892 by Ballowitz and later by Marceau ('04, '05b) and Plenk ('33). The oblique striation has been mistaken to be a diamond lattice or "double oblique striation." Whenever whole isolated cells are viewed through the light microscope, both the front and back of the cell are visible and the oblique pattern appears to cross (Hanson and Lowy, '60). Hanson and Lowy ('57) suggested that the oblique striation was due to a single layer of ribbon-shaped, smooth (nonstriated) myofibrils that wrap the sarcoplasmic core in a helical pattern. They therefore proposed that this muscle type be classified as a special type of smooth muscle: "helical smooth." Hoyle ('64) recognized that a muscle fiber so constructed would be incapable of shortening unless it was prevented from twisting and the sarcoplasmic core maintained a constant volume. Later, the smooth "myofibrils" reported by Hanson and Lowy ('57) were revealed to be actually a staggered alignment of myofilaments, according to detailed ultrastructural studies of the obliquely striated muscles of cephalopods (Amsellem and Nicaise, '80; Gonzalez-Santander and Socastro Garcia-Blanco, '72; Kawaguti and Ikemoto, '57; Kawaguti, '62), annelids (Bouligand, '66; Knapp and Mill, '71; Kryvi, '74; Mill and Knapp, '70; Rosenbluth, '68, '72; Wissocq, '67, '81; Wissocq and Boilly, '77) and nematodes (Rosenbluth, '65, '67; Lanzavecchia, '77, 81; Lanzavecchia and Arcidiacono, '81). The myofilaments themselves are parallel to the long axis of the muscle fiber and the muscle is actually a type of striated muscle.

As Amsellem and Nicaise ('80) have noted, the term "myofibril" has also been used inappropriately in several recent studies of cephalopod muscle (Gonzalez-Santander and Socastro Garcia-Blanco, '72; Moon and Hulbert, '75; Ward and Wainwright, '72). This term is used to describe the fibrous subdivisions of cross-striated muscle cells made up of a sequence of sarcomeres and usually surrounded by sarcoplasmic reticulum and interspersed by mitochondria. The roughly trapezoidal areas of myofilaments seen in transverse sections of regular, obliquely striated cephalopod muscle differ from true myofibrils because they represent an alignment of A bands and thus only a portion of a sarcomere rather than a sequence of sarcomeres (Fig. 4).

Ultrastructure of the cross-striated muscle of the tentacle

The cell size and characteristics of the sarcoplasmic reticulum in squid cross-striated muscle differ from the cross-striated muscle of vertebrates in a number of ways. The sarcoplasmic reticulum of the cross-striated cells of the tentacle does not extend into the central portion of the cell occupied by myofilaments, and there are no divisions into myofibrils. In addition, the cells lack a transverse tubular system. The cross-striated cells of the tentacle are similar in this respect to the cells described in the cross-striated adductor muscles of scallops (Millman and Bennett, '76; Morrison and Odense, '74; Nunzi and Franzini-Armstrong, '81; Sanger, '71). There is likely a relation between the small cell diameter seen in the cross-striated cells

Fig. 12. High-power electron micrograph of transverse section of cross-striated muscle fibers of the transverse musculature of the tentacle of *Loligo pealei*. The thick filaments appear hollow. The A band (A) (where overlap between thick and thin filaments occurs) and the H band (H) (portion of the A band not occupied by thin filaments) are indicated. The scale bar length equals 200 nm.

Fig. 13. Electron micrograph of transverse section of cross-striated muscle fibers of the transverse musculature of the tentacle of *Loligo pealei*. Portions of the A band (A), I band (I), and Z disc (Z) are included in the section. Note the diffuse arrangement of electron-dense Z material. The scale bar length equals 1 μm.

Fig. 14. Electron micrograph of longitudinal section of cross-striated muscle fibers from the transverse musculature of the tentacle of *Illex illecebrosus* illustrating vernier displacements (arrows) within a single muscle fiber. The scale bar length equals 1 μm.

of the tentacle and the absence of a transverse tubular system within the myofilament mass. Sanger ('71) has suggested that the small cross-sectional area (1 × 10 μm) of scallop *(Aequipecten irridians)* cross-striated cells of the adductor is related to minimizing the Ca^{2+} diffusion distance from the sarcoplasmic reticulum to the myofilaments (see also Bone and Ryan, '73; Hill, '48; Kidokoro et al., '74; Prosser, '82). A similar relation between cell size and diffusion distance is suggested here. It is perhaps significant that the myofibrils of mammalian skeletal muscle fibers are typically 1.0 μm in diameter (Close, '72; Goldspink, '70). The single muscle cell of the cross-striated tentacle musculature is similar in size and is perhaps a functional equivalent of a single myofibril of mammalian skeletal muscle.

The above discussion assumes that, as in vertebrate striated muscle, the sarcoplasmic reticulum serves as a calcium store. The peripheral couplings of the striated adductor of scallops *(Aequipecten irridians)* figured by Nunzi and Franzini-Armstrong ('81) look identical to the peripheral couplings observed in this study in squid muscle. Nunzi and Franzini-Armstrong ('81) used freeze-fracture techniques and found that the plasmalemma facing the peripheral sarcoplasmic reticulum is similar to the junctional T-tubule membrane of vertebrate striated muscle. I suggest that the peripheral couplings identified in both the obliquely striated muscle of the arms and the cross-striated muscle of the tentacles play a role similar to that of the triad of vertebrate skeletal muscle.

Transverse sarcomere splitting has been suggested as a mechanism of insertion of new sarcomeres within a muscle for crab muscle (Jahromi and Charlton, '79) and scallop cross-striated adductor muscle (Nunzi and Franzini-Armstrong, '81). In this, a new sarcomere begins formation as a Z line cuts across the bridge-free regions of the thick filaments in the center of an existing A band. Each half of a divided A band then reestablishes bipolarity by adding the missing half. Simultaneously, thin filaments grow from the new Z line. As a result of this growth mechanism, vernier displacements of the cross-striations are formed. Perhaps the vernier displacements observed in squid cross-striated muscle are a result of a similar mechanism of addition of sarcomeres.

The protein paramyosin is present in the core of the thick filaments of most molluscan muscles. Although its function remains somewhat unclear, there is a correlation between thick filament length and paramyosin content (Chantler, '83; Levine et al., '76). In this regard, a determination of the paramyosin content of the cross-striated muscle cells of the squid tentacle would be particularly interesting because the thick filaments of this muscle type are much shorter than those reported for other molluscan muscles. The hollow appearance of the thick filaments when viewed in transverse section under the electron microscope could possibly indicate reduced paramyosin content in the core.

Implications of ultrastructure for physiological parameters

The ultrastructure of the muscle fibers of the transverse muscle mass of the squid tentacle is different from that of the other muscle masses of the tentacle and the muscle masses of the arm. What does the unusual ultrastructure of this muscle indicate about its physiology? There is a striking correlation between a muscle's ultrastructure and its physiology (Franzini-Armstrong and Peachey, '81; Josephson, '75; Smith, '72). There are also data on the structure and physiological properties of other cephalopod muscles and from mollusc muscles in general (Lowy and Millman, '62; Millman, '67; Nisbet and Plummer, '68). This discussion will not be concerned with intensive factors of muscle performance (terminology of Josephson, '75) such as the activity of myosin ATPase or the rate constants for calcium binding by sarcoplasmic reticulum proteins.

Comparison of the structural and physiological properties of molluscan muscles with frog sartorius muscle shows that an approximately inverse correlation exists between thick filament length and unloaded shortening speed (Millman, '67). Apparently, muscles with short sarcomeres have more sarcomeres in series per unit length, and shortening velocities of elements in series are additive (Huxley and Simmons, '72; Josephson, '75). Unloaded shortening speeds (at 20°C) of molluscan muscles range from approximately 5 lengths/second for the cross-striated adductor muscle of the scallop *Pecten* (thick filament length of 1.6 μm) to 0.25 lengths/second for the smooth anterior byssus retractor muscle of the mussel *Mytilus* (thick filament length of 10–30 μm). Frog sartorius muscle (thick filament length of 1.6 μm) shows an unloaded shortening speed of 6.0 lengths/second and is thus comparable with the striated adductor of *Pecten*. The

thick filament length of the cross-striated transverse muscle mass of the squid tentacle is 0.5 μm in *I. illecebrosus* and 0.9 μm in *L. pealei*. This suggests that this muscle has an even higher shortening speed than the cross-striated muscles of the frog and *Pecten*. The approximate thick filament length of the regular, obliquely striated muscle of the squid arm was measured to be 2.8 μm. Other regular, obliquely striated cephalopod muscles show similar thick filament lengths, and it is thus likely that the shortening speed of the obliquely striated arm muscle is similar (2.4 lengths/second for *Octopus* funnel retractor, Millman, '67).

It is possible to estimate the shortening speed of the cross-striated muscle of the tentacles from measurements from the high-speed cine films of prey capture by squid using the model for tentacle extension (Kier, '82). If the tentacle is treated as an elliptic cylinder of constant volume, one may predict the change in diameter of the tentacle from a measured change in length. (The change in diameter could not be resolved on the high-speed cine films; see Kier, '82.) In the sequence illustrated in Figure 1, the tentacles extended by 37% in 19 ms. This elongation would result from a 15% decrease in diameter (contraction of the transverse muscle mass produces the 15% decrease) requiring an approximate contraction speed under load of eight lengths/second (19°C). Although the load is difficult to estimate, the unloaded shortening speed is likely to be higher. This suggests that the cross-striated muscle of the tentacle is indeed a fast-contracting muscle.

CONCLUSION

Although the gross morphology and arrangement of the transverse muscle masses of the arms and tentacles of squid are similar, their functional roles are different. The arms serve in bending and grasping, whereas the tentacles are specialized for prey capture and rapid extension. The muscle fibers of the transverse muscle masses of the tentacle are responsible for this rapid extension, and their ultrastructure reflects this specialization. Unlike the other muscle masses of the tentacle, and all of the arm musculature, muscle fibers of the transverse muscle mass of the tentacles are cross-striated with a short A band length. The approximate loaded shortening speed estimated for these muscle fibers is significantly higher than values reported for unloaded shortening speed of typical cephalopod obliquely striated muscle and is also higher than unloaded shortening speeds of many vertebrate striated muscle fibers. The regular, obliquely striated fibers of the other muscle masses of the arms and tentacles are similar in ultrastructure to those described for other cephalopod body musculature.

ACKNOWLEDGMENTS

I thank R.K. O'Dor and M.E. DeMont for hospitality and lab space while at Dalhousie and R.F. Hixon for sending the specimens used for the methacrylate sections. I thank J.G. Lundberg, H.F. Nijhout, M.K. Reedy, C.F.E. Roper, S. Vogel and S.A. Wainwright for a critical reading of an early version of the manuscript. I am grateful to M.K. Reedy and K.K. Smith for discussion and insight, and to E.M. Lynch for typing the manuscript. I appreciate the patient training in EM technique I received from D.E. Copeland and J.G. Tidball. I especially wish to thank S.A. Wainwright for advice, encouragement, and support. This work was supported in part by a Cocos Foundation Morphology Traineeship and a Woods Hole Oceanographic Institution Postdoctoral Scholar Award.

LITERATURE CITED

Alexandrowicz, J.S. (1927) Contribution à l'étude des muscles, des nerfs et du mécanisme de l'accommodation de l'oeil des céphalopodes. Arch. Zool. Exptl. Gén. *66*:71–134.

Amsellem, J., and G. Nicaise (1980) Ultrastructural study of muscle cells and their connections in the digestive tract of *Sepia officinalis*. J. Submicro. Cytology. *12*:219–231.

Balch, N. (1978) A description of the pool and tower tanks in the aquatron laboratory, Dalhousie University. Proceedings of the Workshop on the Squid *Illex illecebrosus*, Dalhousie University, Halifax, Nova Scotia, May, 1978. Fish. Marine Serv. Tech. Rept. *833*:19.1–19.7.

Ballowitz, E. (1892) Ueber den feineren Bau der Muskelsubstanzen. I. Die Muskelfaser der Cephalopoden. Arch. Mikrosk. Anat. *39*:291–324.

Bennett, H.S., A.D. Wyrick, S.W. Lee, and J.H. McNeil, Jr. (1976) Science and art in preparing tissues embedded in plastic for light microscopy, with special reference to glycol methacrylate, glass knives and simple stain. Stain. Tech. *51*:71–97.

Bone, Q., and K.P. Ryan (1973) The structure and innervation of locomotor muscles of salps (Tunicata: Thalicea). J. Mar. Biol. Assoc. U.K. *53*:873–883.

Bone, Q., A. Pulsford, and A.D. Chubb (1981) Squid mantle muscle. J. Mar. Biol. Assoc. U.K. *61*:327–342.

Bouligand, Y. (1966) La disposition des myofilaments chez une Annélide Polychète. J. Microsc. (Paris) *5*:305–322.

Chantler, P.D. (1983) Biochemical and structural aspects of molluscan muscle. In A.S.M. Saleuddin and K.M. Wilbur (eds): The Mollusca, Vol. 4, Physiology, Part 1. New York: Academic Press, pp. 1–33.

Cloney, R.A., and E. Florey (1968) Ultrastructure of cephalopod chromatophore organs. Z. Zellforsch. Mik-

rosk. Anat. *89:*250–280.
Close, R.I. (1972) Dynamic properties of mammalian skeletal muscles. Physiol. Rev. *52:*129–197.
Dykens, J.A., and C.P. Mangum (1979) The design of cardiac muscle and the mode of metabolism in molluscs. Comp. Biochem. Physiol. *62A:*549–554.
Florey, E. (1969) Ultrastructure and function of cephalopod chromatophores. Am. Zool. *9:*429–442.
Franzini-Armstrong, C., and L.D. Peachey (1981) Striated muscle—contractile and control mechanisms. J. Cell. Biol. *91:*166–186.
Goldspink, G. (1970) The proliferation of myofibrils during muscle fiber growth. J. Cell Sci. *6:*593–604.
Gonzalez-Santander, R., and E. Socastro Garcia-Blanco (1972) Ultrastructure of the obliquely-striated or pseudo-striated muscle fibres of cephalopods, *Sepia, Octopus* and *Eledone.* J. Submicrosc. Cytol. *4:*233–245.
Guérin, J. (1908) Contribution à l'étude des systèmes cutané, musculaire, et nerveux de l'appareil tentaculaire des Céphalopodes. Arch. Zool. Exp. Gén. (Sér. 4) *8:*1–178.
Hanson, J., and J. Lowy (1957) Structure of smooth muscles. Nature, Lond. *180:*906–909.
Hanson, J., and J. Lowy (1960) Structure and function of the contractile apparatus in the muscles of invertebrate animals. In G.H. Bourne (ed): Structure and Function of Muscle. New York: Academic Press, Vol. I, pp. 265–335.
Hill, A.V. (1948) On the time required for diffusion and its relation to processes in muscle. Proc. Roy. Soc. (B) *135:*446–453.
Hochachka, P.W., C.J. French, and J. Meredith (1978) Metabolic and ultrastructural organization in *Nautilus* muscle. J. Exp. Biol. *205:*51–62.
Hoyle, G. (1964) Muscle and neuromuscular physiology. In K.M. Wilbur and C.M. Yonge (eds): Physiology of Mollusca. New York: Academic Press, Vol. I, pp. 313–351.
Hoyle, G. (1983) Muscles and Their Neural Control. New York: John Wiley & Sons.
Huxley, A.F., and R.M. Simmons (1972) Mechanical transients and the origin of muscular force. Cold Spring Harbor Symp. Quant. Biol. *37:*669–680.
Jahromi, S.S., and M.P. Charlton (1979) Transverse sarcomere splitting. A possible means of longitudinal growth in crab muscles. J. Cell Biol. *80:*736–742.
Jensen, H., and A. Tjønneland (1977) Ultrastructure of the heart muscle cells of the cuttlefish *Rossia macrosoma* (Delle Chiaje) (Mollusca: Cephalopoda). Cell Tiss. Res. *185:*147–158.
Josephson, R.K. (1975) Extensive and intensive factors determining the performance of striated muscle. J. Exp. Zool. *194:*135–154.
Kawaguti, S. (1962) Arrangement of myofilaments in the oblique-striated muscles. In S.S. Breese (ed): Proceedings of the Fifth Congress for Electron Microscopy. New York: Academic Press, Vol. *2:*M–11.
Kawaguti, S. (1963) Electron microscopy on the heart muscle of the cuttlefish. Biol. J. Okayama Univ. *9:*27–40.
Kawaguti, S., and N. Ikemoto (1957) Electron microscopy of the smooth muscle of a cuttlefish, *Sepia esculenta* (Hoyle). Biol. J. Okayama Univ. *3:*196–208.
Kidokoro, Y., S. Hagiwara, and M.P. Henkart (1974) Electrical properties of obliquely-striated muscle fiber membrane of *Anodonta gochidium* J. Comp. Physiol. *90:*321–338.
Kier, W.M. (1982) The functional morphology of the musculature of squid (Loliginidae) arms and tentacles. J. Morphol. *172:*179–192.
Kier, W.M., and K.K. Smith (1985) Tongues, tentacles and trunks: The biomechanics of movement in muscu lar-hydrostats. Zool. J. Linn. Soc. *83:*307–324.
Knapp, M.F., and P.J. Mill (1971) The contractile mechanism of the obliquely-striated body wall muscles of the earthworm, *Lumbricus terrestris.* J. Cell Sci. *8:*413–425.
Kryvi, H. (1974) On the myofilament arrangement in obliquely-striated muscle cells of *Sabella penicillum* (Polychaeta). Norw. J. Zool. *22:*67–69.
Lanzavecchia, G. (1977) Morphological modulations in helical muscles (Aschelminthes and Annelida). Int. Rev. Cytol. *51:*133–186.
Lanzavecchia, G. (1981) Morphofunctional and phylogenetic relations in helical muscles. Boll. Zool. *48:*29–40.
Lanzavecchia, G., and G. Arcidiacono (1981) Contraction mechanism of helical muscles: Experimental and theoretical analysis. J. Submicr. Cytol. *13:*253–266.
Levine, R.J.C., M. Elfvin, M.M. Dewey, and B. Walcott (1976) Paramyosin in invertebrate muscles. II. Content in relation to structure and function. J. Cell Biol. *71:*273–279.
Lowy, J., and B.M. Millman (1962) Mechanical properties of smooth muscles of cephalopod molluscs. J. Physiol. *160:*353–363.
Marceau, F. (1904) Sur le mécanisme de la contraction des fibres musculaires lisses dites à double striation oblique ou à fibrilles spiralées et en particulier des celles des muscles adducteurs des lamellibranches. C.R. Acad. Sci. Paris, *139:*70–72.
Marceau, F. (1905a) Recherches sur la structure du coeur chez les mollusques. Suives d'une étude spéciale des coeurs branchiaux et de leurs appendices glandulaires chez les céphalopodes. Arch. Anat. Microscop. *7:*495–588.
Marceau, F. (1905b) Recherches sur la structure des muscles du manteau des céphalopodes en rapport avec leur mode de contraction. Tran. Lab. Soc. Sci., Arcachon, 8th year, pp. 48–65.
Messenger, J.B. (1968) The visual attack of the cuttlefish. *Sepia officinalis.* Anim. Behav. *16:*342–357.
Messenger, J.B. (1977) Prey capture and learning in the cuttlefish, *Sepia.* Symp. Zool. Soc. Lond. *38:*347–376.
Mill, P.J., and M.F. Knapp (1970) The fine structure of obliquely-striated body wall muscles in the earthworm *Lumbricus terrestris* (Linn.). J. Cell Sci. *7:*233–261.
Millman, B.M. (1967) Mechanism of contraction in molluscan muscle. Am. Zool. *7:*583–591.
Millman, B.M., and P.M. Bennett (1976) Structure of the cross-striated adductor muscle of the scallop. J. Mol. Biol. *103:*439–468.
Mommsen, T.P., J. Ballantyne, D. MacDonald, J. Gosline, and P.W. Hochachka (1981) Analogues of red and white muscle in squid mantle. Proc. Natl. Acad. Sci. U.S.A., *78:*3274–3278.
Moon, T.W., and W.C. Hulbert (1975) The ultrastructure of the mantle musculature of the squid *Symplectoteuthis oualaniensis.* Comp. Biochem. Physiol. *52B:*145–149.
Morrison, D.M., and P.H. Odense (1974) Ultrastructure of some pelecypod adductor muscles. J. Ultrastruct. Res. *49:*228–251.
Nicaise, G. and Amsellem, J. (1983) Cytology of muscle and neuromuscular junction. In A.S.M. Saleuddin and K.M. Wilbur (eds.): The Mollusca, Vol. 4, Physiology, Part I. New York: Academic Press, pp. 1–33.
Nisbet, R.H., and J.M. Plummer (1968) A functional interpretation of the organization of molluscan muscles. J. Physiol. Lond. *196:*17–18.
Nunzi, M.G., and C. Franzini-Armstrong (1981) The structure of smooth and striated portions of the adductor muscle of the valves in a scallop. J. Ultrastruc. Res.

*76:*134–148.

O'Dor, R.K. (1978) Laboratory experiments with *Illex illecebrosus.* Proceedings of the workshop on the squid *Illex illecebrosus,* Dalhousie University, Halifax, Nova Scotia, May 1978. Fish. Marine Serv. Tech. Rept. *833:*18.1-18.10.

Plenk, H. (1924) Die Muskelfasern der Schnecken. Zugleich eine kritische Studie über die sogenannte Schrägstreifung. Z. wiss. Zool. *122:*1–78.

Plenk, H. (1933) Zum Bau der Cephalopodenmuskelfasern. Z. Mikroskop. Anat. Forsch. *33:*605–624.

Prosser, C.L. (1982) Diversity of narrow-fibered and wide-fibered muscles. In B.M. Twarog, R.J.C. Levine, and M.M. Dewey (eds.): Basic Biology of Muscles: A Comparative Approach. New York: Raven Press, pp. 381–397.

Reynolds, E. (1963) The use of lead citrate at high pH as an electron-opaque stain in electron microscopy. J. Cell Biol. *17:*208–212.

Rosenbluth, J. (1965) Ultrastructural organization of obliquely-striated muscle fibers in *Ascaris lumbricoides.* J. Cell Biol. *25:*495–515.

Rosenbluth, J. (1967) Obliquely-striated muscle. III. Contraction mechanism of *Ascaris* body muscle. J. Cell Biol. *34:*15–33.

Rosenbluth, J. (1968) Obliquely-striated muscle. IV. Sarcoplasmic reticulum, contractile apparatus and endomysium of the body muscle of a Polychaeta, *Glycera,* in relation to its speed. J. Cell Biol. *36:*245–259.

Rosenbluth, J. (1972) Obliquely-striated muscle. In G.H. Bourne (ed): The Structure and Function of Muscle. Second edition, Vol. 1. New York: Academic Press, pp. 399–420.

Rowe, R.W.D. (1971) Ultrastructure of the Z line of skeletal muscle fibers. J. Cell Biol. *51:*674–685.

Sanger, J.W. (1971) Sarcoplasmic reticulum in the cross-striated adductor muscle of the bay scallop *Aequipecten irridians.* Z. Zellforsch. *118:*156–161.

Schipp, R., and A. Schäfer (1969) Vergleichende elektronmikroskopische Untersuchungen an den zentralen Herzorganen von Cephalopoden *(Sepia officinalis).* Die Feinstruktur des Herzens. Z. Zellforsch. Mikrosk. Anat. *98:*576–598.

Smith, D.S. (1972) Muscle. New York: Academic Press.

Socastro, E. (1969) Observaciones sobre el significado estructural y functional de la musculatura braquial de los Cefalopodes. Bol. R. Soc. Espanola Hist. Nat. (Biol.). *67:*181–191.

Ward, D.V., and S.A. Wainwright (1972) Locomotory aspects of squid mantle structure. J.Zool., Lond. *167:*437–449.

Wissocq, J.-C. (1967) Etude ultrastructurale de l'evolution des muscles longitudinaux lors de la stolonization expérimentale de *Syllis amica* Quatrefages (Annélidae Polychéte). Z. Zellforsch. *83:*449–467.

Wissocq, J.-C. (1981) Muscles à striation oblique et à striation transversale chez les Annélides et Polychétes. Boll. Zool. *48:*57–74.

Wissocq, J.-C., and B. Boilly (1977) Muscles à simple striation oblique et à striation transversale chez une Annélide Polychète: *Magelona papillicornis* F. Muller. Biol. Cell *29:*183–192.