

# ELECTROMECHANICAL COUPLING IN TUBULAR MUSCLE FIBERS

## I. The Organization of Tubular Muscle Fibers in the Scorpion *Leiurus quinquestriatus*

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### ABSTRACT

The tubular fibers of the claw-closer muscle of the scorpion have a central core containing nuclei and mitochondria. The myofibrils have the shape of thin lamellae ( $1 \mu$ ) extending radially from the core to the surface membrane ( $20 \mu$ ). The thick myofilaments are organized in a hexagonal array with orbits of 10–13 thin myofilaments. The ratio of thick-to-thin filaments is 1:5. Transverse tubular system (TS) openings are located between lamellated myofibrils. In each sarcomere two TS's are found, one on each side of the H band. The TS is composed of a transverse tubule and tubular pockets (TP). The TP's form diadic contact with the terminal cisternae of the sarcoplasmic reticulum. The TS can be traced from the cell membrane down to the cell core. The surface area of the TS was calculated to be six times that of the outer surface membrane.

### INTRODUCTION

The current hypothesis concerning electromechanical coupling in muscle proposes a spread of surface depolarization into the transverse tubular system (TS) (Huxley and Taylor, 1958). Two main mechanisms were proposed. One assumes that a regenerative process in the TS is not required for full activation of the contractile system and that inward electrotonic spread of the normal action potential is sufficient to activate the most central filaments (Falk, 1968; Adrian et al., 1969 *a*). The other implies that an active potential change is required to achieve a safety factor greater than one (Adrian et al., 1969 *b*; Costantin, 1970; Sandow, 1970). However, no conclusive evidence for either mechanism exists (Sandow, 1970).

Recently, the problem of transverse spread of excitation has been treated quantitatively by Adrian et al. (1969 *a, b*) and Schneider (1970).

Both assumed that the TS of amphibian muscle fibers is a transversely oriented, homogeneous network of tubules, uniformly distributed throughout the fiber cross-section. However, observations by Revel (1962), Huxley (1964), Peachey (1965), and Peachey and Schild (1968) point out the longitudinal extensions of the TS and the unequal branching of this system. Furthermore, the width of each fibril is about  $1 \mu$ , while Huxley and Taylor's experiments strongly suggest that the openings of the TS are located at  $5 \mu$  intervals. It is, therefore, quite possible that TS tubules from a few fibrils converge onto a single narrow peripheral segment which is twisted and convoluted and situated almost parallel to the sarcolemma to form subsarcolemmal caveolae, the only observed connection between the TS and fiber exterior (Rayns et al., 1968). Such a complicated TS is not

convenient for a quantitative study of current spread into the muscle fiber. This makes the use of a more simple and regular TS, such as the one found in the tubular muscle fibers of scorpion, of great interest.

Tubular muscle fibers are found in several phyla, such as Annelids (leech, Röhlich, 1962) and Arachnids (spider, Zebe and Rathmayer, 1968). In insects, tubular muscle fibers were described in the leg and flight muscles of Orthoptera, Odonata, Lepidoptera, Hymenoptera, and Diptera (Tiegs, 1955; Smith, 1961, 1966 *a*; Pasquali-Ronchetti, 1970). In Mollusca, tubular fibers were reported in squid mantle (Hanson and Lowy, 1957; Hoyle, 1969) and in the radula protractor of *Busycon canaliculatum* (Sanger and Hill, 1971). Tubular fibers also appear in embryos of vertebrates (Walls, 1960) and in adult fish muscles (Franzini-Armstrong and Porter, 1964). Such fibers have a central core of sarcoplasm containing a chain of nuclei. The core is surrounded by contractile elements, which, in arthropods, are arranged in a radial lamellar pattern.

In tubular fibers the mitochondria are found in different discrete locations within the muscle fiber. In Odonata they occupy the space between myofibrils (Smith, 1966 *a*), while in Diptera they are arranged as a ring between the laminar myofibrils. The general organization and the distribution of mitochondria within a muscle fiber might have an effect on the location and geometry of the TS. We describe here a tubular cell in which the lamellar fibrils are arranged radially, the nuclei and mitochondria are concentrated in the central core, and the TS is organized in a simple radial arrangement.

In a previous study (Gilai and Parnas, 1970) we observed that the scorpion muscle fibers are tubular. Preliminary experiments to calculate membrane constants show that the membrane capacity is low relative to that of other arthropods. Accordingly, light micrographs show that the sarcolemma is unfolded. In addition, each muscle fiber is innervated by two motor axons, one initiating a junction potential, the second a spike. Thus, two distinct levels of mechanical coupling were observed. In the case of an all-or-none muscular electrogenesis, it is of particular interest to know whether the electrical signal could propagate with sufficient rapidity and magnitude to bring about full activation of both the peripheral and core filaments. Several mechanisms to ex-

plain the nature of graded contraction were suggested by Hoyle (1967 *a*), but it is not yet known what part of the tension is contributed either by "parallel elements," such as the extent of sarcomere activation and the number of activated myofibrils, or by the "series elements" such as the extent of filament sliding and the number of sarcomeres activated. The tubular muscle fiber of the scorpion with its two distinct levels of mechanical coupling offers a model by which some of these questions could be answered.

With these problems in mind, the morphology and ultrastructural organization of the membrane system in the tubular muscle fibers of the scorpion has been studied in order to enable a quantitative analysis of the transverse spread of excitation to be made.

#### MATERIALS AND METHODS

The long closer muscle (Gilai and Parnas, 1970) of the pedipalp claw of the yellow scorpion *Leiurus quinquestriatus* was used. The muscle was exposed by removing the ventral part of the patellar cuticle. Resting length was maintained by affixing the claw and the femur to a rigid support. Prefixation was done *in situ* with ice-cold 2.5% glutaraldehyde (Sabatini et al., 1963) buffered at pH 7.2 with 0.1 M phosphate for 3 hr. The muscle was then washed several times during 12 hr with 0.1 M phosphate buffer (pH 7.2). It was later cut into small pieces and post-fixed with 1% OsO<sub>4</sub> solution for 1 hr at 0°C. Dehydration was carried out with ascending ethanol series, followed by propylene oxide. The specimens were embedded in Epon 812 (Luft, 1961). Sections (500–700 Å) were cut with glass knives (LKB Ultratome, LKB Instruments, Inc., Rockville, Md.) and stained in saturated uranyl acetate and lead citrate (Karnovsky, 1961). Electron micrographs were taken with an electron microscope type 7A (Japan Electron Optics Laboratory Co., Ltd., Medford, Mass.) at 80 kv.

#### RESULTS

The general anatomy of the long closer muscle of the claw has been previously described (Gilai and Parnas, 1970). The muscle fibers are about 7 mm long with a diameter ranging from 40 to 60  $\mu$ . Connective tissue is found between the fibers.

The fibers have the basic arrangement of lamellar myofibrils with a central region containing nuclei and mitochondria (Fig. 1).

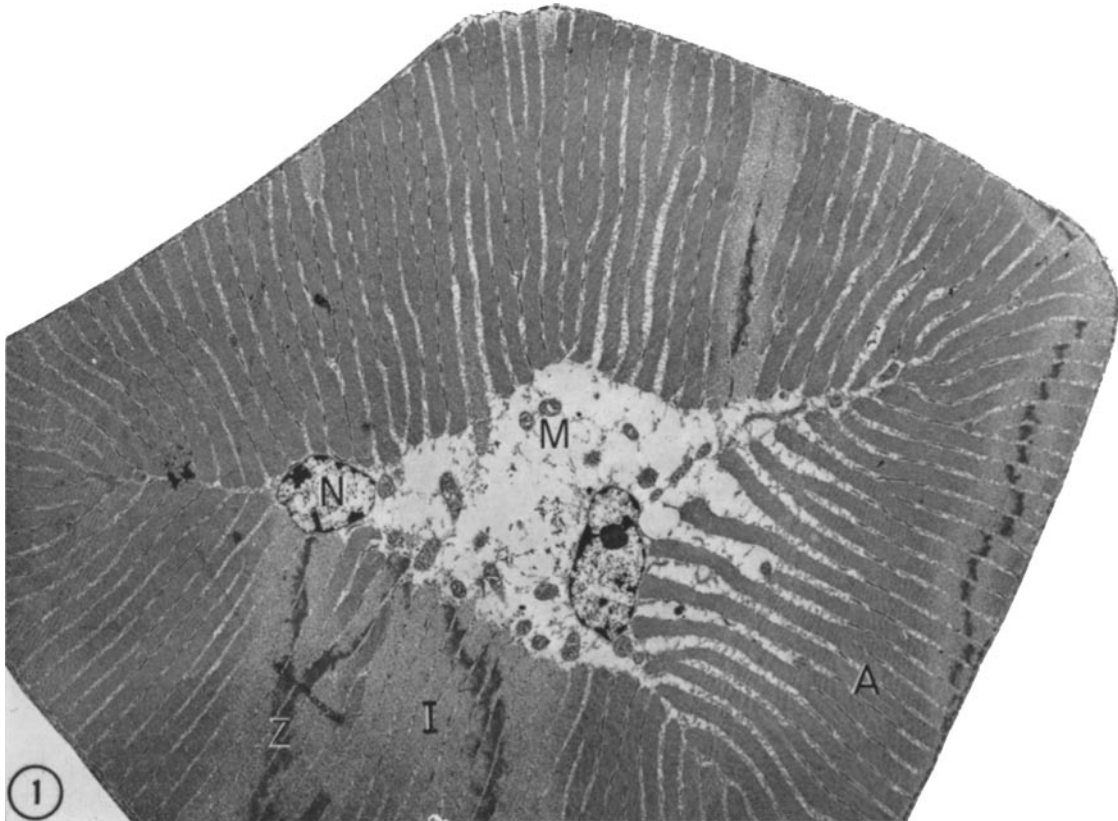


FIGURE 1 Cross-section of a tubular muscle fiber. Note lamellar arrangement of myofibrils and central core with mitochondria (*M*) and nuclei (*N*). A bands (*A*); I bands (*I*); Z bands (*Z*).  $\times 3700$ .

### *The Myofibrils*

The myofibrils are arranged radially in a lamellar pattern (Fig. 1); an average of 145 fibrils per cell can be counted in cross-sections. The dimensions of each fibril range from 10 to 20  $\mu$  radially and from 0.5 to 1.5  $\mu$  tangentially. Each fibril extends radially from the core to the sarcolemma. The myofibrils are separated by a complex sarcoplasmic reticulum (SR), which occasionally extends between the fibril and the sarcolemma (Fig. 8).

In longitudinal sections the classical (Huxley, 1957) sarcomere structure is evident (Fig. 9). At rest length the sarcomere has a mean length of 5  $\mu$ . The I, A, and H bands are clearly visible. The Z band is about 0.1  $\mu$  thick and it broadens near the sarcolemma to a conelike structure with a diameter of about 1.0  $\mu$  (Fig. 8). This widening can also be seen in cross-section through the I band (Fig. 3).

### *The Myofilaments*

The orbital arrangement of myofilaments is irregular. The length of the thick filaments is about 4  $\mu$  and the I band is approximately 1  $\mu$ . The thick filaments are round in transverse section, their diameter ranges from 200 to 220 A, and they have a hollow center (Fig. 2). They are arranged in a hexagonal pattern with interfilament distances of 400–500 A. In the region of overlap the orbits consist of up to 13 filaments. However, this arrangement is not always precise or well preserved. The ratio of thick-to-thin filaments is 1:5.

### *The Transverse Tubular System*

The TS's can clearly be identified by their denser membrane with a more pronounced bilayer structure. The organization of the transverse system is extremely regular. A remarkable sym-

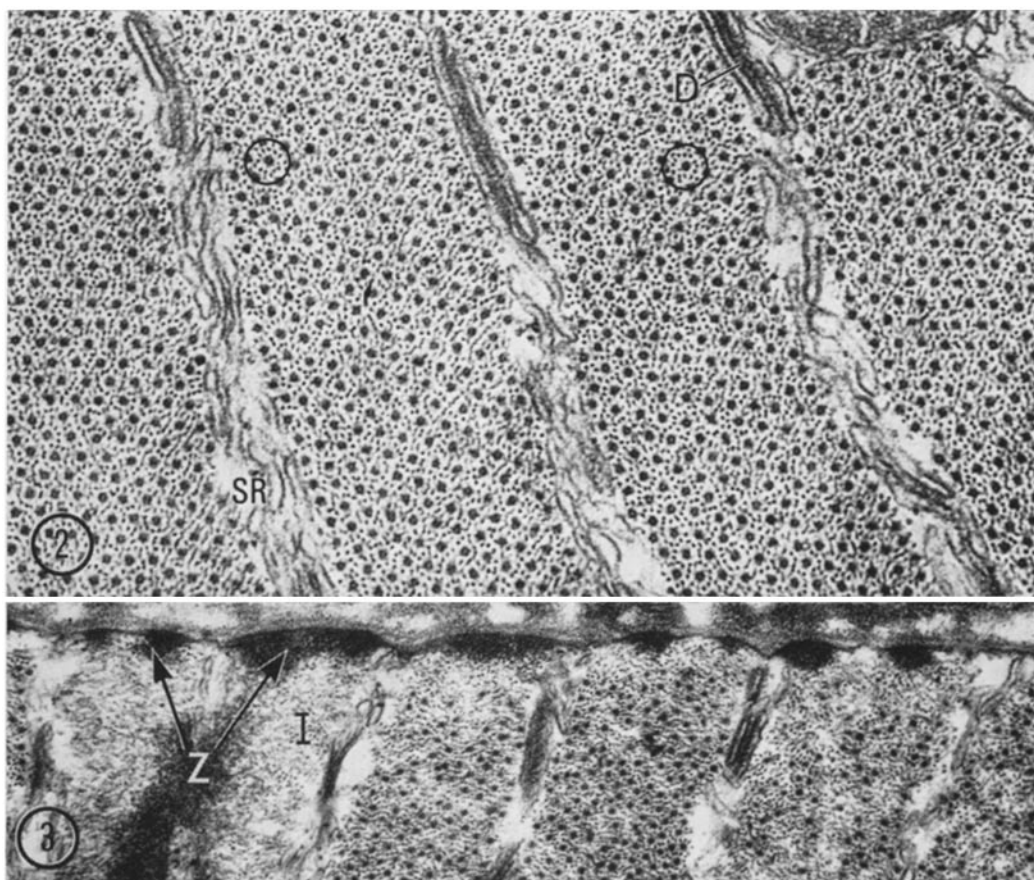


FIGURE 2 Cross-section through a region of A-I overlap. Note the hexagonal array of thick filaments with orbits of 10-13 thin filaments. Note the hollow core and subunits of thick filaments. Sarcoplasmic reticulum (SR) and diads (D) appear between two myofibrils.  $\times 42,000$ .

FIGURE 3 Cross-section through the fiber periphery showing connection of Z line (Z) at the I-band region (I) to the outer membrane. The Z line broadens before reaching the outer border. The section shows different regions of the Z line.  $\times 28,000$ .

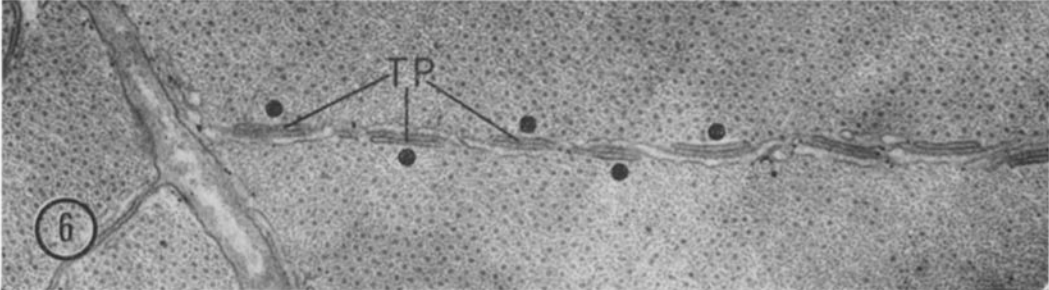
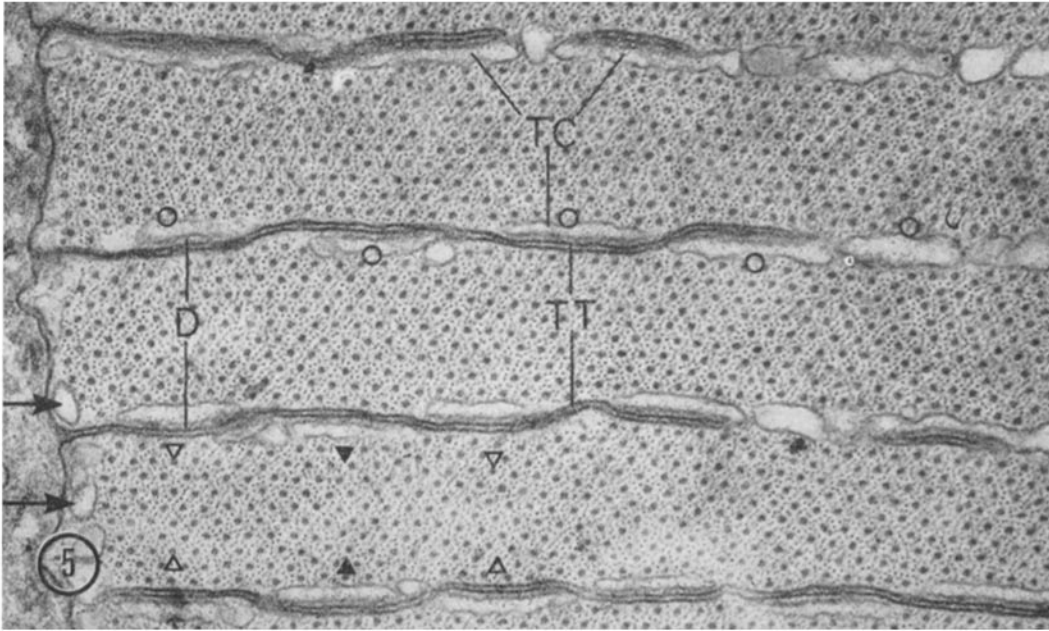
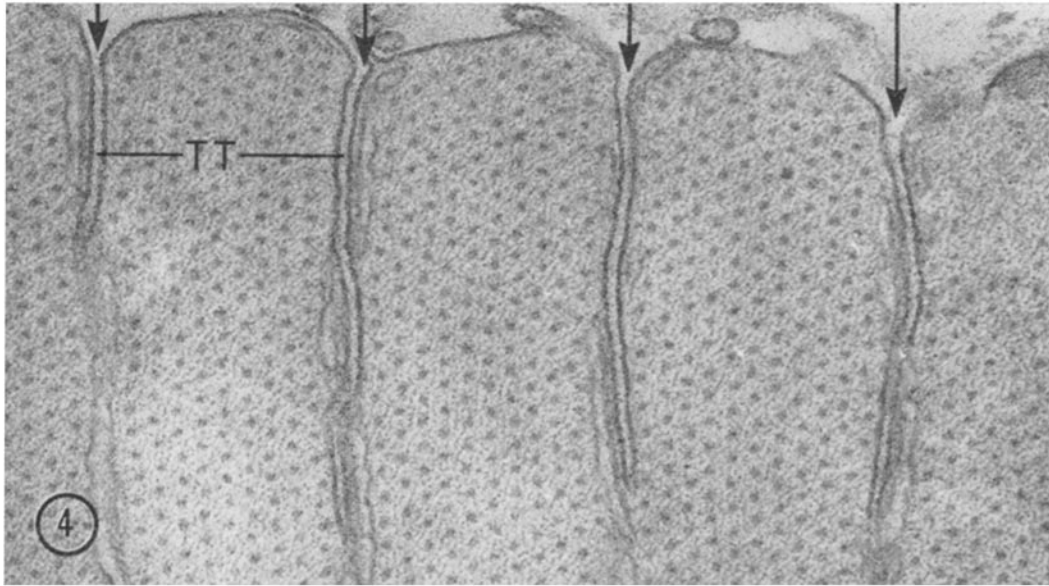
metric arrangement is found in the three planes: in the radial direction, along the circumference, and along the longitudinal axis of the fiber.

The openings of the TS can be seen in one plane of a cross-section (Figs. 4 and 5); each opening is always between two myofibrils. Therefore, along the circumference of the cell at the region of overlap of thick and thin filaments, an average of 145 openings is found. Each TS can be traced in one plane from the opening at the sarcolemma down to the core as a narrow system 400 A in width. In its course, it waves intermittently from one fibril to the other (Fig. 5). In another plane of section (Fig. 6), the TS is not

continuous and rows of cross-sectioned profiles are in evidence.

In describing longitudinal sections, it is convenient to define two longitudinal planes relative to the long axis of the TS: (a) parallel to the long axis of the TS, where a "face view" of the system can be seen (Fig. 7), and the whole TS can be traced; (b) perpendicular to the long axis of the TS, where the TS is cut transversely (Figs. 9 and 10).

In the parallel sections (Fig. 7), the TS is composed of a transverse tubule (TT) oriented radially and tubular "pockets" (TP) extending



sideways in an alternating fashion. The TT is  $0.1 \mu$  wide and runs almost parallel to the Z band. The TP's have a mean diameter of  $0.3 \mu$  and are spaced at regular intervals (triangles in Fig. 7) of  $0.86 \mu$ . Two such TS's are found in each sarcomere and are located on both sides of the H zone.

The perpendicular sections (Figs. 9 and 10) show the TS in cross-section. It can be seen that if the plane of section crosses only the TT, two profiles can be recognized in each sarcomere (Fig. 9, on both sides of the H zone). If the plane of section passes through the TP, up to four profiles per sarcomere are observed. Different combinations of these two extremes were observed (Figs. 9 and 10 *a-f*). Fig. 10 *a-e* demonstrates longitudinal sections of half a sarcomere, showing the transition from a section through a TT (Fig. 10 *a*) to a section crossing one TP (Fig. 10 *b*) and to a section with two TP's and associated terminal cisternae (TC) (Fig. 10 *c*). In Fig. 10 *b* a two-component "diadic" structure is evident, while in Fig. 10 *c* a three-component "triadic" structure is seen. The two TC's in Fig. 10 *c* are actually connected as can be seen in Fig. 10 *d, e*, forming an "inverse triad." (See Discussion.) Fig. 10 *f* (a whole sarcomere) shows a section through four TP's, the lower two of which abut one fibril while the upper two abut the other fibril. Here one can see (left side) a four-component "tetrad" structure.

A scheme of the TS is illustrated in Fig. 11. Note the waving of the TT (cf. Fig. 5) and the organization of the TP. (See also scheme Fig. 12.) The terminal cisternae accompanying the tubular pockets are connected longitudinally over the TT (TC in Fig. 11).

### Surface Area of TS

As mentioned, the fibers are 7 mm long, and the sarcomere length averages  $5 \mu$ . Thus 2000 sarcomeres or  $4 \times 10^3$  openings (two per sarcomere) of TS are found in each centimeter of length of fiber. Transversely, the TS openings are separated by myofibrils about  $1.0 \mu$  apart. Therefore, the total number of TS openings is  $4 \times 10^7$  per  $\text{cm}^2$  of outer surface area. In a cross-section, the TT approximates a rectangle (Fig. 11)  $0.1 \mu$  in length and  $0.04 \mu$  in width. The length of TT was taken as  $20 \mu$  (the average distance between sarcolemma and cell core). The surface area of one TT is thus  $5.6 \mu^2$ . The tubular pockets were treated as circular disks  $0.3 \mu$  in diameter and  $0.04 \mu$  thick. Therefore, the surface area of one TP is  $0.18 \mu^2$ . Since, along the length of one TT, 50 TP's are found, the total surface area of pockets associated with one TT is  $9.0 \mu^2$ . The surface area of one TT with its pockets is, therefore,  $14.6 \mu^2$ , and the total surface area of the transverse system amounts to  $6 \text{ cm}^2$  per  $\text{cm}^2$  of outer surface area ( $14.6 \mu^2 \times [4 \times 10^7] = 5.84 \text{ cm}^2$ ).

### The Sarcoplasmic Reticulum (SR)

The SR is a highly convoluted, well-developed complex network of tubules. The SR extends through the whole length of the fibril but it is more concentrated around the H zone and Z band (Figs. 7 and 9). Approaching the sarcolemma, especially at the center of the sarcomere, the reticulum extends into and occupies the space between the fibril and the sarcolemma, thus enveloping the fibril (Figs. 5 and 8). At the region of overlap of thin and thick filaments the SR converges to form terminal cisternae (TC) (Fig. 10 *c*). These cisternae have a flattened profile

FIGURE 4 Cross-section showing openings (arrows) of transverse tubules (TT). The openings are evenly spaced, each occurring between two neighboring myofibrils.  $\times 48,000$ .

FIGURE 5 Cross-section showing transverse tubules (TT) and terminal cisternae (TC) of the sarcoplasmic reticulum. Note alternate arrangement of TC's on both sides of TT ( $\circ$ ). TC's appear facing each other in some parts ( $\blacktriangle$ ), and appear on opposite sides of the TT in other regions ( $\triangle$ ); this arrangement alternates from periphery to core. The contact region of TC and TT forms diads (D) which contain an electron-opaque material but do not show dentate processes. Arrows point to sarcoplasmic reticulum vesicles juxtaposed to the sarcolemma.  $\times 31,000$ .

FIGURE 6 Cross-section showing continuity of sarcoplasmic reticulum with a wavy path ( $\bullet$ ) between tubular pockets (TP) of the transverse tubular system.  $\times 25,300$ .

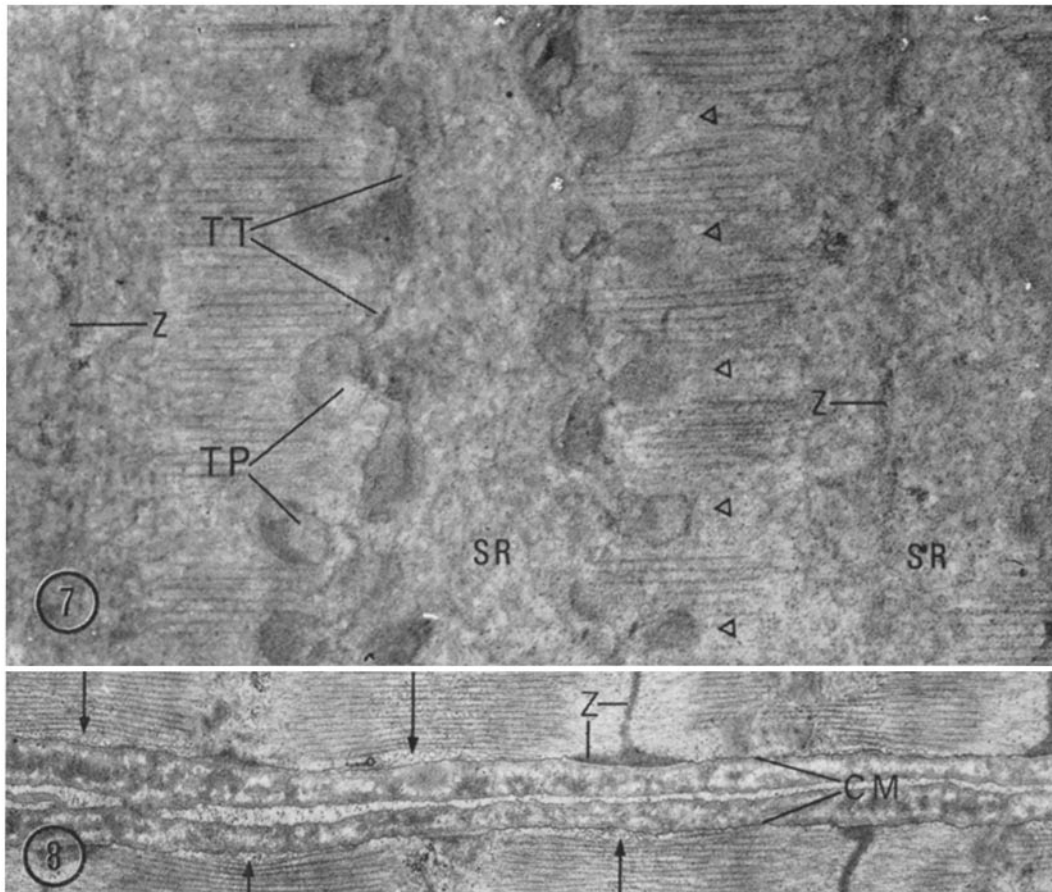


FIGURE 7 Longitudinal section which passes just above the surface of a lamellar myofibril showing an extensive face view of the tubular system. This system is composed of a transverse tubule (*TT*) and tubular pockets (*TP*) which are spaced at regular intervals ( $\Delta$ ). Note that each sarcomere contains two such systems. Sarcoplasmic reticulum (*SR*) is mainly concentrated at the Z band (*Z*) and at the central area of the sarcomere.  $\times 20,700$ .

FIGURE 8 A longitudinal section through peripheral areas of two fibers. Note broadening of Z band (*Z*) when approaching the cell membrane (*CM*); sarcoplasmic reticulum tubules occupy the space between the cell membrane and the fibrils (arrows).  $\times 10,900$ .

that accompanies the *TT* and its associated *TP*'s while oscillating between two adjacent fibrils longitudinally (Fig. 10 *e* and *f*) and transversely (Fig. 6).

#### DISCUSSION

In the present study we described the fine structure of a tubular muscle fiber of the scorpion. This muscle fiber is primitive and its structural components are arranged in a radial symmetry.

In the tubular muscle fibers previously described (Smith, 1961, 1966 *a*; Pasqualli-Ronchetti, 1970), the localization of subsystems such as the transverse tubular system and the sarcoplasmic reticulum depends on the position of the nuclei and mitochondria. These organelles are generally located in defined areas, and during phylogenetic evolution and specialization of tubular fibers (to flight or leg muscles) there has been a migration of nuclei and mitochondria within the cell.

In the flight and leg muscles of primitive insects (Odonata, Orthoptera), the mitochondria are scattered between the myofibrils (Tiegs, 1955). In the higher forms of insects (Diptera), the mitochondria are arranged in concentric rings (Pasquali-Ronchetti, 1970). It is obvious that such an organization determines the geometry of the TS. For example, in fibers where mitochondria occupy the whole space between two myofibrils, two TS's are found, one on each side of the mitochondria, each in juxtaposition to a myofibril. Occasionally, the TS branches off or bifurcates (Smith, 1966 *b*; Rosenbluth, 1969 *a*). In fibers where the contractile elements are not positioned directly beneath the cell membrane and where a layer of mitochondria is found between the sarcolemma and the myofibrils, the length of the TS is actually increased (Hoyle and McNeil, 1968; Nakajima, 1969).

It seems that in primitive arthropods, such as Arachnids (scorpion and spider), the nuclei and mitochondria are found in the cell core, the myofibrils are lamellated, and the TS's are symmetrically distributed around the core.

#### *Thick and Thin Myofilaments*

The structure of the sarcomere of the scorpion tubular muscle fibers follows the general scheme of that of the sarcomere of vertebrates (Huxley, 1957) and other invertebrates (Hagopian, 1966). The thick filaments are round in cross section as in other arthropods and fish (Huddart and Oates, 1970; Hagopian, 1966; Nakajima, 1970; Rosenbluth, 1969 *a*) and not trigonal as in chicken breast (Pepe, 1967); in addition, the thick myofilament appears hollow. In the present study, we have not concentrated on the structural details of filament subunits as was done by Reger and Cooper (1967); however, in several of our electron micrographs we observed structures similar to the subunits found in the cockroach muscle (Hagopian and Spiro, 1967).

The arrangement of the thick filaments within a myofibril is not constant, and variations from a precise thick filament lattice (Smith, 1965) to a completely irregular arrangement (Hoyle, 1967 *b*; Hoyle and McNeil, 1968) are found. In the scorpion fibers, we actually observed all of these structural variations. The orbital arrangement of the thin filaments is not constant (Auber, 1963), and the number of thin myofilaments ranges from 10 to 13 in one orbit.

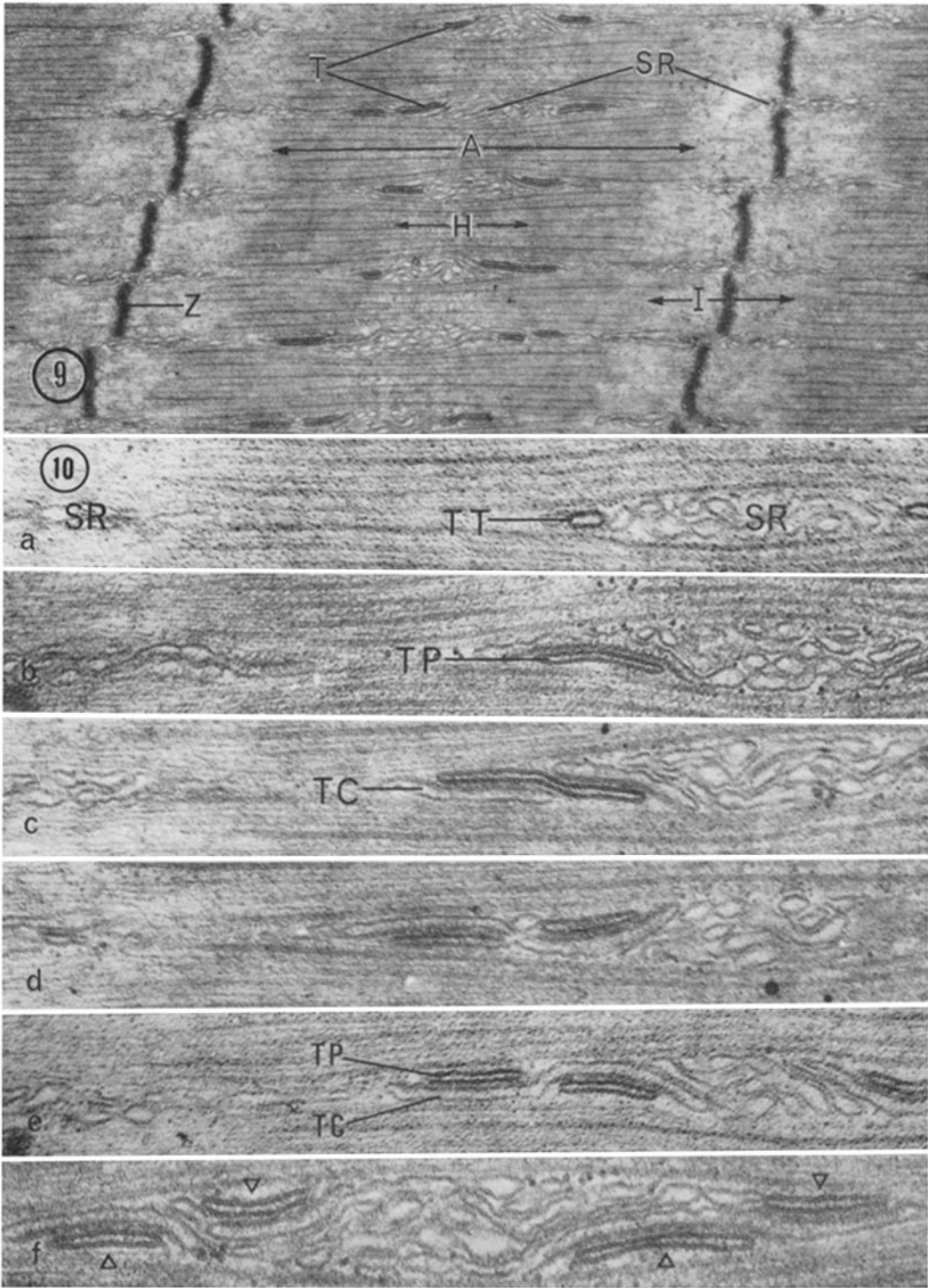
#### *The Transverse Tubular System*

It is accepted that the TS is continuous with the surface membrane. This is based mainly on results of experiments showing penetration of large molecules into the TS (Huxley, 1964; Page, 1964; Endo, 1966; Peachey and Schild, 1968). Nevertheless, many investigators did not succeed in demonstrating the actual openings of the TS in a frog skeletal muscle. This point is discussed by C. Franzini-Armstrong (1970), who points out that the difficulty in finding these openings (130 Å in diameter) is due to the narrowness of the peripheral segment (210–240 Å), which is bent, twisted, and passes almost parallel to the sarcolemma. It is also possible that only some of the TS tubules have openings in the sarcolemma, and that several tubules converge into one peripheral segment. This organization was not taken into consideration by Falk and Fatt (1964), Falk (1968), Adrian et al. (1969 *a*, 1969 *b*), and Schneider (1970), and was not mentioned in the calculation of tubular surface area (Peachey, 1965).

In arthropods the situation is simpler. Many investigators have demonstrated the continuity of the TS with the surface membrane (Smith, 1965, 1966 *a*, 1966 *b*; Pasquali-Ronchetti, 1970; Rosenbluth, 1969 *a*; Huddart and Oates, 1970; Peachey, 1967). In tubular muscle fibers, these openings are regularly arranged between fibrils. The openings are spaced at 2.5  $\mu$  in the longitudinal axis of the cell and at 1  $\mu$  along the circumference. It is therefore possible in these cells to measure accurately the TT and TP surface area. Such TP's were also found in other arthropods (Zebe and Rathmayer, 1968; Pasquali-Ronchetti, 1970), but the connection between TP's and the number of diadic structures in one sarcomere was not always emphasized (Hagopian and Spiro, 1967; Hoyle and McNeill, 1968; Zebe and Rathmayer, 1968). This probably results from the lack of a three-dimensional reconstruction of the TS. Indeed, in only a few works on the TS in arthropods has a three-dimensional reconstruction been made (Smith, 1961; Pasquali-Ronchetti, 1970).

The three-dimensional reconstruction presented (Figs. 11 and 12) shows that, as in other arthropods (Hagopian and Spiro, 1967; Smith, 1966 *a*), the TS alternates between two myofibrils. It alternates transversely (shown in Fig. 5) as well as





longitudinally, so that two adjacent TP's are located near different myofibrils (Fig. 10 *f*).

### The Diadic Structure

It is usually accepted that in vertebrates the point of electromechanical coupling is the *triad*, while the corresponding structure in invertebrates is the *diad* (Smith, 1966 *c*). In the scorpion the two types of structure could be observed, depending on the plane of the section. In cases where the section passed through a terminal cisterna and one tubular pocket, a diadic structure was observed (Fig. 10 *b*); however, in cases where the section passed through two connected TP's, the organization was more like a triad (Fig. 10 *c*). In such "triads" one TC is directed towards one myofibril, while the other faces another myofibril. Such a triad is similar to that of vertebrates, namely it is composed of one element of the transverse system (TS) (in this case TP) and two TC elements. However, in other cases in the scorpion we found "triads" composed of *two* elements of TS (TP's) and *one* TC element (Fig. 10 *e*), thus forming an "inverse triad." In some cases where the section crossed two TP's and two TC's, even an organization of a "tetrad" could be observed (Fig. 10 *f*). When the TS and SR are reconstructed tridimensionally, diads, triads, and tetrads can be obtained from sections in the appropriate planes. In the scorpion, longitudinal connections between two terminal cisternae are common. Similar connections between TC's were also

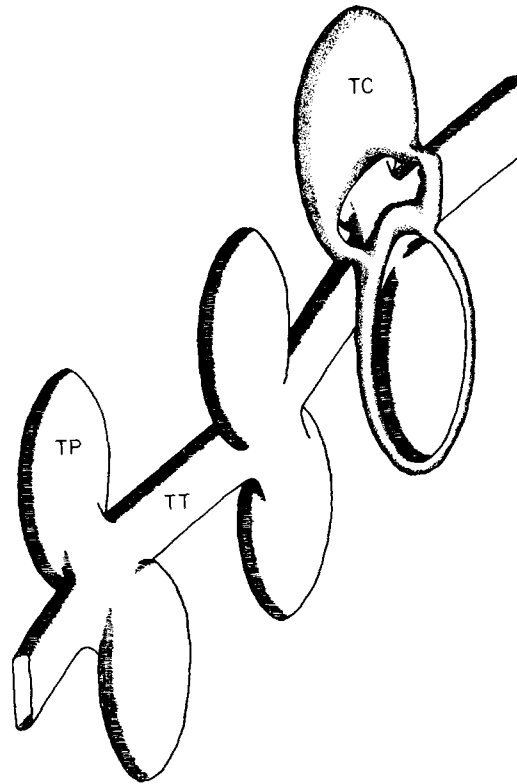


FIGURE 11 Three-dimensional reconstruction of transverse tubular system and associated terminal cisternae. The system consists of two parts, a wavy transverse tubule (*TT*) and tubular pockets (*TP*) arranged alternately on both sides. The terminal cisternae (*TC*) accompanying the TP's are connected and form diads with the transverse tubular system.

FIGURES 9 and 10 Longitudinal sections cut in a plane perpendicular to the long axis of the lamellar myofibrils.

FIGURE 9 Section through entire sarcomere. Z lines (*Z*) spaced about  $5 \mu$  apart. The regions of thin and thick filament overlap, A bands (*A*), have a central lighter H-band (*H*) region. The sarcoplasmic reticulum (*SR*) is mainly located adjacent to the H and I (*I*) bands. Elongated profiles of the transverse tubular system (*T*) are seen adjacent to the region of myofilament overlap (see text).  $\times 18,000$

FIGURE 10 Micrographs of half-sarcomeres taken from different sections, showing relation between sarcoplasmic reticulum (*SR*) and transverse tubular system; center of sarcomere is on the right. (*a*) A section through a transverse tubule (*TT*); the profile resembles a rectangle with dimensions of approximately  $0.1 \times 0.04 \mu$ . (*b*) A diadic structure consisting of a terminal cisterna and a tubular pocket (*TP*). At the region of contact an electron-opaque material is seen. (*c*) A triadic structure consisting of two terminal cisternae (*TC*) and a centrally located transverse tubular system composed of two TP's connected by a *TT*. (*d*) A section showing longitudinal connection between two terminal cisternae and two tubular pockets. (*e*) An "inverse triad" consisting of two tubular pockets (*TP*) and a single terminal cisterna (*TC*).  $\times 50,000$ . (*f*) Section through a whole sarcomere. Note the alternating organization of the four tubular pockets ( $\Delta$ ), two of them adjacent to one fibril (above) and, two adjacent to another fibril (below). A tetrad structure consisting of two tubular pockets and two terminal cisternae can be seen on the left  $\times 60,100$ .

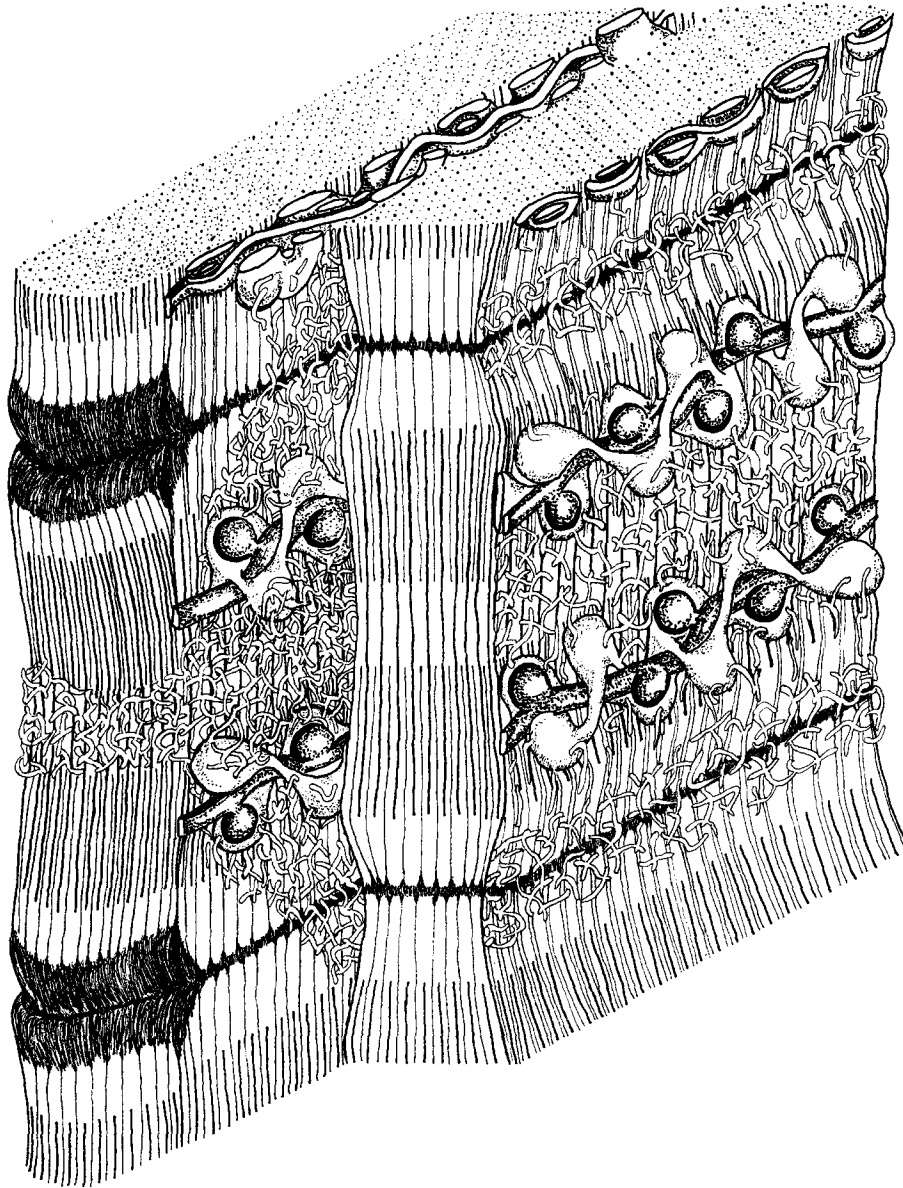


FIGURE 12 Three-dimensional reconstruction summarizing the structural organization of the scorpion tubular muscle fiber. Two lamellated myofibrils are demonstrated, one reaching the cell membrane, with a broader Z line, the second cut to show the relation between the transverse tubular system and sarcoplasmic reticulum.

observed in vertebrate muscles (Peachey, 1965; Nakajima, 1969). It seems, therefore, that the plane of section will determine whether a "triad" or "diad" will appear, and that the same basic two-component diadic structure comprises the site of electromechanical coupling.

The diadic junctional area in the scorpion was not investigated in particular, but it can be seen

that the surface of the TC abutting the TP is flat; no scallops (Revel, 1962) or foot processes (Smith, 1965, 1966 *b*) were observed with the method used in this study. It is quite possible that such structures will be visualized with other preparative methods (Rosenbluth, 1969 *b*; Smith, 1965). However, a more electron-opaque material appears to be present in this junction.

## Surface Area of TS

The continuity of the TS with the external membrane of the cell greatly increases the surface area over that of a simple cylinder. This enlarged surface may explain the high values obtained for membrane low frequency capacity (Peachey, 1968). The surface area of the TS in frog sartorius was estimated to be five (Falk and Fatt, 1964), seven (Peachey, 1965), and nine (Peachey and Schild, 1968) times that of the surface membrane. It is interesting to note that these estimates are of the same order as those found for tubular muscles of arthropods. In dragonfly tubular flight muscles (Smith, 1966 *a*), the surface area of the TS was calculated to be six times that of the surface membrane. Exactly the same figure was calculated here for the scorpion tubular muscle. Is it a mere coincidence?

All of these characteristics make the scorpion tubular muscle fibers a convenient model for the study of electromechanical coupling.

The authors wish to express their gratitude to Dr. M. Friedlander for providing electron microscope facilities and help.

Received for publication 31 August 1971, and in revised form 3 November 1971.

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