FINE STRUCTURE OF RAT INTRAFUSAL MUSCLE FIBERS

The Equatorial Region

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ABSTRACT

An ultrastructural study has been undertaken on the equatorial (sensory) region of the rat muscle spindle. Two kinds of intrafusal muscle fibers, a nuclear bag fiber and a nuclear chain fiber, have been identified in this region on the basis of fiber diameter, nuclear disposition, and M-band appearance. The large-diameter nuclear bag fiber contains an aggregation of tightly packed vesicular nuclei, while the small-diameter nuclear chain fiber contains a single row of elongated, well-separated nuclei. Both muscle fibers contain an attenuated peripheral cylinder of myofilaments surrounding a central core of sarcoplasm. Elements of the sarcotubular system, dilatations of the sarcoplasmic reticulum, and the presence of other sarcoplasmic organelles and inclusions are considerably more abundant in the nuclear chain fiber than in the nuclear bag fiber. Leptomeric organelles and membrane-bounded sarcoplasmic granules are present in both intrafusal fiber types and may be situated between the myofibrils or in intimate association with the sarcolemma. The functional significance of some of these structural findings is discussed.

INTRODUCTION

Muscle spindles consist of a group of specialized striated muscle fibers, termed intrafusal fibers, and their associated motor and sensory nerve endings. They have been divided into three characteristic regions (polar, myotube, and equatorial), and the intrafusal fibers in each of these regions are innervated by a particular form of nerve ending (see 3).

Although three kinds of intrafusal fibers have recently been described in the mammal (4), most of the light microscope (5, 9), histochemical (21, 23, 32, 35, 46, 49), electron microscope (10, 11, 14, 27, 37, 38), and electrophysiological (6, 7, 13, 44) studies, to date, have resulted in the classification of intrafusal fibers into two kinds, a nuclear bag fiber and a nuclear chain fiber.

It is currently thought that the primary function of mammalian intrafusal fibers is to control the different forms of sensory discharge which originate in the afferent (sensory) nerve terminals of the muscle spindle (see 45). These afferent nerve terminals are known to end directly on the intrafusal fibers. Thus, it is likely that the structural and mechanical properties of the intrafusal fibers per se are an important factor in determining the forms of sensory discharge. Unlike extrafusal muscle fibers which are morphologically and histochemically uniform throughout their lengths (16), intrafusal fibers are known to differ markedly throughout the different regions of the muscle

spindle (33, 49). In view of this, it was decided to undertake a fine structural study of the intrafusal muscle fibers in the different regions of the muscle spindle. Ultrastructural features of the polar regions of rat intrafusal fibers have recently been presented (38). In the present study, attention has been directed to the equatorial (sensory) regions of these muscle fibers. A preliminary report of a portion of this study has been published elsewhere (39).

MATERIALS AND METHODS

The IV lumbrical muscles from hindpaws of adult Sprague-Dawley rats were used. The material was fixed in a manner described previously (38), and embedded in Epon 812. Serial transverse and longitudinal semithin sections (1 μ thick) of several muscles were cut with glass knives and stained with a 0.1% solution of Azure II in 1.0% aqueous borax. Muscle spindles in each muscle were located by this method, and preliminary identification of the intrafusal muscle fibers as "nuclear bag" or "nuclear chain" was made with the light microscope on the basis of myofibrillar density in polar regions and cross-sectional diameter and nuclear arrangement in equatorial regions (38). Thin sections through equatorial regions of several muscle spindles were subsequently cut with glass knives on an LKB Ultrotome III (LKB Produktur, Stockholm, Sweden), mounted on naked copper grids, and stained with uranyl acetate and lead citrate. Grids were examined in an RCA EMU 4 electron microscope.

OBSERVATIONS

Nuclear Arrangement

Two kinds of intrafusal muscle fibers were consistently found in all muscle spindles examined. Light (Fig. 1) and electron (Figs. 2, 3) microscope identification was made in equatorial regions, primarily on the basis of fiber diameter and nuclear disposition. Figs. 1–3 depict the two intrafusal fiber types sectioned longitudinally in equatorial zones. The nuclear bag fiber[1] is easily distinguished by its larger over-all size and its large, closely packed, vesicular nuclei (Figs. 1, 2). The nuclear chain fiber[2], in contrast, exhibits a smaller diameter and contains a single row of elongated, well-

[1] Hereafter designated "bag fiber."
[2] Hereafter designated "chain fiber."

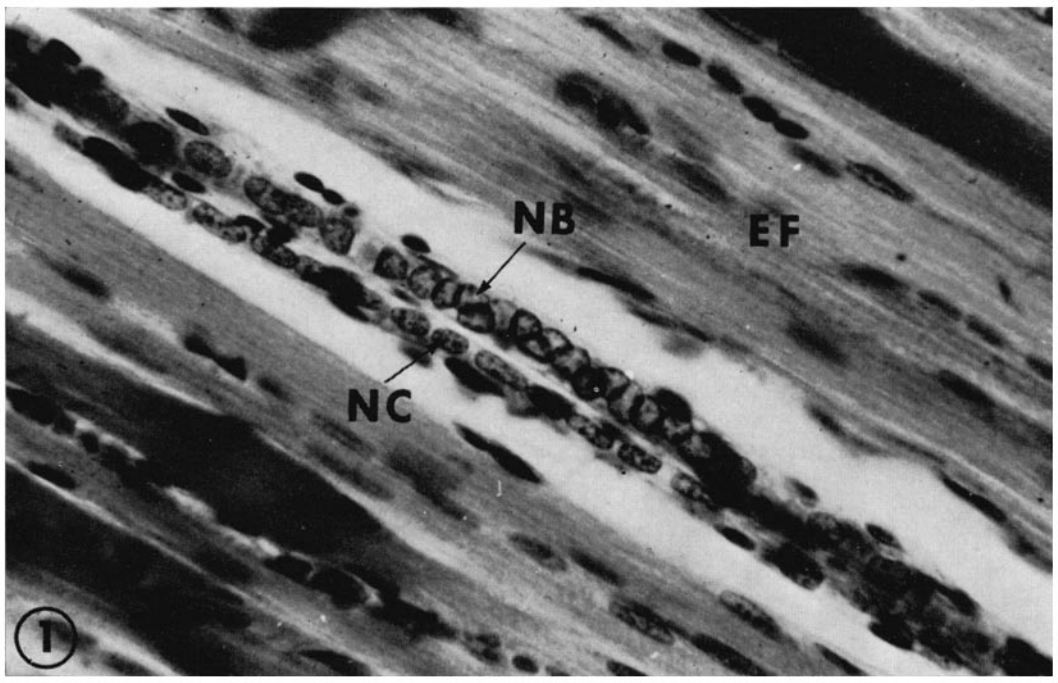

FIGURE 1 Light micrograph of a muscle spindle sectioned longitudinally in the equatorial region. Note the large-diameter bag fiber (*NB*) and the small-diameter chain fiber (*NC*). Surrounding extrafusal muscle fibers are indicated (*EF*). × 700.

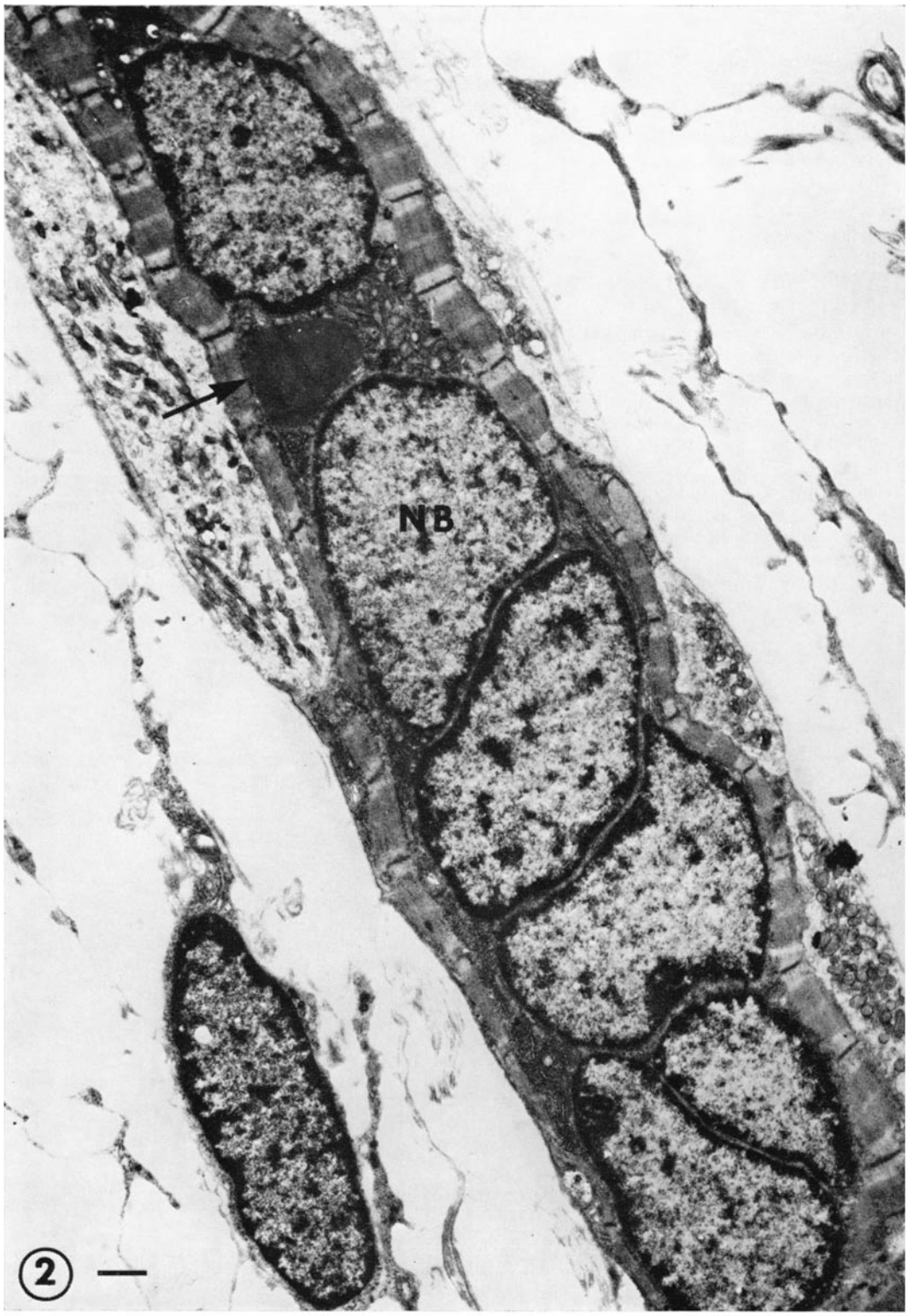

FIGURE 2 Electron micrograph of the equatorial region of a bag fiber (*NB*). Tightly packed, rounded nuclei and an attenuated peripheral cylinder of myofilaments characterize this muscle fiber. Sensory nerve endings can be seen terminating on the outer surface of the muscle fiber in a helical fashion. Dense cytoplasmic body (arrow). (Marker bar in this and subsequent figures indicates 1 μ). × 6500.

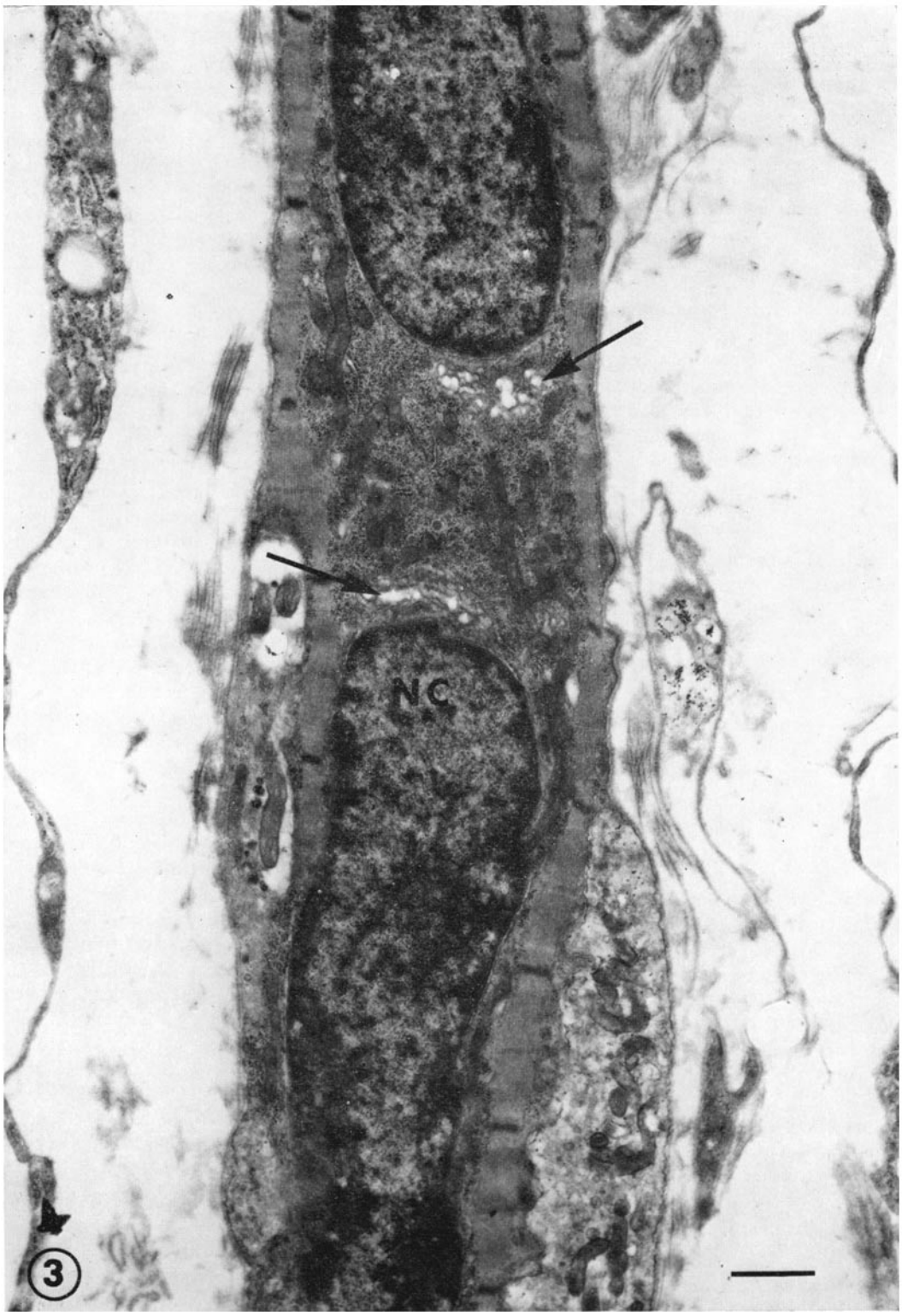

FIGURE 3 Electron micrograph of the equatorial region of a chain fiber (*NC*). Elongated, well-separated nuclei and a peripheral cylinder of myofilaments characterize this muscle fiber. A central core of sarcoplasm is more conspicuous in this fiber where a variety of organelles and inclusions occupy each internuclear space. Portions of sensory nerve endings can be seen terminating on the lower surface of the muscle fiber. Golgi complexes (arrows). × 12,000.

separated nuclei which run in series in the center of the muscle fiber (Figs. 1, 3).

Myofibrillar Organization and M Band

Equatorial regions of both intrafusal fiber types are characterized by an attenuated peripheral cylinder of myofilaments surrounding a central core of sarcoplasm (Figs. 2–5). Each peripheral myofilament cylinder is composed of one (Figs. 2–4) or two (Figs. 5–7) closely packed myofibrils oriented in the longitudinal direction.

It has previously been shown that M-band structure is an important criterion which serves to distinguish polar regions of the bag and chain muscle fibers (37, 38). Similar differences in M-band structure are also apparent in equatorial regions of these fibers (Figs. 4, 5). Chain fibers contain well-defined M bands situated in the center of the pseudo-H zone of each sarcomere (Figs. 4, 6), while bag fibers contain less conspicuous M bands, composed of two parallel thin densities in the center of each sarcomere (Figs. 5, 6).

Sarcoplasmic Organelles and Inclusions

CENTRAL SARCOPLASMIC CORE: The internuclear spaces of both intrafusal fiber types contain a conspicuous central core of sarcoplasm filled with a variety of organelles and inclusions (Figs. 2–5). Since the internuclear spacing is greater in the chain fiber (Fig. 3) than in the bag fiber (Fig. 2), the number and variety of organelles and inclusions, in turn, is usually greater in the former than in the latter. Each sarcoplasmic core is found to contain an abundance of mitochondria, glycogen particles, cisternae of rough-surfaced endoplasmic reticulum, free ribosomes, and elements of the Golgi complex (Figs. 2–5).

GOLGI COMPLEX AND SARCOPLASMIC GRANULES: Most Golgi complexes are juxtanuclear in location and contain a few dilated vacuoles and several small vesicles with clear and moderately dense lumina (Figs. 3–5, 7). They are usually more abundant in the chain fiber than in the bag fiber. Closely associated with each Golgi complex is the presence of small spheroidal membrane-bounded sarcoplasmic granules (Figs. 4, 5, 7). Each sarcoplasmic granule contains a dense granular central core of material surrounded by a less dense zone. Their diameter varies from 0.06 to 0.30 μ, closely resembling that of the "specific atrial granules" originally described by Jamieson and Palade (24) in cardiac muscle cells. Most sarcoplasmic granules are distributed in the central sarcoplasmic cores of both intrafusal fibers. They may also be situated directly under the sarcolemma (Figs. 4, 9) or within the interfibrillar spaces (Figs. 7, 8).

MICROTUBULES: Equatorial regions of both intrafusal fibers contain numerous microtubules; however, microtubules are considerably more abundant in chain fibers in which bundles of them are commonly seen in the interfibrillar sarcoplasm where they run parallel to the myofilaments (Fig. 7). Accumulations of microtubules are also encountered in the vicinity of each Golgi complex and in close association with sarcoplasmic granules (Fig. 7).

DENSE CYTOPLASMIC BODIES: The presence of large, dense cytoplasmic bodies, ranging in size from 2 to 3 μ and devoid of a limiting membrane, is characteristic of equatorial regions of both intrafusal fibers (Figs. 3, 5). Each dense cytoplasmic body is confined to the central sarcoplasmic core and is usually juxtanuclear in location. These "inclusions" are frequently found wedged in between two centrally located nuclei (Fig. 2) and exhibit oval or circular profiles regardless of the orientation of the section. They consist of a dense uniform mass of finely granular and diffuse filamentous material which appears fairly homogeneous.

LEPTOMERIC ORGANELLES: Cross-striated organelles, separate and distinct from the sarcomeres, and termed "leptomeric organelles" by Karlsson and Andersson-Cedergren (25), are common features of the bag and chain fibers (Figs. 9, 10). In longitudinal section they are seen to span the entire length of a sarcomere, originating at the level of one Z band and terminating or extending beyond the level of an adjacent Z band (Fig. 9). Each leptomeric organelle is composed of a series of narrow, transversely oriented, electron-opaque bodies (or striations) which measure 300–475 A in width, and run parallel to the Z bands. Several faintly stained thin filaments (60–75 A in diameter) appear to interconnect the dense bodies in a longitudinal direction. Leptomeric organelles are also encountered directly under the sarcolemma (Fig. 10). In such cases, the striations are perpendicular to, and intimately contact, the inner surface of the sarcolemma, and they are most often situated in or near the region of sensory innervation.

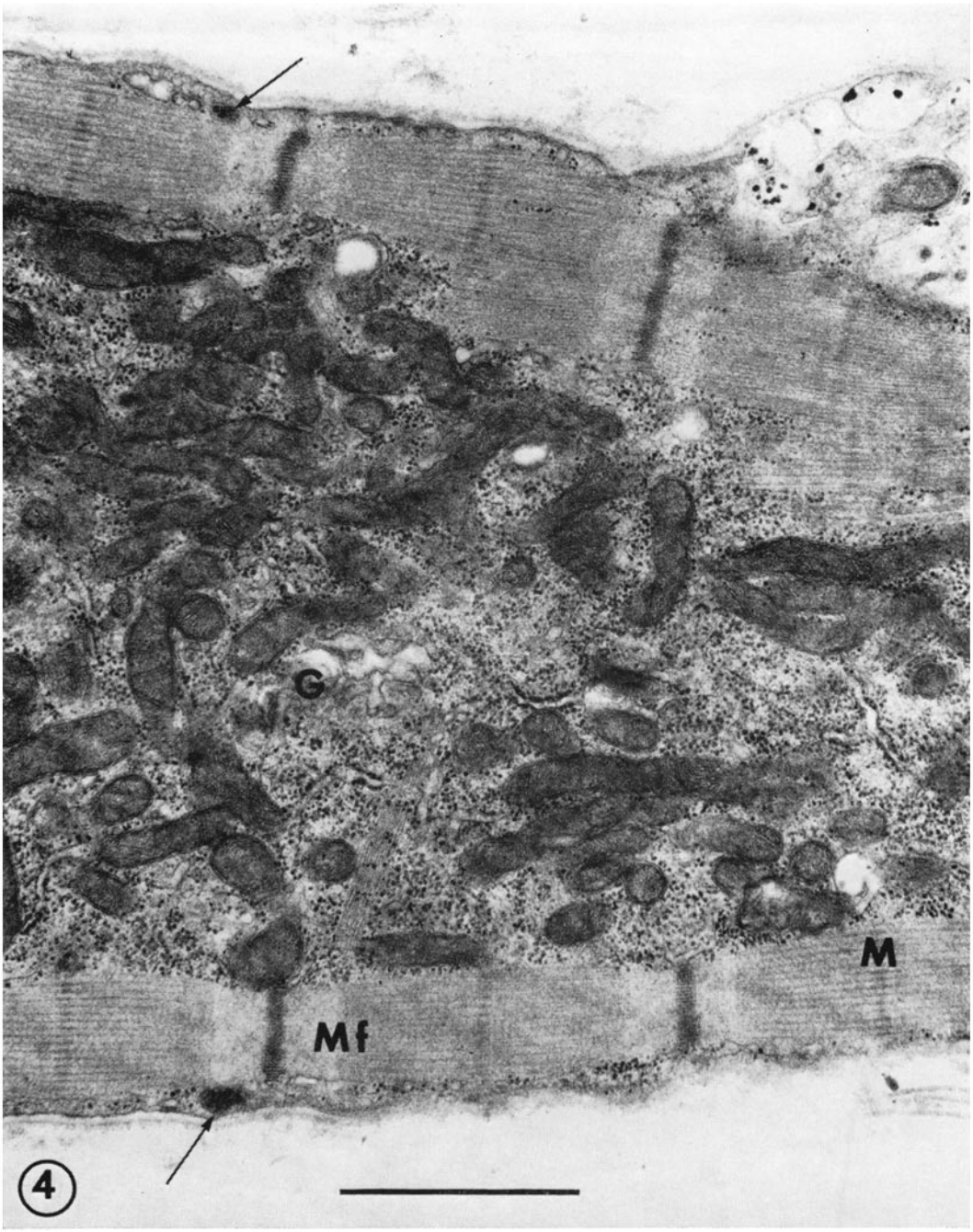

FIGURE 4 Longitudinal section of a chain fiber in the equatorial region. The central sarcoplasmic core contains an aggregation of organelles and inclusions. Typical M bands (*M*) characterize this muscle fiber. Note the presence of sarcoplasmic granules (small arrows) directly under the sarcolemma. Golgi complex, *G*; myofilaments, *Mf*. × 33,500.

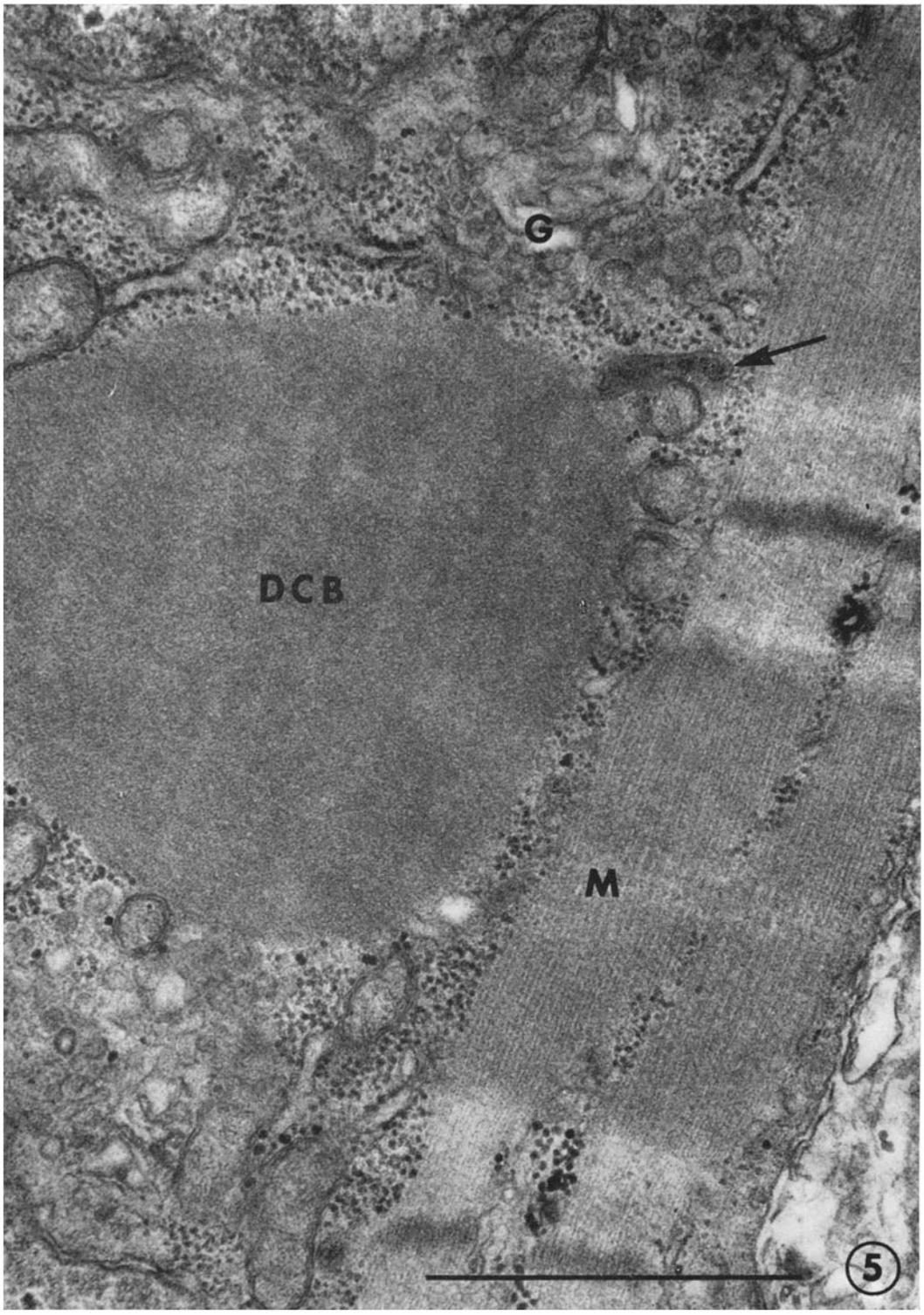

FIGURE 5 Longitudinal section of a bag fiber in the equatorial region. Note the central sarcoplasmic core (to the left) and the reduced peripheral cylinder of myofilaments (to the right). Inconspicuous M bands (*M*) characterize this muscle fiber. Golgi complex, *G*; sarcoplasmic granule (arrow); dense cytoplasmic body, *DCB*. × 57,500.

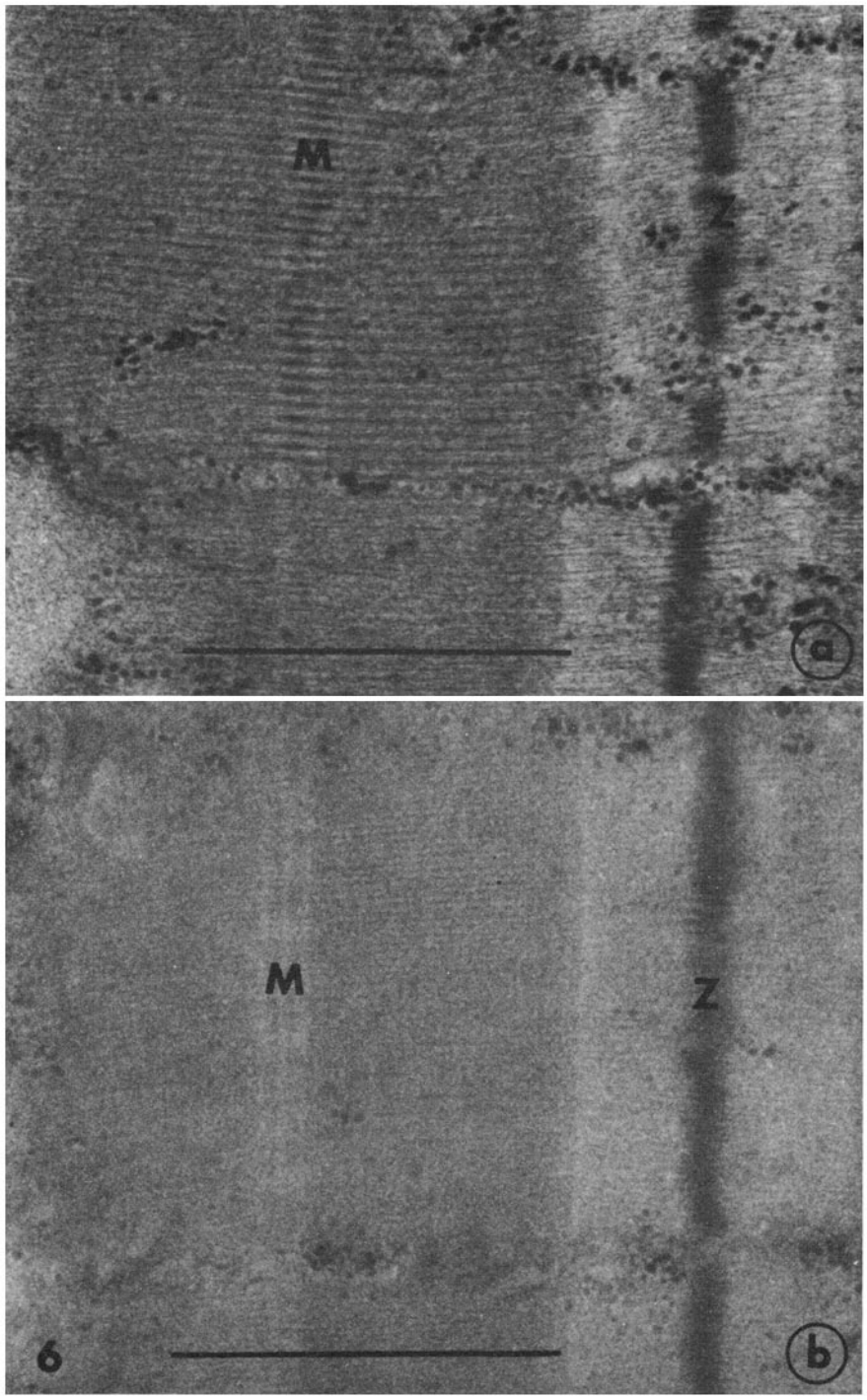

FIGURE 6 Portions of a chain fiber sarcomere (*a*) and a bag fiber sarcomere (*b*), illustrating the differences in *M*-band appearance. The chain fiber (*a*) contains a prominent *M* band (*M*) situated in the center of the pseudo-H zone, while the bag fiber (*b*) contains an ill-defined M band (*M*) composed of two parallel thin densities in the center of the sarcomere. Z band, *Z*. × 50,500.

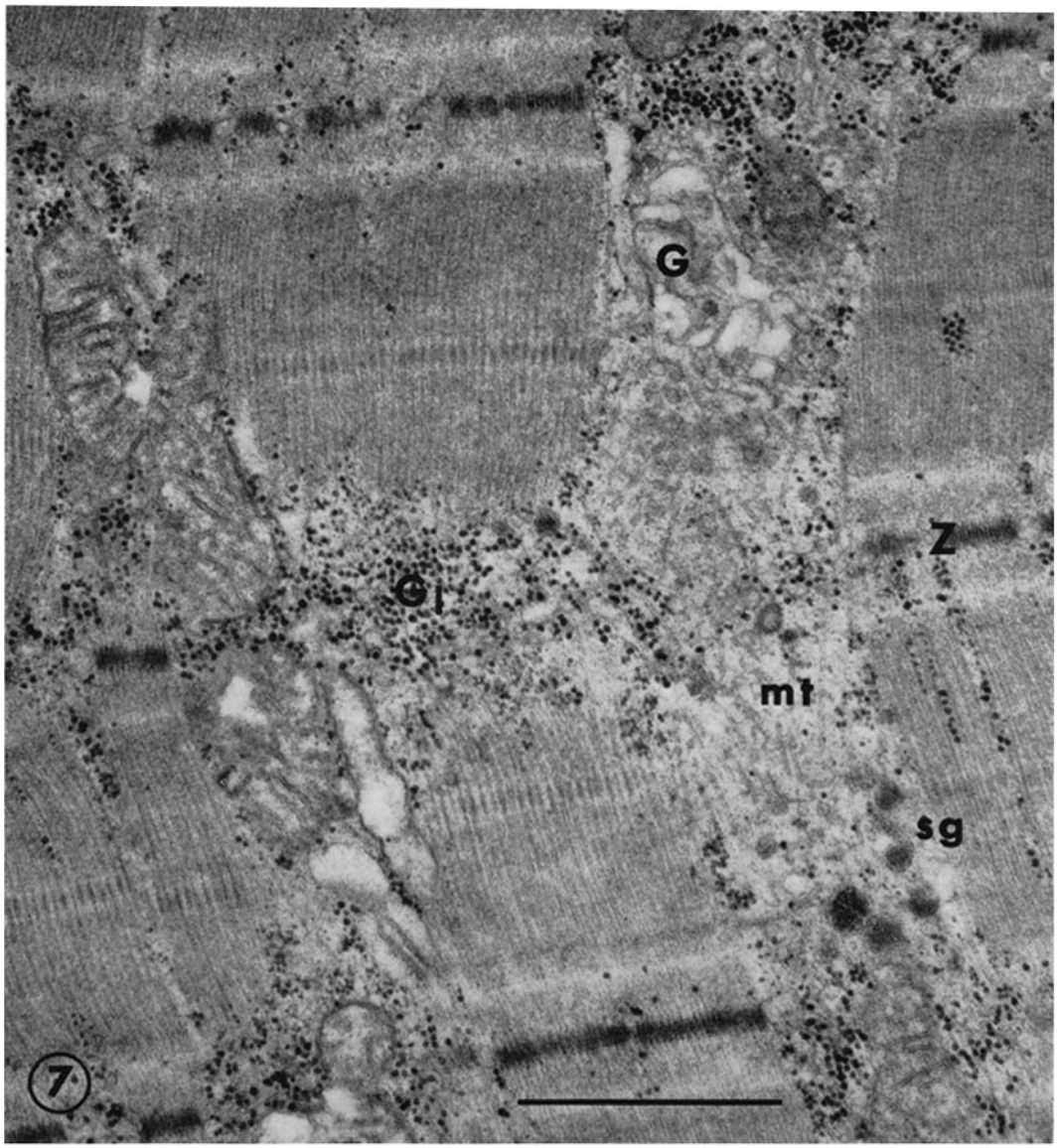

FIGURE 7 Longitudinal section of the periphery of a chain fiber. A prominent Golgi complex (*G*) and numerous microtubules (*mt*) are present in the interfibrillar sarcoplasm. Several sarcoplasmic granules (*sg*) are situated in the vicinity of the Golgi complex. Glycogen particles, G_1; Z band, *Z*. × 33,600.

SARCOTUBULAR SYSTEM: In a previous study (38) it has been shown that elements of the sarcotubular system (i.e., the sarcoplasmic reticulum [SR] and T system) are considerably more abundant in polar regions of the chain fiber than in polar regions of the bag fiber. Similar differences in the organization and extent of development of the sarcotubular system are also apparent in equatorial regions of these fibers. Junctional couplings (between SR cisternae and T tubules) are more numerous in chain fibers where they are located either near the center of most sarcomeres (Fig. 8) or directly under the sarcolemma (Fig. 9). Moreover, marked dilatations of the SR, similar to those found in polar regions of chain fibers (38), are also noted in equatorial regions of

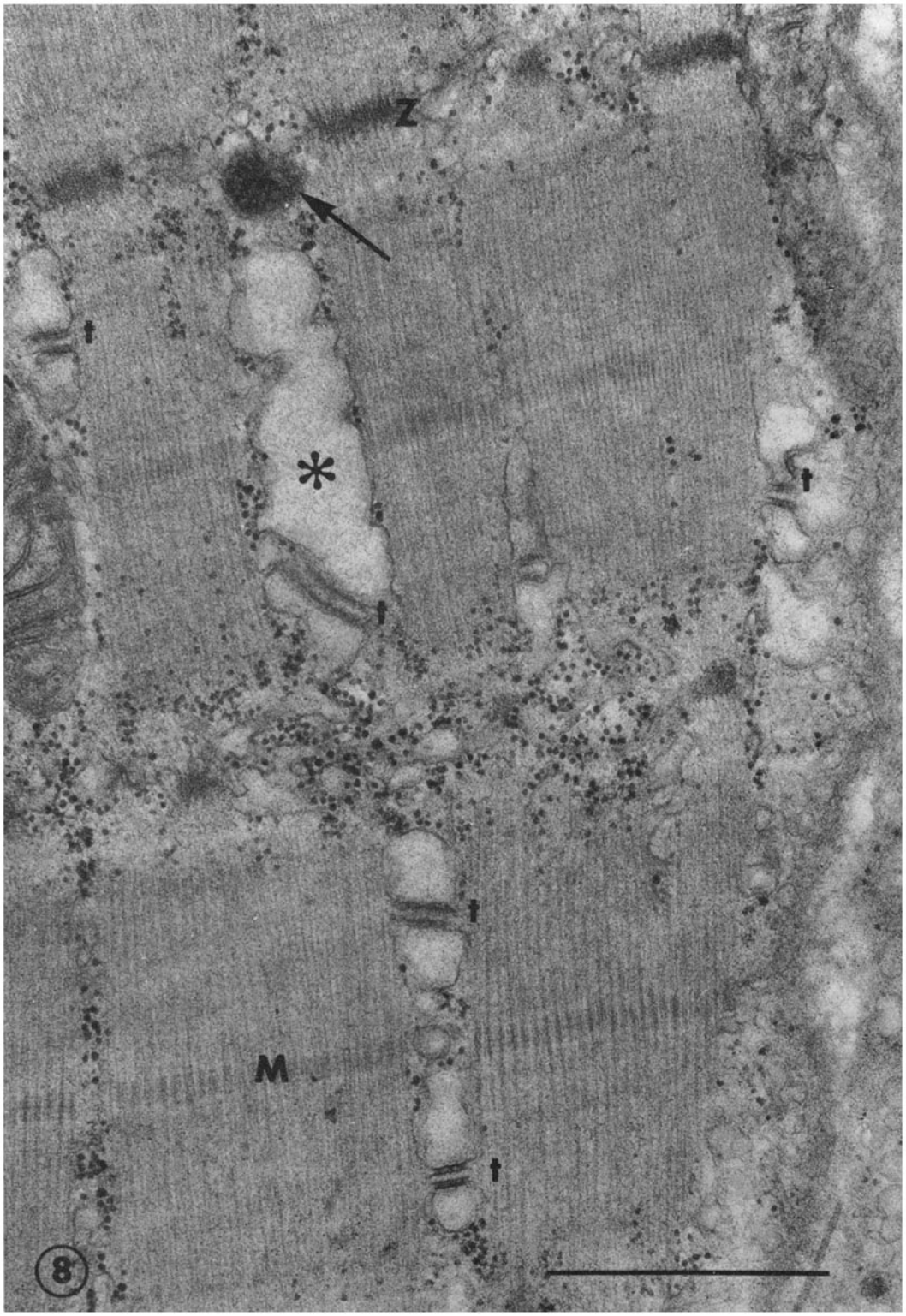

FIGURE 8 Longitudinal section of the periphery of a chain fiber, illustrating its well-developed sarcotubular system. Various dilated SR cisternae (one indicated by asterisk) contact several nondilated T tubules to form triads (*t*). Note the triad (*t*) on the right situated directly under the sarcolemma. Sarcoplasmic granule (arrow); Z band, *Z*; M band, *M*. × 42,200.

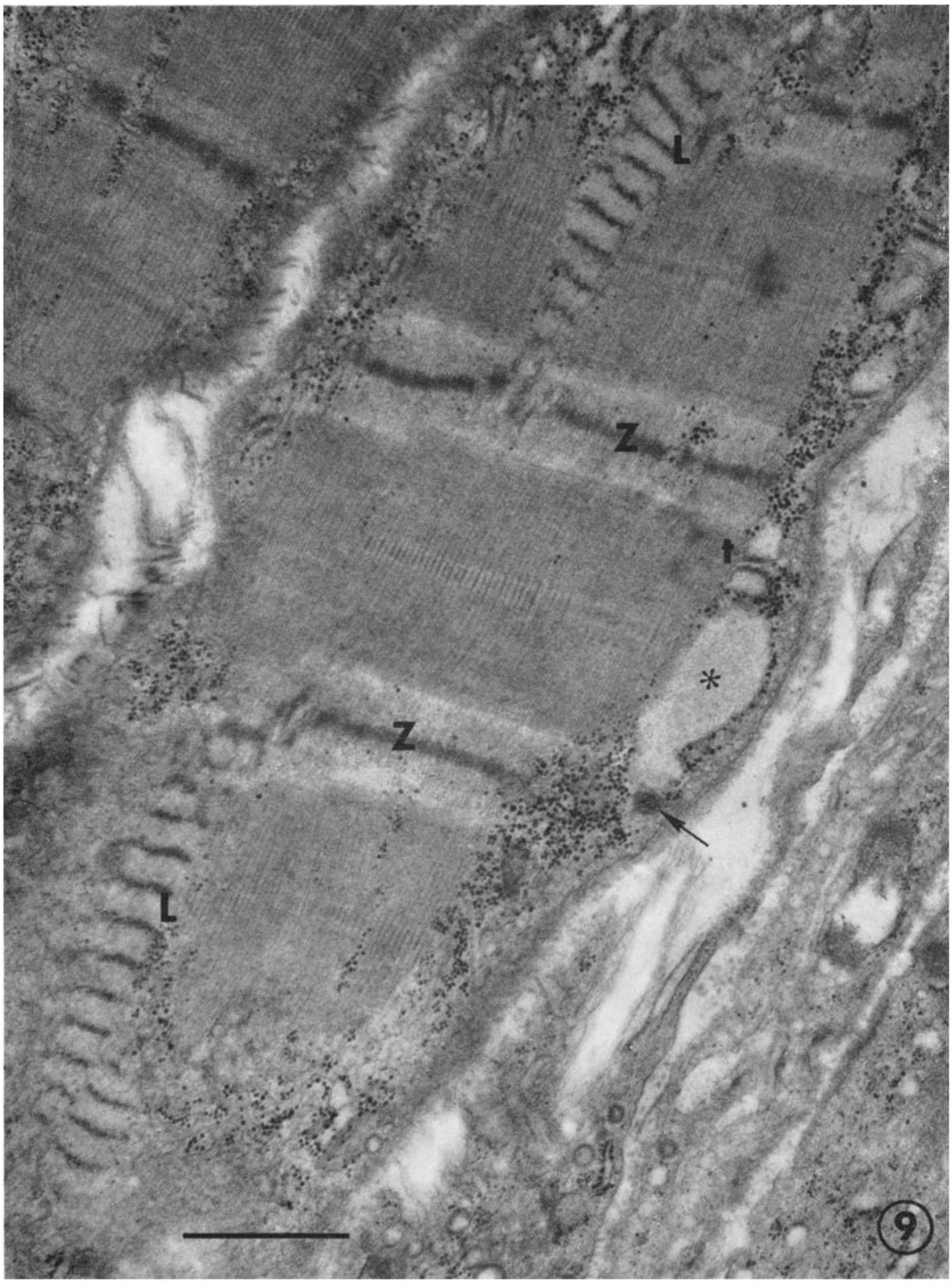

FIGURE 9 Grazing section through the periphery of a chain fiber. Two leptomeric organelles (*L*) are situated between the myofibrils. Both organelles appear to span two separate sarcomeres, originating at one Z band (*Z*) and extending beyond the adjacent ones. Portions of the Z bands appear disarrayed in coincidence with each leptomere. Note the dilated SR cisterna (asterisk), triad (*t*), and sarcoplasmic granule (arrow) directly under the sarcolemma. × 24,900.

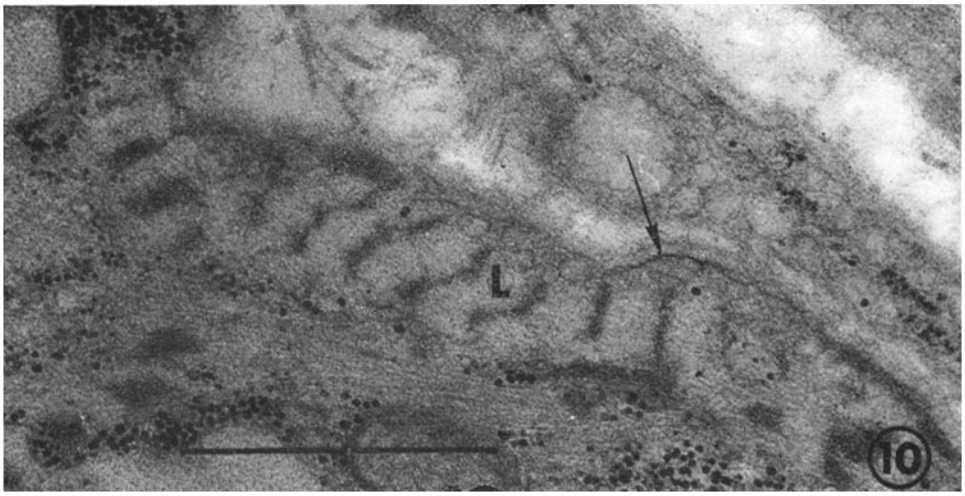

FIGURE 10 A leptomeric organelle (*L*) abuts directly against the undersurface of the sarcolemma (arrow) of a chain fiber. × 40,000.

these fibers (Figs. 8, 9). These dilated cisternae are usually filled with fine granular material, and are variable in location within the muscle cell. They may form junctional contacts with T tubules at the A-I junctions of a sarcomere (Fig. 8), or they may be found directly under the sarcolemma (Fig. 9).

DISCUSSION

Matthews (29, 30) originally suggested that mammalian intrafusal fibers are less viscous in equatorial (sensory) regions of muscle spindles than in polar regions, and furthermore, that the frequency of afferent nerve discharge from sensory regions of muscle spindles would reflect the mechanical (or rate-sensitive) properties of the intrafusal fibers (see 31, 45). In agreement with some of the findings of others (1, 10, 33, 43), it has been shown in the present study that equatorial regions of intrafusal fibers have unique fine structural features which distinguish them from polar regions (see also 38). This would be expected if Matthews's original proposal were correct. Some of these features are the marked reduction and the peripheral attenuation of contractile myofilaments, the accumulation and central disposition of nuclei, and the aggregation of organelles and inclusions in the central sarcoplasmic cores of these fibers. Moreover, distinct differences in the disposition and spacing of nuclei and in the number and variety of organelles and inclusions further serve to distinguish the bag fiber from the chain fiber.

The disposition of microtubules in the interfibrillar spaces of the intrafusal fibers, and their greater abundance in chain fibers than in bag fibers, may have some bearing on the mechanical properties of these fibers. Since microtubules are known to function in giving rigidity or asymmetric shape to many cells (17), one might expect an abundance of such structures in a vigorously contracting muscle cell (such as the chain fiber [6, 7 44]) whose asymmetric shape must be reestablished after each forceful contraction.

The unusual presence of sarcoplasmic granules in equatorial regions of both intrafusal fibers is noteworthy since such granules are not common features of other mammalian skeletal muscle fibers. Such sarcoplasmic granules are similar in size and appearance to the "specific atrial granules" of cardiac muscle cells (24). Moreover, a similar close association between atrial granules and elements of the Golgi complex has led other workers to suggest that they represent a secretory function in these cells (22). Although at present there is little information concerning the composition and function of these granules, it is known that their number is increased after administration of norepinephrine and is reduced by atropine (22). This suggests that they are affected by neurohumoral agents and are related to cholinergic effects. Whether or not intrafusal fibers have a secretory function, similar to that suggested for atrial muscle cells, can only be conjectural. Nevertheless, the close association between the

sarcoplasmic granules and the vesicles of the Golgi complex and their presence directly under the sarcolemma suggest that the granules may indeed be products of secretion of the intrafusal fibers. In addition, their consistent location in areas close to sensory nerve terminals suggests a possible relationship between these granules and the mechanism(s) of sensory nerve transduction.

The nature and significance of dense cytoplasmic bodies in equatorial regions of both intrafusal fibers is, at present, unknown. Similar, but not identical, structures have also been reported in a variety of human skeletal muscle alterations (28, 34, 36), in normal human skeletal muscle (34), and in chick embryonic skeletal muscle grown in vitro (15). Some workers have suggested that such "inclusions" consist of altered myofibrillar material or accumulations of degenerated myofibrils. In view of this, it may well be that these structures in the intrafusal fibers represent a type of nonspecific degeneration or a form of newly synthesized protein sequestered within the central sarcoplasmic cores.

Cross-striated organelles, similar to those structures termed "microladders" (26) or "leptomeric organelles" (25) in frog intrafusal fibers, were observed in both kinds of intrafusal fibers in the present study. Similar structures have been reported in a variety of cell types (8, 18, 42, 47, 48). Moreover, they have previously been reported in intrafusal fibers of the rat (41), cat (10), and human (20). Although the precise function of these structures is still a matter of conjecture, some workers believe that they may perform a contractile function. Karlsson and Andersson-Cedergren (25) demonstrated a direct relationship between the periodicity of these structures and the length of the surrounding sarcomeres, and Katz (26) noted their close association to sensory nerve endings. In the present study, most organelles were observed close to areas of sensory innervation where they either run between the myofibrils or are attached to the sarcolemma. Because these organelles are consistently present near sensory nerve endings and are attached to the sarcolemma, other workers have suggested that such organelles may affect the sensory nerve endings via deformation of the sarcolemma of the muscle cell (10).

In the present study it was noted that, in equatorial as well as in polar (38) regions, chain fibers differ markedly from bag fibers in the extent of development of their sarcotubular systems and in the appearance of the M band in longitudinal sections. It is reasonable to assume that such ultrastructural differences in the two intrafusal fiber types may account for previously observed functional differences (6, 7, 44) in these fibers. Such qualitative differences in the mechanical behavior of mammalian intrafusal fibers have resulted in a number of theoretical models (2, 12, 19, 40) which suggest that the bag fiber is more "rate-sensitive" than the chain fiber. Although it has recently been shown that frequency of sensory nerve discharge is indeed directly related to rate-sensitivity (and, hence, the mechanical properties) of a given intrafusal fiber (31), the precise mechanism(s) by which the two kinds of intrafusal muscle fibers control the different forms of sensory discharge is at present unknown.

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