THE SARCOPLASMIC RETICULUM OF STRIPED MUSCLE

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Dr. Edwards and colleagues have demonstrated that many types of vertebrate and invertebrate muscle possess an extensive representation of the endoplasmic reticulum, and have observed that this may be arranged in longitudinal members running parallel to the myofibrils, and in transverse membranes, often located at the level of the junctions of A and I bands. Dr. Porter has called attention to some earlier work with light and electron microscope which deals with this reticulum, and has supplied us with new details of the structural arrangements prevailing at the points at which the sarcoplasmic reticulum connects with the Z bands of the myofibrils.

So far as I have been able to ascertain, the earliest representation of a component of the sarcoplasm which was disposed with a relationship to the cross-striations of muscle is that of Dobie (4), who in 1849 examined preparations wherein the individual myofibrils of fish and amphibia had been teased apart. He observed between the separated myofibrils, ". . . a beautiful homogeneous membrane (resembling the web between two of the toes of a duck) which is stretched by the violence used in the separation of the fibrillae." This structure in the skate, ". . . was marked with stripes corresponding to the dark and light spaces of the fibrillae between which it was stretched."

The first definitive visualization of the sarcoplasmic reticulum can be attributed to Thin (14), who impregnated it with gold and observed transverse and longitudinal components, but who misunderstood its significance. Melland (7), in confirming these observations in 1885, extended them by noting a fragment of isolated sarcolemma, to the inner surface of which were adherent components of the reticulum in the forms of circumferential lines at levels corresponding to those of the Z bands. Shortly thereafter a more detailed description of the reticulum was presented by Cajal (3), who observed the sarcoplasmic reticulum in living unstained insect muscle, but who erroneously interpreted the reticulum as constituting the active contractile units of the fiber. Other descriptions of importance were published by Retzius (12, 13), Marshall (6), and others. But the most extensive and valuable description of the sarcoplasmic reticulum as seen with the light microscope is that of Veratti (15). This pupil of Golgi prepared elegant metallic impregnations of the reticulum in muscles of various vertebrates and invertebrates, and published his observations with colored

drawings of exquisite delicacy and beauty. He recognized all the important topographical features and variants in this reticulum, including the special relation of portions of the reticulum to sarcolemma and Z band respectively. This paper must be recognized as one of the most important ever published on muscle structure.

When Dr. Porter and I (1) rediscovered the sarcoplasmic reticulum with the electron microscope we deemed it to correspond to the particle-studded membrane system then being recognized in other cells, and termed by Porter (9) the endoplasmic reticulum. This interpretation has since been confirmed by Porter (10, 11), by Palade (8), by myself (2), and by Dr. Edwards and Dr. Porter in the presentations we have just heard.

Fig. 1 presents a model of a block of muscle about $1 \times 3 \times 5 \mu$ in dimensions, showing many structural features of the sarcoplasmic reticulum. The reticulum is represented as consisting of membranes forming tubules with cisterna-like dilatations, peppered rather sparsely on the outside with the particles of Palade, often lying very close to the mitochondria, and sending connections to the myofibrils at the Z bands. Along the left margin of the block of muscle the sarcolemma is represented as a double membrane, to the inner surface of which are attached skeins of the sarcoplasmic reticulum at the level of the Z band. Mitochondria or sarcosomes are to be seen in subsarcolemmal positions, arranged in irregular longitudinal rows between some of the myofibrils, and in irregular transverse array along bands encircling each myofibril at the approximate level of the junction between A and I bands. This represents merely one variant of sarcosomal arrangement in muscle, as Dr. Edwards and others have pointed out. The grosser topographic disposition of the sarcoplasmic reticulum is likewise meant to represent one of many different variants. Some of the variants depicted in Veratti's (15) classic paper show a much less regular disposal of the sarcoplasmic reticulum. The muscle fibers showing a fairly regular arrangement of the sarcoplasmic reticulum usually show longitudinal strands and transverse networks forming anastomosing bracelets around the myofibrils at the levels of the Z bands, or at the levels of the N, as shown in Fig. 1. Transverse members at the levels of the M are encountered less frequently, and may even make connection with the myofibril at this level. Fig. 1 might be improved by incorporating in it details of the relationship of Z band and reticulum just shown us by Dr. Porter.

Retzius (12) suggested that the sarcoplasmic reticulum might transmit an excitatory impulse from the sarcolemma to myofibrils deep within the muscle fiber. Recently Huxley and Taylor (5) have brought forth evidence which has been interpreted as indicating that there is indeed a local transverse conducting system within the muscle fiber.

It seems unlikely that a structural component as well defined as the sarcoplasmic reticulum could be of trivial importance in muscle activity. Thus it may be worthy of careful study by anatomists, biochemists, and physiologists.

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EXPLANATION OF PLATE 57

For explanation of Fig. 1 see text.

A, A band.
B, cisternae.
C, cristae mitochondriales.
D, attachment of reticulum to sarcolemma.
E, attachment of reticulum to Z band.
F, cut ends of myofilaments (in hexagonal array).
G, myofibril.
H, H band.
I, I band.
K, sarcoplasm.
M, mitochondria (or sarcosomes).
N, N band.
R, sarcoplasmic reticulum.
S, sarcolemma.
Z, Z band.

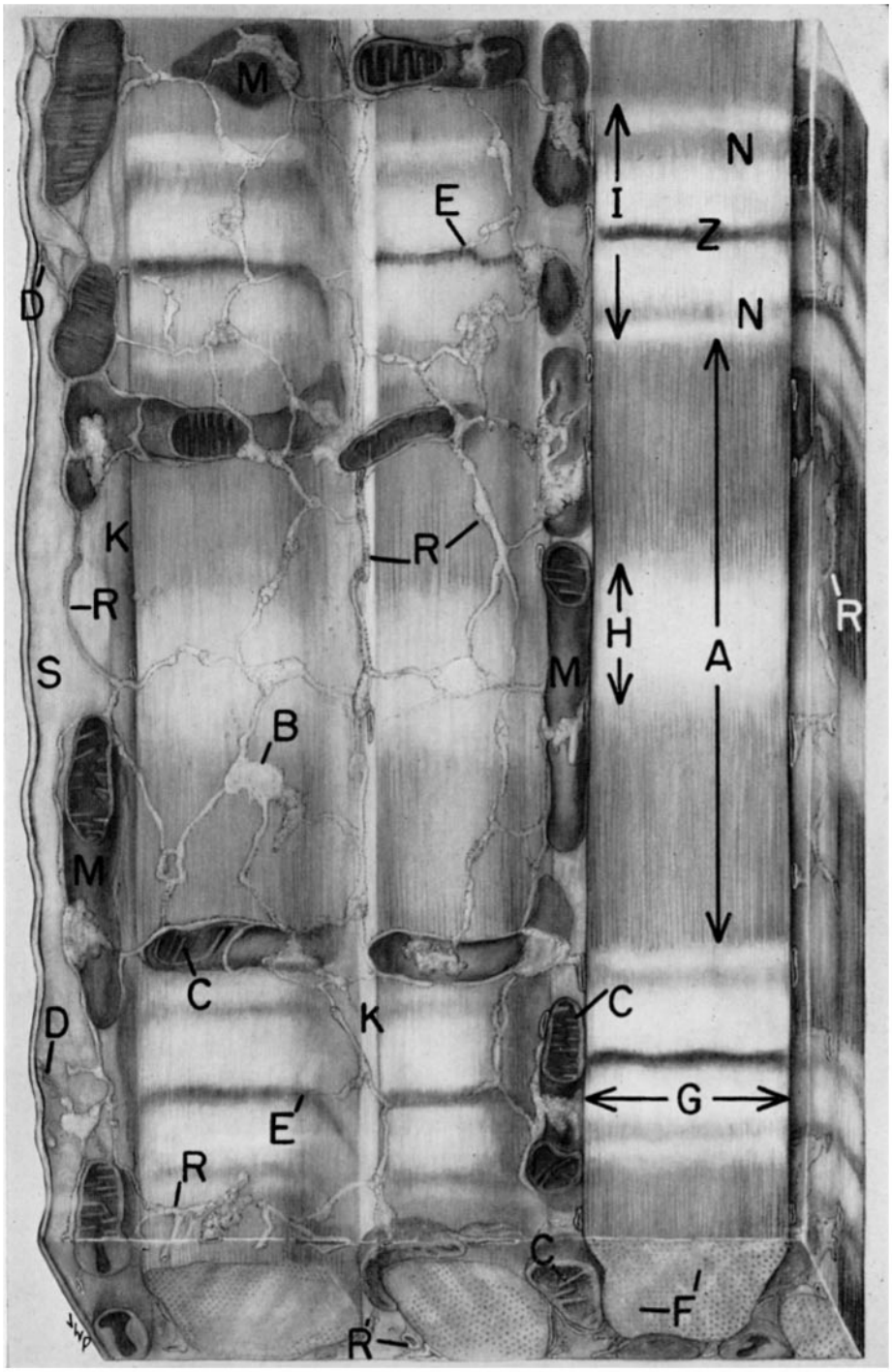

FIG. 1

(Bennett: Sarcoplasmic reticulum)