The Arrangement of Sarcoplasmic Reticulum in Smooth Muscle

The occurrence of a well-developed saccular system of sarcoplasmic reticulum lying immediately underneath the cell membrane and around the caveolae intracellulares of smooth muscle cells has recently been reported[1,2]. These observations were made on the longitudinal and circular muscle layers of guinea-pig ileum. In this as in other smooth muscles it was previously thought that sarcoplasmic reticulum was poorly reported[3,4]. This paper reports the observations carried out on other smooth muscles, in order to investigate the occurrence and the arrangement of sarcoplasmic reticulum. Another report on the sarcoplasmic reticulum in smooth muscles of the turtle has been published[5].

Smooth musculature from stomach, jejunum, ileum, colon, rectum, uterus, and vas deferens was obtained from adult guinea-pigs. Blood vessels supplying those viscera were also examined. Intestinal musculature was also studied in late embryos and newborn guinea-pigs. Tissues were fixed in glutaraldehyde 4–6% in Na cacodylate 0.1*M* at pH 7.3, post-fixed in unbuffered osmium tetroxide 2%, dehydrated in ethanol and embedded in Araldite. Sections, stained with uranyl acetate 1% in 70% ethanol and lead citrate, were observed in a Siemens Elmiskop 1A and a Philips EM 300 electron microscope.

Caveolae are observed in all smooth muscles examined; as it is known from the literature[3,4], they are a characteristic feature of all smooth muscle cells. They are bottle-shaped, and fairly regular in shape and size in different organs. They are grouped in rows parallel to the main axis of the cell and are lacking in the portions of the cell surface where the plasma membrane shows dense bodies and attachment plaques[6]. Caveolae are already present in the musculature of the ileum of 50 mm (CR) embryos; at this stage stage smooth muscle cells are already completely surrounded by a basement lamina.

In all smooth muscles examined a well-developed sarcoplasmic reticulum is found (Figure). It is formed by flat sacs lying parallel and immediately underneath the plasma membrane or underneath the caveolae. Rectilinear tubules skirting rows of caveolae are observed, as well as more complex, labyrinthine saccular networks among the caveolae. Frequently sacs of sarcoplasmic reticulum form a kind of a gutter for a row of caveolae: the sac gets close to the cell membrane with both edges and encloses the caveolae, which are then separated from myofilaments. The closer distance between sarcoplasmic reticulum and cell membrane or caveolae is 8–12 nm.

Mitochondria are very frequently associated with sacs of sarcoplasmic reticulum. The above described superficial sarcoplasmic reticulum is smooth but on occasion it may have ribosomes attached. Although differences in the

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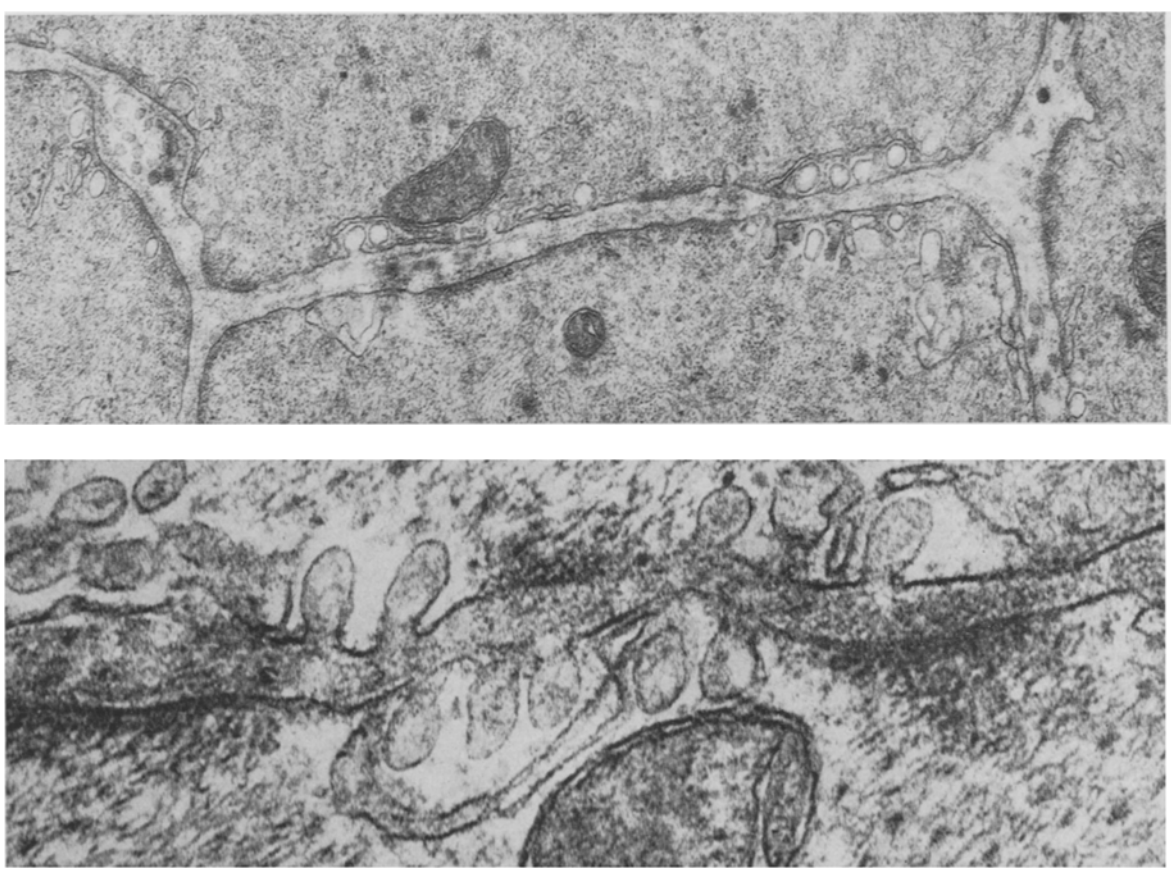

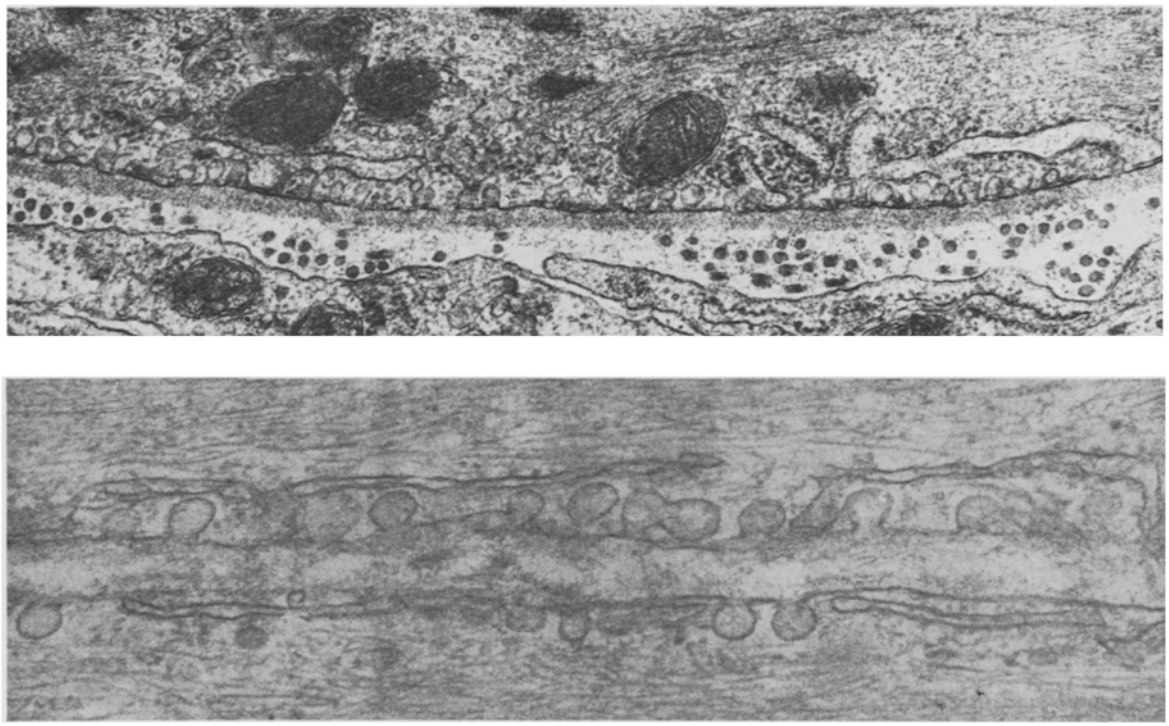

a) Longitudinal muscle of the vas deferens. 4 muscle cells, cross sectioned and surrounded by a basal lamina, show caveolae, sacs of sarcoplasmic reticulum and mitochondria. Among them collagen fibres are oberved. ×29,000. b) Circular muscle of the ileum. 2 muscle cells with several caveolae and sarcoplasmic reticulum. Note the close relationship with the mitochondrion. Dense patches in the cell membrane are observed. ×117,000. c) Arteriole of the oesophagus. The smooth muscle cell shows several caveolae and large sacs of sarcoplasmic reticulum. ×32,000. d) Embryo of 80 mm CR. Circular muscle of the ileum. 2 muscle cells, longitudinally sectioned, show a number of caveolae; sacs of sarcoplasmic reticulum lie underneath the caveolae and the plasma membrane. ×67,500.

amount of sarcoplasmic reticulum among various muscles are observed (it is, for example, more prominent in ileum and vas deferens than in blood vessels and uterus) no attempt has been made at quantiative estimations. Other sacs of smooth and tough sarcoplasmic reticulum and of Golgi complex are found in the cytoplasmic areas near the poles of the nucleus. From their first appearance in embryonic life caveolae are associated with sacs of sarcoplasmic reticulum.

In conclusion, sacs of sarcoplasmic reticulum in the superficial regions of the cells appear to be a general feature of smooth muscle cells. Being situated between extracellular space, cell membrane and caveolae on one side and mitochondria and filaments on the other side, this sarcoplasmic reticulum may be related to the excitation-contraction coupling mechanism. Given the similarity in the contractile mechanisms in striped and smooth muscles, it may have a similar function in both tissues. In this sense it has previously been suggested that sarcoplasmic reticulum could function as an intracellular compartment for ion, notably calcium, storage[1]. Alternative mechanisms for ion storage have previously been put forward, mainly because of early reports of a scanty sarcoplasmic reticulum in smooth muscle. The morphological evidence suggests that mitochondria may also be implicated in the process.

The function of caveolae is still unknown. They communicate with the extracellular space since they are penetrated by extracellular-space tracers such as lanthanum. However, no physiological evidence is available on how easily molecules and ions diffuse from the caveolae to the main bulk of the extracellular space and vice versa. The very shape of caveolae seems unfavourable for a quick exchange with the extracellular space. Thus the space delimited by the caveolae, although extracellular (i.e., outside the cell membrane) may be considered a relatively isolated part of the extracellular space. It is possible that caveolae provide the smooth muscle cell with a sort of microenvironment, whose chemical composition is more readily controlled by the cell itself.

Some similarity between caveolae in smooth muscle and T tubules in skeletal muscle as superficial cellular compartments has been previously discussed[2]. In this context it is worth mentioning that in the rat heart the number of caveolae is inversely related to the development of the T system[7]. In the ventricular muscle of lizard, where T tubules are absent, many caveolae are observed[8].

Riassunto. Nella muscolatura liscia di vari visceri e vasi viene osservato un notevole sviluppo del reticolo endoplasmatico. Esso è costituito da cisterne direttamente sottostanti la membrana plasmatica e le caveolae intracellulares.

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