MICROCIRCULATION

Volume II

Edited by
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PREFACE

The purpose of this treatise is to present a comprehensive view of the field of microcirculation. The study of small blood vessels, which forty short years ago was the domain of morphologists only, has grown in the intervening years into a most important subject from physiologic, pharmacologic, and pathologic as well as clinical points of view. Microcirculation is currently an intensively investigated field and yet a comprehensive approach to this subject, one that would focus on its functional entities and interrelatedness to other disciplines, has not yet, to our knowledge, been attempted.

Our concept concerning individual sections of this treatise was to evaluate critically work done in the past, to describe the present state of the art, and to point out future directions that seem profitable and challenging. It is hoped that *Microcirculation* will not be merely a collection of monographs and a reference source but that it will facilitate a synthesis of all the information available and will provide new approaches to the study of small blood vessels. We also hope that the sheer size of *Microcirculation* will not discourage students, research workers, and biologists in related areas, as well as clinicians, from becoming acquainted with the field of microcirculation.

It is inevitable that some duplication of material will occur in a work of this size. It is also not possible, mostly because of limitations of the size of this treatise, to include among the authors all investigators who have contributed significantly to this research field. Nevertheless, we have been fortunate in being able to bring together so many active and outstanding workers in this field to join us in this endeavor.

There is another, equally compelling reason to put together a volume on microcirculation. It is to honor Benjamin W. Zweifach, the individual who, more than any other, has left his personal mark on this research field. It is rare in science for any one man to become as influential as he has through the years. Almost everyone who has contributed significantly to the field of microcirculation has taken a turn in Dr. Zweifach's laboratory and has been enriched by his exceptional knowledge of, and insight into, research problems. His own contributions, which span four decades and a host of scientific disciplines, encompass every important new development in the field of microcirculation and are the cornerstones of our knowledge in this area of biology. The measure of his success is also exemplified by the number and quality of his students, all of whom, including the editors of this treatise, are proud to trace their lineage to him. This book is a collaborative effort of his students and colleagues, to whom he served as mentor and for whom he continues to be a constant source of help and inspiration.

We are proud to dedicate this treatise to Benjamin W. Zweifach.

G. Kaley and B. M. Altura

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VASCULAR SMOOTH MUSCLE

chapter 1

VASCULAR SMOOTH MUSCLE MORPHOLOGY AND ULTRASTRUCTURE

Carrick E. Devine

This work was carried out under a grant from the Medical Research Council of New Zealand for hypertension research.

INTRODUCTION

Vascular smooth muscle has a wide spectrum of ultrastructural and physiological properties, the details depending on the species of animal and on the part of the vascular bed that is being considered. The microcirculation is usually that part of the vascular bed comprising vessels less than 100 μm in diameter. Because of the relative ease of controlling the physiological and pharmacological environment of larger vessels, however, much important work has been done on them, and results from these studies are included in this chapter, especially with regard to the myofilaments and the sarcoplasmic reticulum. Much of what is being described for many cytoplasmic organelles has changed little from the early review by Rhodin (1962). More recent reviews of the physiology and pharmacology of vascular smooth muscle (Somlyo and Somlyo, 1968, 1970, 1975, 1976; Shepherd and Vanhoutte, 1975; see also chapters in this volume by Paul and Rüegg, Vanhoutte, and Bohr et al.) contain important background information for ultrastructural studies.

The success of recent work has depended on improved methods of fixation (see "Electron Microscopic Techniques," Volume III, and Somlyo and Somlyo, 1975). The tissues illustrated in the figures in this chapter were fixed in cacodylate-buffered glutaraldehyde (pH 7.4), except for two instances of freeze-fractured smooth muscle (Figures 20 and 27). Tissues prepared for sectioning were further post-fixed in osmium tetroxide in cacodylate buffer and block-stained with aqueous uranyl acetate. Any variations in this procedure are noted in the figure legends (for example, Figures 10 and 29).

GENERAL ARRANGEMENT OF SMOOTH MUSCLE CELLS

The arrangement and size of the long spindle-shaped smooth muscle cells and of the extracellular components in blood vessels vary considerably. In large vessels, smooth muscle cells are about 3–5 μm wide and up to 130 μm long, but in the smallest arterioles, they are only 40 μm long (Rhodin, 1967). In large "elastic" blood vessels such as the aorta and pulmonary artery, where the wall tension is high, the circularly oriented smooth muscle cells are arranged in lamellae separated from each other by elastic tissue (Pease and Paule, 1960; Karrer, 1961; Cliff, 1967; Devine, Somlyo, and Somlyo, 1972). In young animals the aortic smooth muscle cells are cuboidal, but they flatten and develop numerous processes during maturation (Cliff, 1967). This is a different picture from that of medium-sized arteries, which are characterized by more regularly shaped smooth muscle

cells and less elastic tissue, mainly limited to the elastic laminae. In the microcirculation, the medial coat is only one or two cells thick, and, finally, the stage is reached where the smooth muscle investment disappears, leaving a lining of endothelial cells in the capillaries (see Baez, and Wolff, Volume 1). The venous side of the circulation has less elastic tissue and smooth muscle than the arterial side of the circulation and exhibits many physiological and pharmacological properties that are different from those of the latter (Shepherd and Vanhoutte, 1975; Altura, 1978).

CYTOPLASMIC COMPONENTS

The single *nucleus* lies centrally and has an elongate, variable shape (depending partly on the stage of contraction) (Figures 1 and 3). It has a prominent

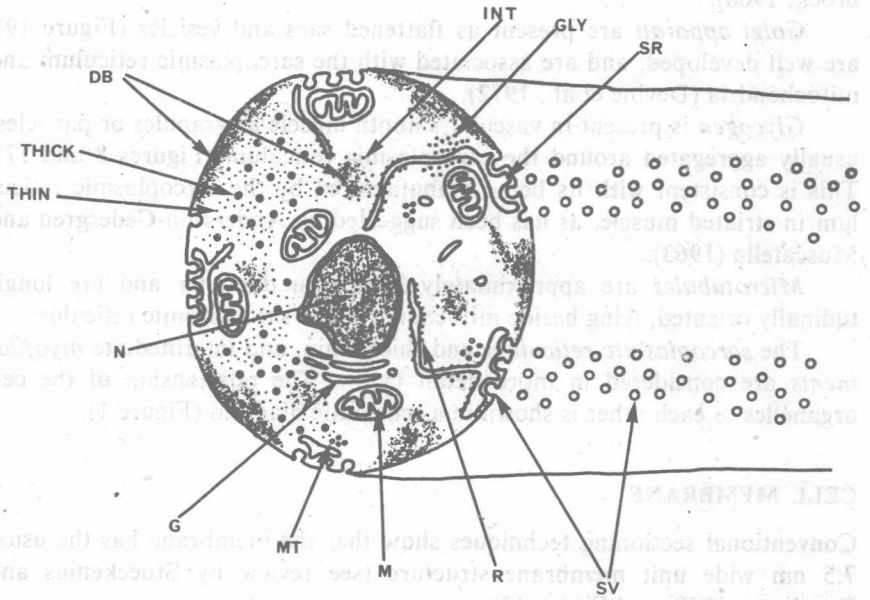

Figure 1. Schematic diagram of a smooth muscle fiber, showing the relationship of the cell organelles to each other. The rows of surface vesicles (SV) in close relationship to sarcoplasmic reticulum (SR) and mitochondria (M) are separated from each other by dense bodies (DB), some of which also lie deeper within the cell. The Golgi apparatus (G) lies close to the nucleus (N), and microtubules (MT) are found close to SR. Thin filaments (THIN) form rosettes around the thick filaments (THICK). Intermediate filaments (INT) predominate around the dense bodies. Ribosomes (R) and glycogen particles (GLY) lie on or close to the SR. (These abbreviations are used throughout the figures in this chapter. Additional abbreviations are noted when they first occur in the legend.)