The Reticuloendothelial System

A COMPREHENSIVE TREATISE

Volume 3
Phylogeny and Ontogeny

The Reticuloendothelial System

A COMPREHENSIVE TREATISE

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Volume 3
Phylogeny and Ontogeny

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The American pioneers charted new directions. They cleared forests and allowed the sun to shine on their newly constructed homesteads. They tilled their fields, planted crops, nourished their children and watched them grow. Bill Hildemann is such a pioneer for he has mapped the wilderness of immunophylogeny, made it habitable, revealed its frontiers, and taught and encouraged its settlers. We dedicate this volume to him.

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Foreword

This comprehensive treatise on the reticuloendothelial system is a project jointly shared by individual members of the Reticuloendothelial (RE) Society and biomedical scientists in general who are interested in the intricate system of cells and molecular moieties derived from these cells which constitute the RES. It may now be more fashionable in some quarters to consider these cells as part of what is called the mononuclear phagocytic system or the lymphoreticular system. Nevertheless, because of historical developments and current interest in the subject by investigators from many diverse areas, it seems advantageous to present in one comprehensive treatise current information and knowledge concerning basic aspects of the RES, such as morphology, biochemistry, phylogeny and ontogeny, physiology, and pharmacology as well as clinical areas including immunopathology, cancer, infectious diseases, allergy, and hypersensitivity. It is anticipated that by presenting information concerning these apparently heterogeneous topics under the unifying umbrella of the RES attention will be focused on the similarities as well as interactions among the cell types constituting the RES from the viewpoint of various disciplines. The treatise editors and their editorial board, consisting predominantly of the editors of individual volumes, are extremely grateful for the enthusiastic cooperation and enormous task undertaken by members of the biomedical community in general and especially by members of the American as well as European and Japanese Reticuloendothelial Societies. The assistance, cooperation, and great support from the editorial staff of Plenum Press are also valued greatly. It is hoped that this unique treatise, the first to offer a fully comprehensive treatment of our knowledge concerning the RES, will provide a unified framework for evaluating what is known and what still has to be investigated in this actively growing field. The various volumes of this treatise provide extensive in-depth and integrated information on classical as well as experimental aspects of the RES. It is expected that these volumes will serve as a major reference for day-to-day examination of various subjects dealing with the RES from many different viewpoints.

Herman Friedman
Mario R. Escobar
Sherwood M. Reichard

Introduction

During the last two decades immunology has truly come of age, with its own individuality, reaching the open stage where a number of eminent contributors from different but related backgrounds have felt justified in attempting to integrate and compare the immunologic or paraimmunologic responses of invertebrate and vertebrate host organisms. Although the steps in the evolution of the reticuloendothelial system (RES) in animals cannot be retraced with any certainty, the study of immunity in extant species has supported the concept of an orderly progression in immunologic development as one ascends the phylogenetic tree from unicellular organisms with a nucleus (eukaryotic) to man.

Phylogeny and Ontogeny, the third volume in a series on the RES, constitutes an essential part of the comprehensive treatise as it critically reviews the state of the art for each taxonomic group of invertebrates and scrutinizes the most current information on the lymphoreticular system of vertebrate animals. The carefully edited contents of this volume attest to the worldwide growth of basic immunology which is perhaps unique in the history of biology.

It is worth considering that although in many cases there is no structural or functional homology between the elements of host defense in invertebrates (e.g., antisomes) and those in vertebrate animals (e.g., antibodies), the development of these elements can be threaded along the evolutionary staircase by analogous similarities. Furthermore, immunologists studying mammals have already learned a great deal about many of the individual functional units in the immune system thanks to the detailed study of lower species that have a limited capacity for immune reactions, for example, in invertebrates, one can examine a primitive form of cellular immunity in the absence of specific antibodies.

We hope that the combined efforts of all the specialists who have contributed generously to this gigantic task and the talent of the editors of this volume to give it organization, unity and perspective will, at least, widen the horizon of classical immunologists by revealing to them the incredible teleological wisdom that is inherent to the evolutionary development of the RES.

Because of the uniqueness of the pioneering efforts by the editors of this volume, their conviction is expressed in the Editorial Comments section that follows. The volume editors wish to underline the importance attached to sources of information derived from pertinent research on species that evolved

early in phylogeny. They believe that the knowledge acquired from that research may pave the way toward a better understanding of immunologic mechanisms operative in the more advanced or complex animals, and not conversely.

Herman Friedman
Mario R. Escobar
Sherwood M. Reichard

Editorial Comments

Higher vertebrates effortlessly perform what seem to be amazing feats of magic as they distinguish self- from modified-self antigens and respond to appropriate signals by manufacturing a panoply of antibody specificities and other effector molecules. We are just beginning to learn that some of the magic involves cellular and molecular on/off signals that exert profound regulatory and directional influences on the generation of immune responses. Only time and human ingenuity will reveal the extent of this biological wizardry.

Immunophylogeneticists attempt to answer when, how, and why this incredibly well integrated complexity came to be. Between the lines of many of the chapters of this volume, one can sense the heady experience of racing up or down what is hopefully a sturdy evolutionary staircase in pursuit of information about the very existence (let alone function) of ancestral lymphocytes, macrophages, and lymphoid organs in the myriad creatures that now inhabit our world. We have learned that ectothermic vertebrates display relatively minor variations on avian and mammalian themes of organization, specialization, and regulation. That the outlines of the mammalian reticuloendothelial systems are well delineated in primitive fishes and amphibians does not make them less worthy of serious scrutiny. Rather, it simply means that we must look elsewhere—to more primitive invertebrates—if we are to decipher the origins of the RES from extant organisms. And look we shall, since there is much to see. Although the diversity of specialized cells in simple invertebrates is certainly less than that of more advanced multicellular creatures, simple and complex multicellular animals alike, must perform, in a coordinated fashion, the universal physiological functions of respiration, digestion, reproduction, and self-protection if they are to survive. Thus, we cannot help but marvel at the abilities of these early metazoans to effectively carry out so many different defense reactions without the vertebrate attributes of antibody, suppressor and helper T cells, etc. We must continue to probe the uniqueness of these defense systems, for an understanding of how they work might help us to arrive at some understanding about the origins of immunity.

M. Michael Sigel
Nicholas Cohen

Preface

Concurrent with the recent veritable explosion of information about all facets of the mammalian immune system, has been the resurgence of interest in the problems posed by the phylogeny and the ontogeny of immunity. This volume reviews research on comparative and developmental aspects of components of the lymphoreticular system—components that are, by and large, responsible for protecting an organism in its antigenically hostile environment.

Each of this book's four sections has a distinctly different focus. In the first section (Chapters 1–9), a separate chapter is devoted to the primordial cellular defense systems of representatives from each taxonomic group of invertebrates. A perusal of these chapters devoted to sponges, coelenterates, worms of all sorts, molluscs, arthropods, echinoderms, and protochordates reveals unique features of organization and specialization as well as a common denominator—the phagocytic cell. This section, which is indeed a book unto itself, is both introduced by and concluded by a chapter in which defense systems of all invertebrates are viewed from a broad biological and biochemical perspective.

The first four chapters of the second section (Chapters 10–14) of this volume are definitive reviews of the structure and function of the lymphoreticular systems of fishes, amphibians, reptiles, and birds. Chapter 14 addresses the critical issue of the molecular basis of self/nonself discrimination of all ectothermic vertebrates. There are two omissions in the second section. First, the structure and function of the RES of mammals has not been covered; this is, of course, the purview of the nine other volumes of this treatise. Second, data bearing on the nonlymphoid components of the RES of ectothermic vertebrates are not presented in any depth. This omission is not an oversight. Rather, it is simply the result of our almost complete ignorance about these cellular entities in creatures other than birds and mammals.

The comparative theme that unites the first and second sections (and provides the rationale for our presumption in using the word, phylogeny, in the title of this volume) is continued in the second half of the book. In the third section (Chapters 15–17), the ontogeny of cells (primarily lymphocytes) of the lymphoreticular systems of amphibians, birds, and mammals is reviewed. In the fourth section (Chapters 18–21), the ontogeny of immunity in representatives of these three vertebrate classes is addressed. A final chapter discusses aging of the RES as an important and continual developmental event. Each of these chapters

not only provides a state of the art summary but it reveals a wealth of new, often unique, models with which to study immunological problems that are not restricted to mammals. The second half of this book is also characterized by certain noteworthy omissions. On the one hand, these again reflect our desire to avoid redundancy in view of the abundant well reviewed literature on the ontogeny of immunity of mammals; on the other hand, they speak to our ignorance about the ontogeny of the immune system and immunity of fishes and reptiles. Fortunately, there are shimmerings on the comparative and developmental immunology horizon* that suggest that by the time this treatise will need to be revised and updated, Volume 3 will contain several new chapters, as well as many new references.

Nicholas Cohen
M. Michael Sigel

*See grouped papers on fish immunology in *Aspects of Developmental and Comparative Immunology I.* (J. B. Solomon, ed.) Pergamon Press, Oxford, 1981.

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