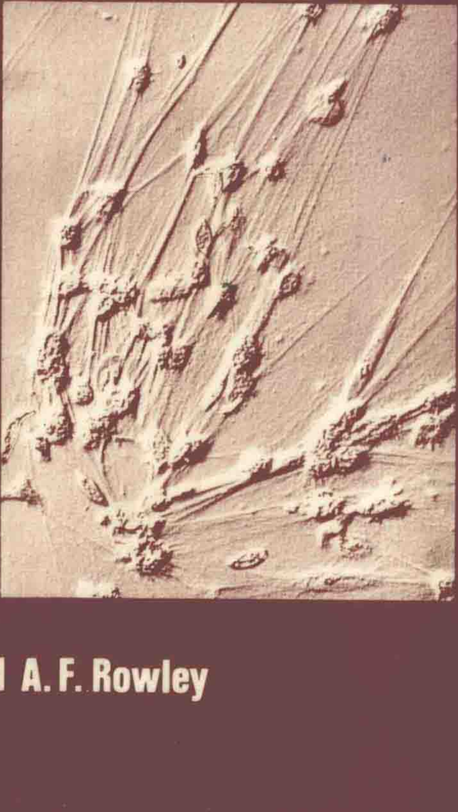
INVERTEBRATE BLOOD CELLS 1



GENERAL ASPECTS, ANIMALS WITHOUT TRUE CIRCULATORY SYSTEMS TO CEPHALOPODS

edited by N. A. Ratcliffe and A. F. Rowley

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Volume 1

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Preface

Renewed interest in invertebrate "blood cells" has developed for a number of reasons. First, there has been a recent escalation in research into comparative immunology, including many studies on invertebrates. These animals provide relatively simple experimental models, they may supply clues to the ancestry of the lymphoid system, and they may have novel defence reactions not yet discovered in the more complex immune systems of vertebrates. Secondly, many invertebrates, but especially the molluscs and crustaceans, are now being extensively farmed to augment the food resources of man. Clearly, a better understanding of the host defence reactions of such species would help to avoid and overcome disastrous outbreaks of disease which are likely to occur under the artificial and potentially stressful conditions of commercial culture. Thirdly, many invertebrates act as vectors of parasitic organisms which are the scourge of mankind. The insects and molluscs, in particular, include species responsible for the transmission of malaria, sleeping sickness, filariasis, onchocerciasis and schistosomiasis. The means by which these parasites invade and multiply in their hosts and yet fail to elicit an effective "immune" response is now the subject of intensive research. Fourthly, with the increasing resistance of invertebrate pests to chemical pesticides, and the accumulation of these noxious substances at higher levels in the food chains, greater efforts are being made to develop and utilize biological control agents such as the viruses, bacteria, fungi, nematodes and parasitoids. The potentially immense practical value of such agents has provided yet a further stimulus for researches into the host defence reactions of invertebrates. Finally, many biologists are beginning to realize that invertebrate blood cells not only function in "immune" or host defence reactions but also serve, at least in some species, to store, transport and/or synthesize food, waste products and hormones and are thus involved in many other vital life processes. Our lack of knowledge of the role of invertebrate blood cells in these basic functions provides a major area for future research utilizing modern biochemical techniques.

Much of the recent work on invertebrate blood cells, particularly in the fields of comparative immunology and cellular defence reactions, has been summarized in a number of excellent volumes including *Contemporary*

Topics in Immunobiology, Vol. 4, Invertebrate Immunology (E. L. Cooper, Ed., Plenum Press, 1974); *Invertebrate Immunity* (K. Maramorosch and R. E. Shope, Eds, Academic Press, 1975); *Comparative Immunology* (J. J. Marchalonis, Ed., Blackwell Scientific, 1976); *Comparative Immunobiology* by M. J. Manning and R. J. Turner (Blackie, 1976); and *Insect Hemocytes* (A. P. Gupta, Ed., Cambridge University Press, 1979). However, not since the publication of Warren Andrews *Comparative Hematology* (Grune and Stratton, 1965) has an attempt been made to summarize comprehensively our knowledge of the structure and function of invertebrate blood cells. Such a synopsis is urgently required in the light of current research interests and the many advances which have been made utilizing sophisticated modern techniques.

Volumes 1 and 2 of *Invertebrate Blood Cells* have been prepared specifically to bridge the gap since the publication of *Comparative Hematology*, with each chapter written by an expert in his or her particular group of animals. We have attempted to present information on as many invertebrate groups as possible and to this end have included much unpublished material, some of which was researched specifically for these books, e.g. Chapters 5, 14 and 15 on the leeches, lophophorates and echinoderms, respectively. We hope these volumes will generate further interest in many areas of invertebrate haematology and provide a source of comparative data for those workers already researching into particular aspects of invertebrate blood cells.

February, 1981 N. A. Ratcliffe and A. F. Rowley

Contents of Volume 1

Contents of Volume 2

Section IX: Comparative Aspects of the Structure and Function of Invertebrate and Vertebrate Leucocytes

Section I

Aspects of the Evolution and Development of Body Cavities, Circulatory Systems and "Blood Cells"

1. Aspects of the evolution and development of body cavities, circulatory systems and "blood cells"

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CONTENTS

I. Introduction

While the invertebrates vary enormously in structure all must maintain the body in working order by tissue repair, by elimination of waste, and by internal defence against invading foreign organisms. Each phylum represents a basic body plan, a particular morphological theme with variations according to different life styles. But, whatever the body structure may be, all animals have cells capable of phagocytosis. Most of these cells are independent in the sense that they can move about, either by active migration or by passive transport in circulated body fluid. If phagocytes are to play a role in internal defence then they must be able to move to the right place when required. This presents no particular problem to an animal which is very small, but with increasing size there is an obvious advantage in having very many of these cells throughout the body or capable of being distributed when needed. The evolution of circulatory systems to convey both nutrients and to mediate respiratory exchange lent itself to this need, phagocytes or other defensive cells being distributed by the blood or body fluids. What we know of these cells, their types and functions, is summarized in the chapters which follow. This introductory chapter is designed simply to remind the reader of the morphology of the different invertebrates we shall be considering and, in particular, the relationships of the various body cavities and vascular systems in which the cells are found (Table I).

The phagocyte is an eating cell and antedates the evolution of body cavities and indeed organ systems. The universality and importance of the phagocyte was emphasized by Metchnikoff (1893) in his well known book "Lectures on the Comparative Pathology of Inflammation". The most primitive invertebrates are without discrete organ systems and in the siliceous and horny sponges, digestion occurs solely through the agency of phagocytes (Pourbaix, 1931). In sponges food particles are trapped by choanocytes, then passed to the amoebocytes which distribute the products of digestion throughout the body (Fig. 1). Sponges have no body cavity other than the central "spongocoel" and the canals leading to and from it. In coelenterates with a single internal cavity which functions as a gut, the epithelial lining has become a specialized digestive layer and the products of digestion are distributed through canals radiating from this central cavity. In larger coelenterates with extensive mesogloea formation there is a need for scavenging, and amoebocytes are found which act as phagocytes (see Chapter 2).

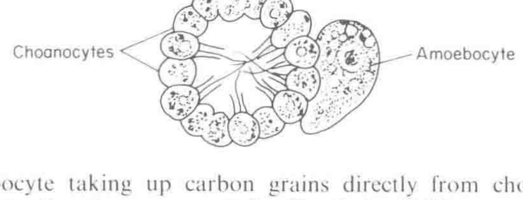

Fig. 1. Amoebocyte taking up carbon grains directly from choanocytes in the calcareous sponge *Grantia compressa* (after Pourbaix, 1931).

The accelous turbellarians have an amorphous "gut" without a defined epithelium. The wandering amoebocytes break down and distribute the products of digestion. It is but a simple step for such cells programmed to engulf non-self particles as food, to take on the role of eliminating unwanted materials, foreign organisms and parasites, in order to maintain fitness.

We are probably most familiar with the defence systems characteristic of advanced vertebrates, and in particular those of mammals and birds. We now understand a great deal about their elegant immune responses and the role of the different cell types found in the blood and lymph. Both mammals and birds are characterized by their high activity maintained by elevated, constant body temperatures with a high pressure blood vascular system connected with a low pressure lymphatic system draining the tissue fluid. Defence cells can thus be transported quickly via the blood to sites of injury and potential infection, while the lymph can participate in the distribution of other white cells concerned with the more long-term responses to foreign organisms or materials. Both the vascular and lymphatic systems develop within the embryonic mesoderm separately from the coelom which serves as a body cavity in which the viscera are slung. Unlike many invertebrates where the coelomic cavity is spaceous and in which the fluid may represent the major part of the animal's mass, the volume of the coelomic fluid in birds and mammals is very small as compared with that of the blood and lymph.

II. The coelom

In invertebrates the coelom developed as a space around the gut serving both to separate it from the muscular system and also to provide a hydrostatic skeletal system on which the muscles of such soft-bodied creatures could act. The coelom was thus a mechanical development which functioned primarily in relation to movement and locomotion. Subsequently the spaceous fluid-filled coelom assumed other functions including excretion and osmotic regulation. It also served as a space in which the gametes could develop.

III. The blood vascular system

The blood vascular system, on the other hand, developed in relation to two needs: first, to distribute products of digestion from the gut to other parts of the body, and secondly to convey the respiratory gases to and from the tissues. The adaptation of the circulation to these functions in invertebrates