THE MOLECULAR ARCHITECTURE *of* PLANT CELL WALLS

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Electron micrograph of the outermost lamellae in the Wall of *Valonia ventricosa*. Pd-Au shadowed; magnification 25,000 ×

[*Frontispiece*

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To all the members of my family who, in their various ways, have given me encouragement this book is humbly dedicated

"FOR WHAT we obtain of *Nature*, we must not do it by commanding but by courting of Her. Those that woo Her, may possibly have her for their *Wife*: but She is not so common, as to prostitute her self to the best behaved *Wit*, which only practiseth upon it self, and is not applied to her. I mean, that wherever Men will go beyond Phansie and Imagination, depending upon the Conduct of *Divine Wisdom*, they must Labour, Hope and Persevere. And as the *Means* propounded, are all necessary, so they may, in some measure, prove effectual. How far, I promise not; the way is long and dark; and as Travellers sometimes among Mountains, by gaining the top of one, are so far from their journey's end; that they only come to see that another lies before them: so the way of *Nature*, is so impervious, and, as I may say, down Hill and Up Hill, that how far soever we go, yet the surmounting of one difficulty, is wont still to give us the prospect of another."

NEHEMIAH GREW, M.D., F.R.S.
Anatomy of Plants, 1682.

Preface

THE STRUCTURAL features of cellulose and of the substances associated with it have been the subject of much intensive study for at least thirty years and have given rise to a literature now so enormous that it is difficult even for the expert to keep up with it. From time to time various sections of this study have been reviewed in text-books, but a good deal is still available only in the original papers. In particular no text-book has yet appeared in English confined to those aspects of wall studies of greatest appeal to botanists, and the growing demand for such an account has stimulated me to write the present book.

I have made no serious attempt to cover the ground already so adequately surveyed in a number of texts. The methods and results of physico-chemical investigations of cellulose have already been presented in a series of excellent treatises, and the most recent book by Frey-Wyssling has already laid down the basis of the botanical approach. Nevertheless there remains much that is of importance still not presented, and a good deal of information has already become available even in the short time which has elapsed since Frey-Wyssling's book appeared.

Since the present book is written, however, chiefly for botanists, it has been necessary to present in the first few chapters a brief and, it is feared, wholly inadequate résumé of the more important physical and chemical approaches to cellulose structure. At the same time it is hoped that it may prove of interest also to physical scientists and, though no specific reference is made to any of the obvious technological connections, also to fibre technologists; and for this reason some explanatory account is also given of the anatomy and development of the tissues under review. The rest of the book is concerned with the detailed architecture of cell walls in a wide variety of plants, including growing cells, and an attempt is made to interpret growth processes in terms of the structure thus revealed.

A good deal of the work described in these later chapters has been performed in my laboratory and I have not hesitated to draw on the latest work of my colleagues to whom I owe a very great debt of gratitude. I would particularly mention Dr. M. Middlebrook and Dr. M. F. E. Nicolai, who are still with me, and Dr. K. Singh, now at Dehra Dun, India, and Dr. A. B. Wardrop, now in the Forest Products

Division, C.S.I.R.O., Melbourne, Australia. In particular I would say that I have not hesitated to express opinions on controversial points and I hope they will forgive me if I have taken undue liberties. The inclusion of a good deal of hitherto unpublished material has possibly led me into statements which may eventually need to be modified: but again I have preferred to liven the book at the risk of some later corrections rather than adhere rigidly to fully established interpretations.

I am deeply indebted to Mrs. F. R. Langstadt for the very able way in which she has converted my almost illegible pages into typescript, and to Mr. B. Clarke for the preparation of many of the prints with which the book is illustrated and in particular for the colour plate (Plate III). To Dr. M. F. E. Nicolai, Dr. L. C. Spark and Miss L. I. Scott I am grateful for assistance in proof-reading; any errors which remain are my own responsibility.

It has been my privilege during my research life to be in close association with some of the leading authorities in various fields of science. To all of them, and particularly to Professor W. T. Astbury and, of late years, to Professor I. Manton, I owe a debt I can never repay. It is my sorrow and misfortune that I can no longer convey an expression of my gratitude to the one to whom I owe the most—the late Professor J. H. Priestley.

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CHAPTER I

Introduction and Historical Background

THE THEME of this book centres round the extraordinary advances which have been made, during the past twenty-five years, in the understanding of the molecular structure of the solid envelope which surrounds every plant cell. It is fitting therefore, that we should consider in the first place some of the multitudinous reasons for the current preoccupation with such a topic. Reasons in plenty are not far to seek—they must in fact be obvious after a little thought even amongst those of us unacquainted with plant science. From time immemorial man has made use of plants, not only for food—for that would not help us here since the bulk of the material we shall deal with is not digestible in man's alimentary tract—but also in many other ways. From the Garden of Eden downwards, use has been made of plant products to cover human nakedness, a use widened enormously in scope by the discovery of weaving since fibres of all kinds could then be manufactured into sheets of cloth. Nowadays we are familiar with the weaving of flax fibres into linen, with the weaving of hemp into ropes and jute into bags and with the multitudinous uses of cotton fibres. All of these processes exploit the very fibres which we shall be investigating here. More than this, however, from times well before recorded history man has made use of another plant product—timber—for the building of houses, for furniture, and even for weapons of offence and defence. He has become acquainted with the great strength and durability of such plant products and has made use of their peculiarities, of the lightness and resilience of wood for instance. There can be no doubt but that the peculiar combination of physical properties in these materials—and this short list does not by any means cover all the queer mixture of properties—is due in no small degree to the molecular structure of plant products and, in particular, to the structure of the cellulose so ubiquitous in all of them. As in many other branches of human endeavour, the uses of these materials, and knowledge and exploitation of their peculiarities, came long before any attempt could be made to explain them. Nevertheless explanation is surely needed, and all the more surely in this modern age when so much of our economy depends on the faultless processing of huge quantities. Without such explanation it becomes impossible to control adequately the varied, and nowadays very complicated, treatments which the raw material receives; and, in particular, if anything goes wrong it is not otherwise easy to put it right again without serious loss. Finally, it is impossible to devise new uses, or to explore the old ones thoroughly, without a good deal of ordered and accurate information concerning the most intimate details of the materials concerned. Realization of these matters has led to the founding throughout the world, in the growing areas as well as in the processing, of scientific laboratories devoted to the problems involved.

This is by no means all, however, and this fails by a long way to exhaust the reasons for study of this particular field; it is certainly not the major reason for writing this book nor does it express in any large measure the fascination of the subject for the author, for any of those whose help it will be an honour to acknowledge, or for any of the long sequence of scholars—for scholars they are even though also scientists!—whose names will grace these pages and in whose footsteps the author and his associates now humbly tread. Apart altogether from its immense impact on the welfare of human beings, a knowledge of how things grow, whether animal or plant, can hardly fail to be of interest to all of us, and this means in the long run a knowledge of the reactions of the protoplasm—the stuff of which all living things are composed and by whose activity they develop. There are naturally many avenues along which such a study can properly be approached, and are being approached; but none of them can be more fundamental than the approach through structure. Until the structure of the living material is fully understood there can be no real appreciation of the course of growth. From this point of view, and since in very general terms protoplasm is very much the same in whatever body it is organized, it is immaterial whether we concern ourselves with plants or with animals, and in some respects plants offer more favourable material for exploratory purposes. Just as animal bodies produce structural proteins such as hair, whose study at the hands largely of Professor W. T. Astbury has led to such sweeping developments in the field of protein physics and chemistry, so in plants we find structural polysaccharides. These are, chemically speaking, a far cry from the proteins, and therefore several steps removed from the molecular species which undoubtedly confer upon protoplasm its particular and still cryptic features. Nevertheless their production in intimate contact with the protoplasm makes it very probable that, as an end product in carbohydrate metabolism, they have a good deal to tell us concerning protoplasmic structure and activity if only we can read them aright. Further, and of more immediate importance, forming as they do an outer envelope surrounding each little unit of protoplasm in the plant body and remaining so from the beginning during the whole of its life, they can hardly fail to be vitally concerned in the increase in bulk of cells and tissues and to carry with them a record of cellular activity. It is from these points of view, and these alone, that this book has been written.

The astounding progress during recent years in the whole field of structure in biological materials, using the methods which modern physics has placed in our hands, is perhaps sometimes apt to blind us to the very solid foundation which our distinguished predecessors have laid with their completely inadequate tools, and upon whose firmness of construction our ivory towers depend. It is therefore a salutary lesson to go down and consider, even if very briefly, the stones—and the rubbish—which lie in the basement. The historical period concerned can be divided roughly into four sub-periods—the period before the discovery of the microscope, of which we shall have nothing to say, the period from the first use of the microscope in about 1666, to the application of the polarizing microscope in about 1830, the period from this time until the year when the method of X-ray analysis began to develop, and the modern period since that time.

The beginnings of cell wall studies

It was naturally only after the improvement by *Robert Hooke* of the microscope recently devised by the *Janssen* brothers, to give reasonable magnification with tolerable definition, that anything useful could be written about our subject. Although *Henshaw* is said to have discovered the vessels in the wood of walnut trees as early as 1661, the study properly begins with the publication by *Hooke* of his *Micrographia* (1667) and the drawing which he there published, and as so often figured in later treatises of elementary botany, of cell structure in cork. *Hooke*, however, was not in any sense a botanist and contented himself with the description of the honeycomb structure he perceived and with fanciful comparisons with bone-lace. The few years which followed, however, saw rapid advances though almost solely at the hands of two investigators, *Malpighi* in Italy and *Grew* in England. These two together laid the foundation of all that was known concerning cellular structure for the next hundred years. *Grew* in particular, though his presentation lacked the tasteful elegance of *Malpighi*, produced a mass of minute detail on the anatomical features of plants, and we shall confine our attention to him for that reason. Among the many cell types he saw and figured for the first time (he was the first to use the term parenchyma for instance) he gave early attention to the walls of vessels. On mechanical treatment of these he found them to unwind like flat ribbons and of these ribbons he says (1682) (Plate I):

> . . . the Vessles, oftentimes, unroave in the form of a Plate. As if we should imagine a piece of fine narrow Ribband, to be woun'd spirally, and Edg to Edg, round about a Stick; and so, the Stick being drawn out, the Ribband to be left in the Figure of a Tube, answerable to an Aer-Vessel. For that which, upon the unroaving of the Vessel, seems to be a Plate, or one single Piece, is, as it were, a Natural Ribband, consisting of several pieces, that is, a certain number of Threds or Round Fibres, standing parallel, as the Threds do in an Artificial Ribband. And as in a Ribband, so here, the Fibres which make the Warp, and which are Spirally continu'd; although they run parallel, yet are not coalescent; but contained together, by other Transverse Fibres in the place of a Woof.

He became convinced that all other cell types follow this structure, and concluded in general that the threads in parenchyma cell walls lie horizontally while those of fibres lie vertically. Let us notice particularly the fineness to which he considered these threads could be split.

> So in the Pith of a Bulrush of the Common Thistle, and some other Plants; not only the threds of which the Bladders; but also the single Fibres, of which the Threds are composed; may sometimes with the help of a good Glass, be distinctly seen. Yet one of these Fibres, may reasonably be computed to be a Thousand times smaller than an Horse-Hair.

This latter estimate can hardly be accepted since the fibres would then have been of the order of 0·1 or 0·2μ in diameter. It does seem reasonable to assume, however, that *Grew* had seen threads grading in fineness down to the limits observable. Some two hundred years later *Sachs*, the foremost plant physiologist of his time, was to ridicule these suggestions made by *Grew*; yet it is very instructive to examine his figures, of which one is presented in Plate I, in the light of modern observations with an electron microscope (Frontispiece). It is always easy, of course, to read modern ideas into older and vaguer writings, but here *Grew* expresses himself so unequivocally that one can hardly avoid the conclusion that this interpretation, in terms of what we would now call fibrils, was inspired vision. We are to see the idea of fibrillar structure turning up again and again in the years that followed, both in the wall and in the protoplasm, and equally often being ridiculed. *Grew* was undoubtedly an acute observer; among other things, he realized that the walls of parenchyma cells were complete, without perforations, a point