WARWICK and WILLIAMS

GRAY'S ANATOMY

35th British edition

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35th British edition

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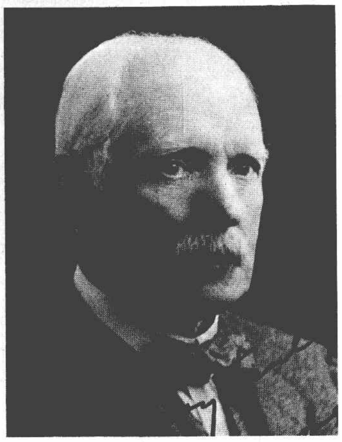

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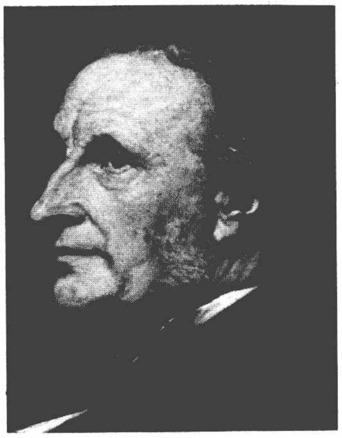

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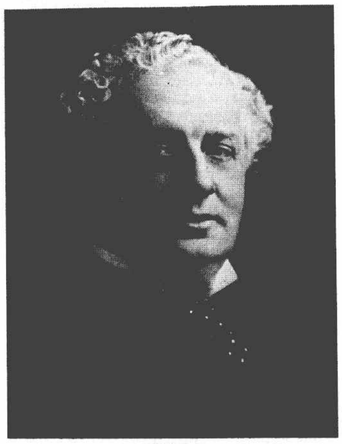

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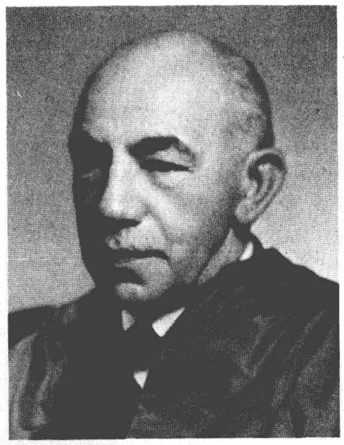

T. B. Johnston 1930–1958

Henry Gray, 1858–1860, seen here in the Dissecting Room of St. George's Hospital 1860

J. Whillis 1942–1954

D. V. Davies 1958–1967

Francis Davies 1958–1962

PREFACE

When our predecessor, Professor David Vaughan Davies, began his preface to the last edition, his first words were to regret the death of his co-editor (Professor Francis Davies) and to acknowledge, with characteristic generosity, the latter's editorial virtues. It is now our equally saddening task to record the death of an editor and friend for whom we shared, with so many others throughout and beyond the confines of human anatomy and medicine, a deep respect both as a scientist and teacher, and as a man of many accomplishments outside his profession. During a period of fifteen years he brought to this editorship the same unyielding standards of scholarship which he applied so outstandingly in his own discipline and school. For both of us his death had also immediate personal associations, for one (P.L.W.) had enjoyed twenty-five years as his student, colleague and companion, and for a number of years acted as his indexer, while the other (R.W.)—frequently a co-examiner—was expecting him on the second day of an examination of our own students when he was so suddenly stricken. We both regard it as an honour to carry forward his editorial obligations.

At the time of his death Professor Davies had completed a small number of revision notes, and these and his collection of references have been valuable to us. However, the decision had already been taken to modernize the format of this volume, with a complete resetting of the text; and it was therefore opportune to undertake a more extensive revision than would have been otherwise possible. The original role of *Gray's Anatomy* as a treasury of 'descriptive and applied' systematic human topography has become amplified through more than a century of usefulness by the early addition of histology and embryology, and by the gradual development of introductory sections to the various 'systems'. To many readers, both graduate and undergraduate, this elder textbook has, however, represented *in excelsis* the field of naked-eye or *dissectional* anatomy. We have neither disturbed nor curtailed this aspect of the volume: rather have we added to it—by the correction of errors, the addition of a host of new observations, the inclusion of hundreds of new references to cover details beyond the scope of even a large textbook, and by reinstatement of variations in respect of many structures. On the other hand we have endeavoured to reduce prolixities of language, as far as the shortened period of revision remaining to us has permitted; no page has escaped such attention, frequently extensive in degree. A considerable saving of space has been thus effected—to offset large additions of new writing and to keep this new edition within a single volume. To rewrite the whole text would have been an impossibly lengthy task, and there has inevitably resulted an increase in size. Subsequently we hope and intend to render all of the established text in a simpler and more succinct style, but to do this throughout with no loss of factual detail is a massive undertaking, and for our limited success in this regard we ask our readers' forbearance. Moreover, we were convinced that other tasks were more urgent and important.

Particularly in this century, the conviction has increased amongst anatomists that isolated observation and description is not enough, and that an experimental approach to problems of structure is as necessary as in other biological sciences. In addition, the great advances in technique—especially in the study of finer detail, in living and developing organs, tissues and cells—have enlarged the scope of anatomy far beyond the parent stem of macroscopic structure. These advances have engendered a spate of new specialities, such as histology, cytology, ultrastructure, embryology, neurology, electromyography, kinesiology, ergonomics, and so on, to a degree dependent only upon the choice of individual minds and the canalization of techniques. The expanding scope of structural knowledge and the exacting demands of more elaborate techniques do indeed dictate such specialization; but all such knowledge remains a continuum—except insofar as extensive gaps of ignorance and uncertainty persist. Unfortunately, and perhaps particularly in the medical sphere, the compartmentalization of anatomy into several disciplines or subjects—with attendant titles, individual chairs, and even separated departments—tends towards disintegration. To study some such region as a limb, in all its proportions, activities, and even evolution, and then its major structures—bones, joints, muscles, vessels and so forth—and to proceed to the microscopic, ultrastructural and ultimately biochemical details of its tissues and cells, appears to us a continuous process, and most desirably so to a balanced education for medicine, however elementary the standard. Unfortunately, these different levels of organization and function are perforce usually considered in separate laboratories, departments, lectures and books.

The defects of this compartmentalization are widely recognized, and have resulted in much effort to 'integrate' teaching. In this persuasion we have re-arranged certain contents of this volume, and in particular have transferred most of the existing section of histology to the appropriate systems. Hence, in *Myology* will be found not only a systematic description of the muscles of the human body, but also of muscle as a tissue. Moreover, there are certain general considerations such as, in this instance, the variable form and the mode of action of muscles and accessory structures—tendons, aponeuroses, bursae, and the like—which have already in recent editions been set out in introductory sections. It is precisely in these generalized aspects of human anatomy that the greatest interest often lies, attracting the major volume of research. We have concentrated special attention upon these sections, which are the more difficult to keep in accord with current progress in research. For this reason, and because the *significance* of structural data is more apparent in generalizations, we have found it necessary to rewrite all such introductory sections and to extend them—to a marked degree in most instances.

The accelerating tempo of enquiry in all respects of structure has a dual effect: there is not only a continuous correction and, more especially, accumulation of data, but also in the main a sharpening awareness of defects in knowledge and deficiencies in its interpretation. It is our belief that ignorance and uncertainty should be more prominently stated in textbooks than they usually are. We have tried to imbue this new edition with rather more of this attitude, not merely in introductory sections, but throughout the systematic text. Where the actions of a muscle are not convincingly demonstrable by direct observation or experiment, we believe uncertainty should be admitted; and where, for example, intricate central nervous organization has been investigated in another animal—perhaps quite remote from man—we consider that the need for caution in extrapolation to mankind should, in a textbook of human anatomy, be clearly appreciated.

It would be burdensome to categorize the changes and additions in this edition; approximately seven hundred pages of completely new writing have been contributed, covering all systems and a wide spectrum of topics. Doubtless our efforts have been uneven; we have, for example, not been able to revise some aspects of cardiac anatomy as thoroughly as we wished, but these and other defects will be remedied in the next edition. While hoping that many will welcome the substantial changes and additions in histology (and especially ultrastructure), in the sections on the teeth (completely rewritten), joints, muscles, lymphatic system, nervous system, special senses and endocrine organs, we also hope that our readers will freely and constructively criticize our mistakes, excesses and deficiencies. To keep abreast of all the new work reported is a formidable undertaking, and we trust that no one will hesitate to inform us of our shortcomings in this or any other regard.

In one particular this edition is unique; for the first time since the first edition, in 1858, this, the *direct* descendant of the original '*Gray*', will be available in the United States side by side with the American scion, which has also persisted through almost an equal period, having begun in 1859 as a reprint of the first edition, but having diverged markedly in its evolution from the direct British descendant. The American parallel version ceased to refer to the British senior heir as long ago as 1896, though preserving the name of Henry Gray on its title-page. With subsequent editions, and particularly this, the divergence has become so great that the two books cannot be regarded as parallel versions; each has its own character.

Our editorial labours have been lightened by much help from others. Doctor Lawrence H. Bannister has contributed the new section on cytology and many of the histological and ultrastructural passages in the sections devoted to myology, neurology, and splanchnology. Doctor Jeffrey W. Osborn has recast the section on dental anatomy. Doctor Susan M. Standring has prepared the bibliography, which appears as a new feature at the end of the text, and has meticulously supervised all reference material. Doctor E. Lowell Rees has not only undertaken the complex revision of an expanded index, but has also provided many special dissections, histological preparations and advice. However, the majority of the revision remains the work of the editors, who are wholly responsible for any errors of judgment, incorrect terminology, omissions, misquotations, or lack of clarity throughout the volume. With the complete resetting of the text, index, illustration captions and tabbing, and the addition of a new bibliography, it is inevitable that, despite prolonged and repeated proof reading, some typographical errors will have eluded us; for these we apologize.

In accord with the comprehensive textual changes in this edition, the illustrations have also received much attention. More than 200 of the 1,305 figures of the 34th edition have been removed, with the addition of over 600 new items; thus, in this 35th edition almost a third of the illustrations are new. Moreover, new blocks have been prepared for all illustrations retained—from the original artwork wherever possible. Apart from those radiographs and reproductions from external sources, acknowledged below, all new illustrations have been prepared in our Medical Centre. We are much indebted to Doctor Aszal Riaz and Doctor John D. Dow (Department of Diagnostic Radiology) and to Mr. Kenneth Twinn and Mrs. Joy Taylor (Department of Physics) for much help with radiographs. In our own department Doctors E. Lowell Rees and Michael C. E. Hutchinson have produced many special dissections and other preparations, assisted in this by Doctors Andrew M. Seal and William J. Owen. Most of these have been photographed by Mr. Kevin Fitzpatrick, our photographer, to whom we are much indebted. Mr. Derek Lovell and Mr. David Ristow have provided skilled technical assistance in respect of electron microscopy and histology. Many other workers on our staff, past and present, have also helped with illustration material, including Doctors Mary Dyson, Murray Brookes, Karen Hiiemae, Wimal Jayaratnam and Kenneth J. W. Taylor; Doctors David R. Turner and Roy O. Weller (now in Pathology), Doctor David N. Landon (now in the Department of Neurobiology, National Hospital for Nervous Diseases, London), Doctor Eric W. Baxter, Mr. Eric C. Tatchell and Miss Hilary Phillip (Department of Biology) and Doctors J. P. Black and P. Barkhan (Department of Haematology) have all afforded us generous aid with preparations for photography. We also gratefully record the expert help of our School's Librarian, Miss Jean M. Farmer and her willing staff.

Mr. S. W. Woods had already prepared six new illustrations (chiefly in embryology), with the same high standards with which he embellished several previous editions while serving Professor Davies. Most of the new artwork, however—amounting to about 210 items—has been carried out by our colleague, Mr. Richard E. M. Moore, D.F.A.Lond., M.M.A.A., member of l'Association Internationale pour l'Etude de la Mosaique Antique, and Fellow of the Royal Society of Arts. His combination of meticulous draughtsmanship, a most unusual ability to comprehend the scientific intent of projected illustrations, and his extraordinary patience and stamina throughout two and a half years of continuous effort, have made our collaboration most fruitful and enjoyable.

Many other authorities in various fields have allowed us to reproduce, copy or adapt illustrations from papers and monographs, or have made special materials available for photography. It is a pleasure to acknowledge the generosity of Professor Janos Szentágothai (University of Budapest), Doctor Elizabeth Crosby (University of Michigan), Doctor W. J. W. Sharrard (University of Sheffield), Doctor Michael J. Hogan, Doctor Jorge J. Alvarado and Mrs. Joan E. Weddell (University of California), Doctor Alan M. Laties (University of Pennsylvania Medical School), Mr. Emanuel Rosen (Royal Eye Hospital, Manchester), Doctor N. A. Locket (Institute of Ophthal-

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We have had the benefit of special advice from many of the authorities acknowledged above, and in addition from Professor M. A. MacConaill (University College, Cork), Professor Jack J. Pritchard and the late Doctor James H. Scott (University of Belfast), Doctor F. Torrent Guasp (University of Barcelona), Professor John Z. Young (University College, London), Mr. D. G. Wilson Clyne, Professor Patrick D. Wall (University College, London) and Professor J. V. Basmajian (Emory University, Atlanta). Among colleagues in other departments in our centre we are especially indebted to Doctor R. T. Grant (late of the Department of Experimental Medicine) and Professor Paul E. Polani and his staff (Department of Paediatric Research) for much help respectively in regard to arteriovenous anastomoses and genetics. Similarly we have had the advantage of advice from many other colleagues in their own specialities, including Doctor Sidney Liebowitz (Immunological Pathology), Doctor John R. Henderson (Physiology) and Doctor David Watts (Biochemistry).

Although we have striven to acknowledge with punctilio the many publishers of scientific journals and books who have allowed us, with customary generosity, to use copyright material, we trust that any neglect in this respect of which we may have been guilty will be forgiven in the same generous spirit.

Throughout the ardours and pressures of this ambitious revision we have enjoyed the most cordial relationship with our publishers and printers, who have both given us the greatest freedom and encouragement. In particular we wish to mention Mr. John A. Rivers of Churchill, and Mr. William G. Henderson, Mr. Gerald J. Hooton and Mr. Alfred S. Knightley, of Churchill-Livingstone, who have been our companions in many anxious, sometimes convivial, and always protracted discussions.

We are most grateful to our departmental secretaries, Miss Margaret Collins and Mrs. Patricia Elson, for much sporadic and demanding help, and to our official secretarial assistant, Mrs. Peter Williams, who has patiently translated innumerable notes and drafts into immaculate typescript for the printers.

It is customary to eulogize the patience of wives—faint praise which is scarcely *galante.* Far from tolerating our preoccupation, our wives have supported us unfailingly with a true and critical interest and sympathy in our labours. To them and all our friends and colleagues, who have helped more than they know to sustain our enthusiasm, we remain profoundly grateful.

PETER L. WILLIAMS and ROGER WARWICK

HENRY GRAY F.R.S., F.R.C.S.

Since readers of *Gray's Anatomy* will be interested to learn something of the original author, Henry Gray, the following information as to his career has been extracted from an article which appeared in the *St. George's Hospital Gazette* of May 21st, 1908.

Gray, whose father was private messenger to George IV, and also to William IV, was born in 1827, but of his childhood and early education nothing is known.

On the 6th of May, 1845, he entered as a perpetual student at St. George's Hospital, London, and he is described by those who knew him as "a most painstaking and methodical worker, and one who learnt his anatomy by the slow but invaluable method of making dissections for himself".

While still a student he secured, in 1848, the triennial prize of the Royal College of Surgeons for an essay entitled, "The origin, connexions and distribution of the nerves to the human eye and its appendages, illustrated by comparative dissections of the eye in other vertebrate animals."

At the early age of twenty-five he was, in 1852, elected a Fellow of the Royal Society, and in the following year he obtained the Astley Cooper prize of three hundred guineas for a dissertation "On the structure and use of the spleen."

He held successively the posts of demonstrator of anatomy, curator of the museum, and lecturer on anatomy at St. George's Hospital, and was in 1861 a candidate for the post of assistant surgeon. Unfortunately he was struck down by an attack of confluent smallpox, which he contracted while looking after a nephew who was suffering from that disease, and died at the early age of thirty-four. A career of great promise was thus untimely cut short. Writing on June 15th, 1861, Sir Benjamin Brodie said, "His death, just as he was on the point of obtaining the reward of his labours . . . is a great loss to the Hospital and School."

In 1858 Gray published the first edition of his *Anatomy*, which covered 750 pages and contained 363 figures. He had the good fortune to secure the help of his friend, Dr. H. Vandyke Carter, a skilled draughtsman and formerly a demonstrator of anatomy at St. George's Hospital. Carter made the drawings from which the engravings were executed, and the success of the book was, in the first instance, undoubtedly due in no small measure to the excellence of its illustrations. This edition was dedicated to Sir Benjamin Collins Brodie, Bart., F.R.S., D.C.L. A second edition was prepared by Gray and published in 1860.

The portrait of Gray published in the present section is a reproduction of one which appeared in the *St. George's Hospital Gazette* of May 21st, 1908, where the original is described as being "a very faded photograph taken by Mr. Henry Pollock, second son of the late Lord Chief Baron Sir Frederick Pollock, and one of the earliest members of the photographic society of London".

INTRODUCTION

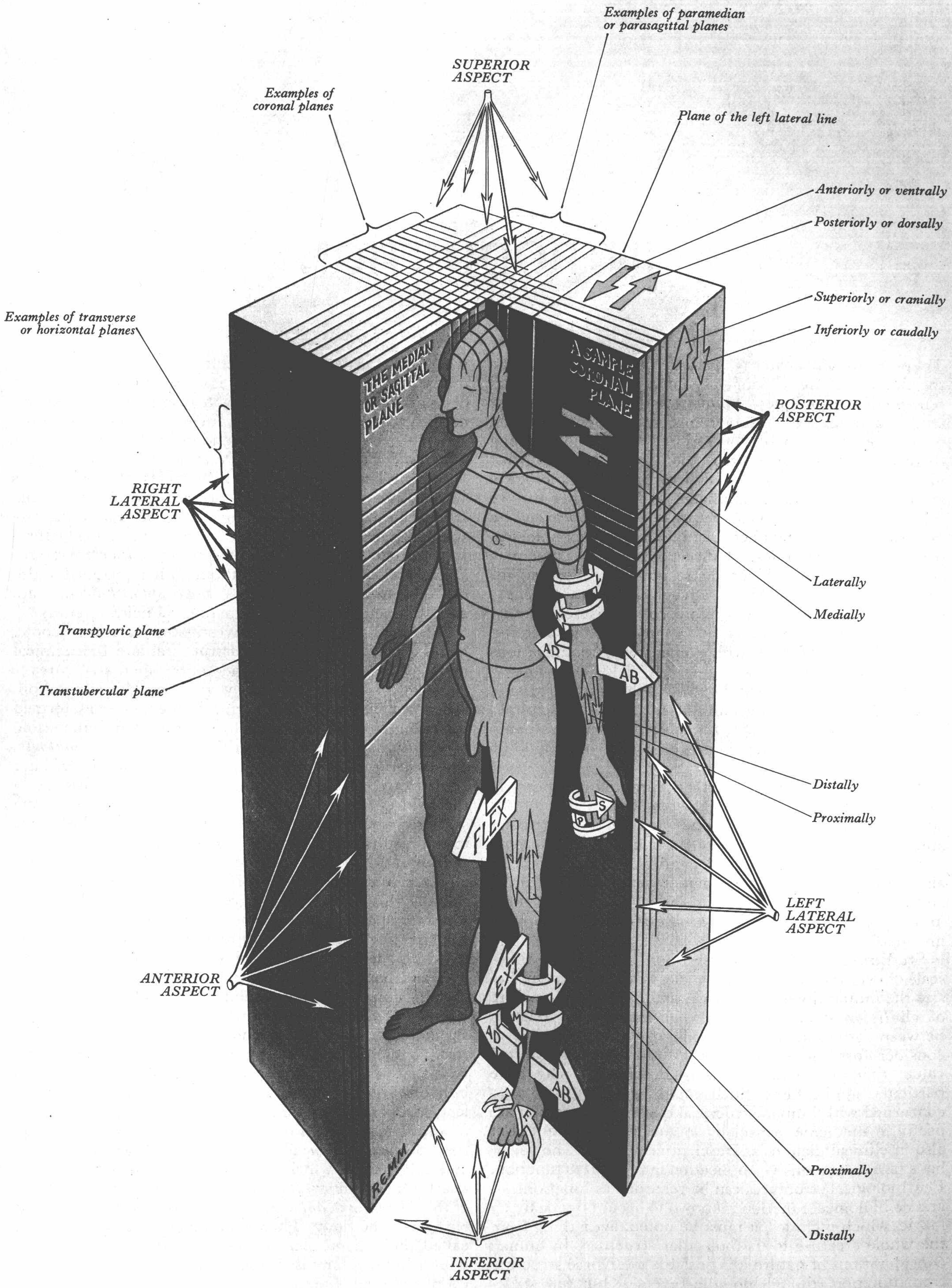
To perform an 'anatomy' was to make a 'dissection'; the two words are no longer synonymous. *Dissection* has remained a technique; *Anatomy* has become a field of study—a corpus of observations, still dependent upon technique, but capable of rational correlation among themselves and with other biological studies. Most narrowly, anatomy may be the investigation of biological structure—in plants or animals—with no other motive than description of form. Even so, such *topographical anatomy* has not remained insulated from technological progress; the usefulness of direct visual dissection persists, but its relatively crude results have become incalculably augmented by the advent of light microscopy, micro-dissection, electron microscopy, histochemistry, radiology, autoradiography, and many other techniques. The application of these, with ever-growing modifications and extensions, has revealed great new fields of discovery. Some, such as *histology* and *cytology*, the study of tissues and cells, are true extensions of the parent discipline; others—*electron microscopy*, *histochemistry* and *autoradiography*—are merely techniques capable of providing particular types of data.

The theme of growth and differentiation, both in individual development or *ontogeny* and in that of the species or kind—*phylogeny*—has led to the particular studies of *embryology*, *comparative anatomy* and *morphology*. Embryology, the study of individual development, also embraces problems of gametogenesis, fertilization and embryonic nutrition, and in the investigation of these in relation to mankind, *comparative embryology* has proved invaluable.

Studies of growth, whether upon the epochal time-scale of evolution or the rapid cycles of ontogeny, emphasize the mutability of structures; and the dynamic nature of all *living* structures entails an inescapable relation between form and function. It is, of course, possible to consider form in isolation, an exercise of most limited value, though the data of pure description may have particular applications. Such *applied anatomy* is usually concerned with human structural observations which are useful in medicine, especially in surgical technique, but also in clinical diagnosis. Descriptive anatomy, however, has a far more extensive application in relation to function. Few biological structures can be regarded as functionless, and no biological function is known to occur outside living fabric, which includes, it must be noted, everything from the whole creature to its molecular structure. In human considerations of nature it is possible to divorce structure from function (though not the reverse); but few structuralists are disinterested in function. The mere fact that topography can be described upon a *regional* or *systematic* basis necessarily entails functional considerations, for while the former is of particular vocational interest in medicine, *systematic anatomy* is based upon recognition of function. The *locomotor system* embraces structures directly concerned with movement—skeletal elements, articulations and ligaments, and muscles, the study of which may be formalized as *osteology, arthrology* and *myology*. Similarly, *neurology*, which treats of the nervous system, including its sensory organs, and *angiology*, the study of cardiovascular arrangements of organs and tissues, are correlated as much by function as by structure. It is equally clear that the *respiratory*, *alimentary*, *urogenital* and *endocrine systems* (though often grouped under the unilluminating anatomical term *splanchnology*), are clearly functional as well as anatomical fields of study.

All such 'systems' are investigated at macroscopic, histological, cytological, ultrastructural and biochemical levels. Furthermore, experimentation upon structures—classically illustrated by early work on the circulation, reflex behaviour and endocrine influences—has formed the vanguard of anatomical research, with increasing momentum in this century. *Experimental anatomy*, *experimental cytology* and *experimental embryology*, have contributed greatly to the advancement of knowledge in the field of human anatomy. Throughout the following sections, where relevant, numerous allusions will be made to the results of such experimental studies.

Descriptive anatomy obviously demands an internationally acceptable repertoire of names for structures, and there is also a need for an agreed convention upon terms for their spatial relationships (*see* accompanying figure). For this purpose the human body is assumed to be in its usual bipedal or erect position with the arms pendent and eyes and hands facing forwards. This position is open to certain objections; for example, the arms are rotated laterally at the shoulder joints and the forearms are fully supinated and are thus not in their usual position of rest (*see* p. 315). Moreover, comparisons of human anatomy with that of other animals, which are mostly quadrupedal in habit, are confronted with some difficulties. Nevertheless, the erect 'anatomical position' does provide an unambiguous system of correlation for man. In this posture the *median plane* divides the body vertically into right and left halves which are approximately symmetrical, apart from certain visceral details. The superficial contours of this plane form *anterior* and *posterior median lines* on the surface of the body. The median plane is also frequently called the *sagittal plane* (after the cranial suture of that name), but this term is also sometimes applied to any vertical plane parallel to the median, and it is hence preferable to refer to the latter as *paramedian* or *parasagittal planes*. Vertical planes at right angles to the median plane are usually described as *coronal planes*, after the coronal



The terminology widely used in descriptive anatomy is illustrated in the figure above. The abbreviations on the solid arrows: AD—adduction, AB—abduction, FLEX—flexion (of the thigh at the hip joint), EXT—extension (of the leg at the knee joint), M and L—medial and lateral rotation, P and S—pronation and supination, I and E—inversion and eversion.

suture (p. 261). To complete the three-dimensional reference grid, *horizontal planes* are those which traverse the body at right angles to both the median and coronal planes.

The adjectives *anterior* and *posterior* are applied to the front or back surfaces of the body, including the limbs. Synonyms for these are *ventral* and *dorsal*, which, since they can be applied equally to quadrupeds, are sometimes preferable. All these terms are in fact used more extensively to specify the aspects or surfaces of individual structures *within* the body, and often to denote their relative positions. Thus—the heart is posterior (or dorsal) to the sternum, the posterior surface of which is close to the anterior (or ventral) aspect of the heart. Similarly, *superior* (or *cranial*) and *inferior* (or *caudal*) are adjectives qualifying the positions of structures in the vertical sense. Of the two venae cavae one is *superior*, *cranial* (headward) with respect to the other which is *inferior*, *caudal* (tailward) in position. (Incidentally, the *superior* and *inferior* venae cavae are *anterior* and *posterior* in the quadruped, but the terms cranial and caudal, which obviate this confusion, have not been adopted in this instance in mankind.) To define the relation of structures to the median plane the terms *medial* and *lateral* are employed: the heart is *medial* to the lungs, which are *lateral* to it, and so on.

Any number of oblique planes can be imagined, and likewise the spatial relations of structures are not always so orthogonally simple as anterior, posterior, superior, medial, and so forth. Combined terms are therefore sometimes used for intermediate positional arrangements, such as anterolateral (ventrolateral), postero-inferior (dorsocaudal), etc., and these are self-explanatory. In the limbs certain variant terms are current—and since these do not involve reference to the 'anatomical position', they have some value in obviating confusion. Thus, structures which are superior, and hence nearer the limb root, are dubbed *proximal*; those relatively inferior in position are clearly more *distal*. Anterior and posterior aspects or regions may be described respectively as *flexor* or *extensor* in upper limbs, but the terms do not correspond in the lower limbs, which have undergone a contrasting form of morphological rotation (pp. 123, 315), such that the primitively extensor or dorsal aspect is now anterior. In the forearm, the terms *radial* and *ulnar* are occasional synonyms for lateral and medial, as are *fibular* (peroneal) and *tibial* in the lower limb. *Palmar* and *plantar* are variants for the flexor surface of the hand and foot. Finally, *superficial* and *deep* specify distance from the surface of the body; the somewhat similar terms, *external* and *internal*, are usually applied to the walls of hollow structures such as the head, thorax and abdomen and various viscera, including vessels and ducts.

It will be noted that throughout the text, the units of linear measurement are those of the Système Internationale (S.I.). These include the *micrometre* (micron, μm) (1 μm = 1×10^{-6} metre; 1000 μm = 1 mm), and the *nanometre* (nm) (1 nm = 1×10^{-9} metre; 1000 nm = 1 μm). Accordingly the use of the Ångstrom unit (Å = 1×10^{-10} metre; 10 Å = 1 nm) has been discontinued.

We have, in the main, continued the policy of adherence to *Nomina Anatomica* (3rd ed., by G. A. G. Mitchell, Excerpta Medica Foundation, 1968). Familiar variants and some eponyms have also been included where deemed advisable. We have also attempted to follow the proposed *Nomina Histologica* and *Nomina Embryologica*, prepared by the subcommittee of the International Anatomical Nomenclature Committee and presented to the Eleventh International Congress of Anatomists held in Leningrad in August 1970, at a plenary session at which these two drafts were approved. Unfortunately, both contain many common terms at variance with each other, important omissions, and some terms which have aroused belated dissatisfaction. Moreover, some ultrastructural details were overlooked, often obliging us to follow current practice, itself confused by synonyms and vernacular jargon. Therefore, we have regarded the recommendations of *Nomina Histologica* and *Nomina Embryologica* as less obligatory than *Nomina Anatomica*, which has been exposed to much more critical revision. Nevertheless, the latter does not meet all contingencies, especially in the central nervous system; it also still retains some intrinsically unsatisfactory terms. Notwithstanding, we have continued to adhere to most of these, though we have preferred not to handicap a whole section with the title of 'Syndesmology', for which 'Arthrology' has priority in time and in clarity of communication. We have also disregarded official disapproval of the hyphen, employing it frequently, though not perhaps consistently, to separate vowels likely to be compounded as diphthongs. Even in Europe and the Americas, most university students fall short of even 'a little Latin and no Greek', and this takes no account of the large number of schools outside these continents. Consequently, it must be assumed that a large majority of undergraduates and younger postgraduates find words of Greek and Latin derivation unfamiliar, and that this difficulty will increase in the future. Even the Latinist may find *bulbourethral* bothersome; *ou* is a diphthong not only in English but in other European languages; similarly, *sacro-iliac* aids in both pronunciation and understanding. The diaeresis is often frowned upon these days: but while *cooperate* perhaps no longer requires hyphen or diaeresis, *spermatozoön* and *oöcyte* are awkward words. We believe that an increasing number of readers need this help if unfamiliar words are to be pronounced with confidence, to the betterment of international communication. Officially, all anatomical terms are expressed entirely in Latin; but there is little objection to translating *extensor digitorum superficialis* into 'the superficial extensor of the digits', and this kind of vernacularization is practised in many countries, especially in Europe. Human anatomy, however, is a worldwide science, and the Latin terms are recognizable everywhere. A little effort with the first few pages of an elementary Latin grammar will quickly unveil the mysteries of masculine and feminine plurals, genitives and so on—a small personal concession to international understanding, in a world which must surely welcome unequivocal terms, even if based on a 'dead' language—perhaps all the more acceptable because no longer a contender in petty national rivalries.

REPRINT CORRECTIONS

The favourable response to the 35th edition, having occasioned an early reprint has provided an opportunity to rectify not only the short list of errata previously included but also to amend a number of typographical and other errors subsequently noted.

Three illustrations have been modified, and Fig. 1.24, p. 23, has been replaced to give a more accurate rendering of the behaviour of chromosomes in meiosis. In this connection it is our pleasure to acknowledge the advice and help of Dr. Keith Jones, Keeper of the Jodrell Laboratory, Royal Botanic Gardens, Kew, Surrey.

Finally, we thank all those who have written, since the appearance of the 35th edition, to help by pointing out errors and drawing attention to new observations. We greatly welcome such constructive criticisms and suggestions, and while only a part of these could be encompassed in this reprint, the remainder and all future comments will prove invaluable in the preparation of the next edition.

CONTENTS

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CYTOLOGY

Introduction

All living organisms show distinctive patterns of organization with respect to time and space. Temporally, these involve orderly sequences of physical and chemical events which are conventionally described in terms of movement, metabolism, growth, differentiation, reproduction, reactivity to external change, and evolutionary progression (see also pp. 54–63). Spatially, these sequences are not haphazard, but arranged in a complex structural framework which determines their direction and their coordination. The integration of these phenomena, and their dependency upon environmental energy sources, constitutes what we call 'life' in the biological sense.

The microscopic study of living things concerns such intimate organization of their life processes, and since their ultimate structure is on a molecular scale, various special means have to be used to analyse them.

The *biological molecules* are arranged in complex aggregations playing specific roles in the living process; these aggregations are the *organelles*; multiples of different types of organelles are further combined in specific membrane-bound units, or *cells*. The cell is an important unit, since it is the smallest aggregation to show all the major features of living organisms mentioned above. In some simple organisms, e.g. bacteria, protozoa, the cell is also the whole organism, and capable of an independent existence. In more complex organisms, multiples of cells are grouped together, with spatial differentiation of different regions to perform particular roles, such as digestion, reproduction, and so forth. These may have the form of simple cooperative layers of cells, or *tissues* (a term introduced by Bichat (1771–1802) for the different groups of cells, muscular, nervous, and so on, in post-mortem man). Multiples of tissue layers are further grouped together to carry out more complicated co-operative actions; these constitute the *organs* of the body. Finally, the whole consortium of organs, coordinated and unified by specialized communication systems, is capable of the directed and self-directing activities which characterize human life. To analyse adequately the biological basis of such activities, it is necessary to understand its parts, and the subjects of *cytology* and *histology* have as their aim the clarification of these at the microscopic level.

Advances in cytology, as in all scientific pursuits, have awaited technical progress.[1] The early microscopes of the sixteenth and seventeenth centuries only allowed examination of large cells, such as those of protozoa and plants, and the English microscopist Robert Hooke was the first (1665) to use the term 'cell', which was applied by him to the compartments of cork wood. With the refinement of the optical microscope by Abbé and Leitz, and the introduction of staining and sectioning techniques in the late nineteenth century, the field was set for the rapid expansion of cytology and histology as a serious discipline. The further introduction of bright field, phase contrast, and interference microscopy in the 1930–50 period allowed direct detailed observation of living cells. By this time histology had lost some of its initial impetus, but the growth of electron microscopy, increasing resolution by three orders of magnitude, together with the development in biochemistry of cell-fractionation techniques, and of methods of biophysical analysis of molecules, allowed observation and interpretation at the molecular as well as the cellular level.

The concept of the cell is a convenient starting point; each cell comprises a discrete body enclosed by a membrane which 'separates' it from the environment, and contains the living material or *protoplasm*, included in which is one or more *nuclei*. The protoplasm is a heterogeneous aqueous phase in which are found the chemical machinery for metabolic processes and the material of heredity, which specifies the character of the cell from one generation to the next. In some very primitive cells (*prokaryotes*) such as bacteria and actinomycetes, the hereditary and metabolic materials are not separated from each other; in more complex cells (*eukaryotes*) the hereditary instructions are almost entirely sequestered in a special membrane-bound region, the *nucleus* (*karyon*), which is distinct from the remainder of the cell, the *cytoplasm*.

The protoplasm of cells consists chemically[2] of large and small organic molecules, and inorganic ions in aqueous solution; water comprises about 70 per cent of the total cell volume. Of the large organic molecules, the most abundant are those of carbohydrates, lipids, and proteins which provide important structural materials and metabolic machinery in the form of enzymes. Nucleic acids are also important in directing the activities of the cell. The cytoplasm of each cell is relatively unstable in its composition, and must be held ionically and osmotically within a narrow range for the effective functioning of its metabolic apparatus. However, each cell is also in a constant dynamic interchange with its external environment (p. 54), including other cells, and the continuous expenditure of metabolic energy is needed for a cell to maintain its steady state. If this is lost, the cell dies.

Most mammalian cells lie within the size range of 5–50 μm in diameter. Although many cells possess only one nucleus, some, formed either by fusion of uninucleate cells (*syncytia*), or by nuclear division without corresponding cell division (*plasmodia*), are multinucleate. The latter may achieve a much larger volume than a uninucleate cell, although the ratio of nuclear to cytoplasmic volume is similar.

One great advantage of cellularity is that diffusion of materials between and within the living units is relatively rapid, so that control systems can operate rapidly within a mass of cells, and also that gaseous, nutritive, and excretory exchange processes can keep pace with the high demands of active cells. In this regard it should be noted that as a cell increases in size, its surface area (available for diffusion), increases by the square of the diameter, whereas the volume of protoplasm increases by the cube; this relationship puts a limit on the maximum size a cell can attain[3] (see also p. 58). Preservation of cellularity also allows the emergence of different cell types welded together into functionally distinct tissues.

In the living state most individual cells are greyish in appearance when examined by transmitted light, and each is bounded by a deformable elastic membrane. Physical measurements of protoplasmic viscosity[4] indicate that it is a heterogeneous material which can be highly viscous (the *gel* state), or relatively non-viscous (the *sol* state), or both states may coexist and interchange. Metabolic processes can profoundly alter these physical characteristics.

Motility is also a characteristic of most cells. This may take the form of intracellular streaming, with the movement of materials within the cell,[5] or may produce movement of the whole cell by the progressive formation of finger-like projections (*pseudopodia*), or other extensions, of the cell surface. Cell movements are also involved in the multiplication of cells by division to form two—*binary*

[1] C. Singer, *A Short History of Biology*, Clarendon Press, Oxford. 1931.
[2] W. Bloom and D. W. Fawcett, *A Textbook of Histology*, Saunders, London. 1968.
[3] W. D'Arcy Thompson, *Growth and Form*, Cambridge Univ. Press. 1942.
[4] L. Picken, *The Organisation of Cells*, Clarendon Press, Oxford. 1960.
[5] R. Allen and N. Kamiya (eds.), *Primitive Motile Systems in Cell Biology*, Academic Press, New York. 1964.