

**THE
ORGANIZATION
OF CELLS
AND OTHER
ORGANISMS**

L. E. R. PICKEN

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THE ORGANIZATION OF CELLS

AND OTHER ORGANISMS

BY
LAURENCE PICKEN

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黄绮教授惠赠

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PREFACE

THIS book is a work of compilation. It is addressed to postgraduate students and research workers. Though its scope is by no means limited to a consideration of recent developments, its writing has largely been made possible by the modern practice of publishing specialized reviews of recent work in the separate fields here brought into relation. In some circles, this type of relatively ephemeral review is criticized for its lack of integration. It performs none the less a valuable service, and will continue to do so until the practical need for a means of access to past work—a means more direct than the voluminous printed word—forces the sciences to abandon current conceptions, tacit and overt, of the aims and purposes of scientific publication. A scientific paper is many things other than a mere instrument serving to communicate to others the nature and results of a limited inquiry. The time may come, however, when the bulk of scientific literature is seen to act as a hindrance to accurate knowledge of the past, and with its coming habits may change.

In the course of this book, I have sought to make plain my indebtedness to reviewers in particular, by drawing attention in a footnote at the beginning of each chapter to the principal books and articles by which I obtained access to the literature of a particular field. Every effort has been made to limit the bibliography rather than to extend it, and the number of entries has been reduced whenever possible during revision. The aim has been to leave a sufficiency of references for credit to be given where it is due, and for the reader to be able to find his way into the relevant literature; the bibliography has no wider aim of completeness.

A major part of my intention has been to illustrate the change and development of concepts, since it is still not widely appreciated that the working biologist is at least as much concerned with concepts as he is with things. In some instances the narrative has dipped briefly into the earlier literature in the hope, perhaps vain, of mitigating belief in the present as an epoch of superior intelligences by demonstrating the considerable age of many current conceptions. But again, I have not sought to be exhaustive in historical bibliography, or even consistent in the use of the historical approach.

I am aware that my coverage of recent publications in English is more complete than that of publications in other European languages, and that my treatment of Russian, Chinese, and Japanese publications, for example, is casual rather than systematic. Although this implies that the bibliography has a strongly Anglo-American bias, I do not think the book is a different book from what it would have been if all languages were equally covered. Indeed, I believe it might have been written in the language of any

one of the major nineteenth-century powers, and based on an almost exclusively national bibliography, without loss in range or restriction in outlook.

Many authors will find that I have but slightly paraphrased their words, or have used their own words in tacit quotation, in writing of their work or reporting their views. In covering a field so large that most topics lie outside the range of first-hand experience, it appeared essential to remain as close as possible to the author's own formulation, rather than to accept the risk of a deforming periphrasis. If I have paraphrased without acknowledging indebtedness, I here and now express that indebtedness, and also a more general indebtedness to all authors who have led me to new aspects of the literature, or who have provided references that might otherwise have been missed.

It is to be expected that such a compilation will contain errors of emphasis, interpretation, or fact. I have tried to reduce their number by seeking criticism from specialists in the various fields of the chapters. From their distinguished names the reader will gain assurance that the number of errors is less than it would have been but for their help. I trust that those readers who find their work misrepresented will kindly inform me of my inadequacies of presentation.

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Except where described as 'original', the text-figures have been re-drawn by Mr. M. J. Wells, who spared no pains in reproducing original shading and texture, and in translating from lithograph or half-tone to line.

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I wish finally to record that this book was completed and the bibliography checked in the incomparable library of the Stazione Zoologica di Napoli.

L.E.R.P.

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 11. 1 a, b, c. Shots from a ciné film of the fall of the nucleolus under gravity through the nucleus of an oocyte of *Echinus esculentus*. The time interval between (a) and (c) is about 3 minutes. The diameter of the nucleus is 70 μ . Unpublished photographs from the negative provided by Professor J. E. Harris. See p. 104.
 - 2a. X-ray diffraction photograph of calf thymus DNA (sodium salt) in the A configuration, at 75 per cent. relative humidity.
 - 2b. X-ray diffraction photograph of DNA from avian tubercle bacilli, at 75 per cent. relative humidity.
 - 2c. Comparison of the X-ray diffraction photographs of (below) unfixed *Loligo* sperm in the intact spermatophore; (above) fibres (prepared from sperm removed from the spermatophore) washed in water, dried and rehumidified at 98 per cent. relative humidity.
 - 2d. X-ray diffraction photograph of wet trout sperm heads. The first intense ring out from the central blackened area corresponds to the first equatorial reflection in (a), (b), and (c). Unpublished photograph by M. H. F. Wilkins and H. R. Wilson (1955).

- No. Photographs (a), (b), and (c) from Wilkins (1957) where a list of collaborators concerned in the preparation of the various specimens will be found (op. cit., p. 184). Photographs provided by Dr. M. H. F. Wilkins. See pp. 108, 109.
12. 1. Chromosome XII entire from *Triturus cristatus carnifex* —/+ heterozygote at the giant loops locus (marked by an arrow.) The opposed arrows mark the centromeres. Unpublished photograph provided by Professor H. G. Callan. See p. 114.
 2. A bundle of air-dried locust sperm in glycerol, photographed in polarized ultra-violet light (2,652 Å) with a reflecting objective. The width of a single sperm head is 0.7 μ . The electric vector is horizontal, and in two quadrants absorption (due to oriented DNA) is strong. Photograph by Wilkins (1953) provided by Dr. M. H. F. Wilkins. See p. 109.
 3. Late zygotene or pachytene in *Chortippus parallelus*—an aceto-orcein testis squash. The lack of definition is characteristic of these chromosomes in zygotene-pachytene-diotene. Unpublished photograph provided by Professor H. G. Callan. See p. 136.
 4. Birefringence of the nuclear membrane in an isolated nucleus of *Triturus cristatus carnifex*. Unpublished photograph provided by Professor H. G. Callan. See p. 111.
13. 1a. Transmission electron micrograph of the nuclear membrane of *Xenopus laevis* isolated in distilled water, fixed for 2 minutes in 0.1 per cent. phosphotungstic acid. Photograph from Callan and Tomlin (1950) provided by Professor H. G. Callan. See p. 111.
 1b. Ultra-thin section of the nuclear membrane of *Trichonympha* (Zoomastigina) showing the appearance of a vesicular, perinuclear cisterna. In some instances the 'pores' seem to be patent; in others closed by a thin membrane. The nuclear contents appear to be finely fibrillar. Unpublished photograph by Dr. A. V. Grimstone. See p. 112.
 2. Prometaphase of mitosis in *Triturus cristatus carnifex* (aceto-orcein tail-tip squash) showing centromeres. Unpublished photograph provided by Professor H. G. Callan. See p. 133.
14. 1 a, b, c. Three stills from a ciné film taken by the late Professor W. Seifriz and projected during a lecture in the Stazione Zoologica at Naples in 1952, showing streaming in the mycetozoon, *Reticulomyxa filosa*. The stills are at intervals of approximately 3 sec. Arrows mark vacuoles moving in adjacent cytoplasmic streams of opposite direction. Unpublished photograph provided by Dr. N. Kamiya from his copy of Professor Seifriz's film. See p. 172.
 2 a, b, c. Protoplasmic thread between two masses of the mycetozoon, *Physarum polycephalum*, forming loops as a result of intrinsic torsion. The photographs were taken at intervals of from 5 to 10 min. Photographs from Kamiya and Seifriz (1954) provided by Dr. N. Kamiya. See p. 175.
 3. Pseudopodium of *Amoeba proteus* photographed between crossed Nicols (with compensation) to show birefringence of the cortex. Unpublished photograph provided by Dr. J. M. Mitchison. See p. 165.
15. 1a. *Discophrya piriformis* before treatment;
 1b. after exposure to a pressure of 10,000 lb. in.² for 31 min. The cytoplasm is rounded up within the expanded pellicle, and some of the tentacles are now curved. Photographs from Kitching (1954a) provided by Dr. J. A. Kitching. See p. 167.
 2a. Transverse section of the gut of a frog tadpole, fixed with sublimate and acetic, stained with haematoxylin and orange-G, photographed in the light microscope.
 2b. The same between crossed Nicols with compensation (1/16th λ mica-plate). Positive birefringence of the cytoplasm with respect to the long axis of the cell. Photographs from W. J. Schmidt (1943) provided by Professor Schmidt. See p. 176.

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15. 3. Cytoplasmic nucleic acid or nucleotides not precipitable by centrifugation. Photograph of a paper chromatogram made in ultraviolet light (2,650 Å). Regions absorbing light of this wavelength appear black. The experimental spot in the middle of the base-line is the clear intermediate cytoplasmic layer from an axolotl neurula centrifuged at 1,000 g, and the spot to the right of this is from the same cytoplasmic layer recentrifuged at 50,000 g. Both show strong absorption by nucleotides or nucleic acids remaining on the base-line; and from both, spots have moved from the base-line with an R_F of 0.18, calculated from the movement of the adenine control—the large spot on the left near the bottom of the photograph. The strong ultraviolet absorption of the spots from the intermediate cytoplasmic layer confirms Brachet's conclusion that early embryos contain a considerable amount of nucleic acid or nucleotide not precipitable by centrifugation. Unpublished photograph from Goodhart (1950) provided by Dr. C. B. Goodhart. See p. 183.
16. 1 a, b, c. Photomicrographs from a ciné film of a fibroblast from a chick embryo (phase contrast) showing the plasticity of the mitochondria. The time interval between (a) and (b) is 1 min.; between (b) and (c) $1\frac{1}{2}$ min. Part of the nucleus and nucleolus is visible on the left-hand margin. Note local and transitory expansions and attenuations, rupture, bending, branching, alteration in refractive index, and displacement relative to the nucleus. The black granules are lipidic droplets. Photographs by J. Frederic and M. Chèvremont (1952) provided by Professor M. Chèvremont. See p. 196.
 - 2a. Transverse section of part of the cortical zone of *Stentor polymorphus* near the adoral region showing mitochondria with tubular internal structure. Note also the complexity of the pellicle, composed of two paired membranes, the outer pair being well separated from the body cytoplasm between the ciliary rows.
 - 2b. These mitochondria also exist in an 'empty' condition, expanded in volume, and with the tubular sub-elements reduced to a peripheral layer. Both conditions, 'normal' and 'empty', are shown in this photograph. Photographs from Randall and S. F. Jackson (1958) provided by Professor J. T. Randall. See p. 201.
 - 3 a, b, c, d, e. Transformation of thread-like mitochondria to spherical vesicles in a preparation of mitochondria from rat liver isolated in 0.44 M sucrose and progressively diluted with distilled water. Mitochondria prepared by Dr. J. B. Chappell and photographed by Dr. A. V. Grimstone. The stages visible may be compared with the diagram by Cleland and Slater (1953). See p. 197.
17. 1. Ultra-thin section of the Golgi region of an exocrine cell from the pancreas of a mouse. The upper half of the photograph is occupied by a single mitochondrion surrounded by α -cytoplasmic membranes. A stack of three or four pairs of γ -cytoplasmic membranes (Golgi membranes) partly bounding vacuolar spaces, in the lower half of the photograph, is the characteristic element of the Golgi region. Below and to the right is a uniformly dense zymogen granule, and to the left a Golgi granule of lower opacity and coarser texture than the zymogen granule, and with a dense surface layer. Photograph from Sjöstrand and Hanzon (1954) provided by Professor F. S. Sjöstrand. See pp. 200, 230, 243, and 244.
 2. Ultra-thin transverse section of a single parabasal of *Trichonympha* (Zoomastigina). The supporting filament occupies the cup-shaped cavity in the upper side of the group of saccules. Note the gradual increase in size of the saccules towards the side away from the filament. In the lower right-hand corner is part of the saccules of a second parabasal. Between the two are a few saccules of the system of α -cytomembranes or endoplasmic reticulum. Unpublished photograph provided by Dr. A. V. Grimstone. See p. 238.
18. 1. Single chromatophore from the egg of *Fucus vesiculosus* seen in ultra-thin section. In this type of chloroplast grana are absent, and the groups of chlorophyll-bearing lamellae extend throughout the substance of the plastid. This structure also occurs in the chloroplasts of the parenchyma sheath in the leaf of *Zea mays*. Photograph from Leyon and von Wettstein (1954) provided by Dr. H. Leyon. See p. 213.

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18. 2. Part of a mesophyll chloroplast from a 3 to 4 weeks old leaf of *Zea mays* seen in ultra-thin section. The denser regions with accurately parallel lamellae are the grana. Note the connexion of these lamellae with the extra-granular lamellae embedded in the stroma. The nature of the dense spherical particles has not as yet been established. Photograph from Hodge, McClean, and Mercer (1955) provided by Dr. A. J. Hodge. See p. 213.
3. Ultra-thin section of a young chloroplast of *Aspidistra elatior* showing a central crystalline body composed of scarcely resolved granules arranged in layers. Note the continuity between the crystal layers and the lamellae of the chloroplast. Photograph from Leyon (1954a) provided by Dr. H. Leyon. See p. 216.
4. Stages in the spontaneous disintegration of chromoplasts of the carrot in aqueous suspension: (a) shows splitting from the edge; (b) suggests the presence of parallel fibrils or strip-like lamellae. Photographs from Straus (1950) provided by Dr. W. Straus. See p. 220.
19. 1a. Phase-contrast photograph (light contrast) of the spindle in a living *Barbulanympha* (Zoomastigina). The spindle has formed between voluminous asters arising at the ends of ribbon-like centrioles. Extra-spindle fibres extend towards the nuclear membrane. Unpublished photograph provided by Professor L. R. Cleveland. See pp. 260, 265.
- 1b. Phase contrast photograph (dark contrast) of chromosomes in *Barbulanympha* attached to the nuclear membrane by their telomeres. Unpublished photograph provided by Professor L. R. Cleveland. See p. 261.
2. Mitotic figures of *Psammochinus miliaris* in polarized light with compensation showing the development of asters and spindle during first cleavage. The first photograph (a) was taken at 50 min after fertilization; the rest succeed as follows: (b) 52 min; (c) 54 min; (d) 55 min; (e) 56 min 20 sec; (f) 57 min; (g) 58 min; (h) 59 min. Photographs from Swann (1951a, b) provided by Professor M. M. Swann. See pp. 264, 265.
3. Micro-X-ray photographs obtained from the several levels of a single human hair root with the X-ray beam at right angles to the axis of the hair and at a specimen to film distance of 1 cm: (a) from the bulb; no fibrillar orientation; (b) immediately above the bulb; fully developed α -keratin pattern, although this region is unconsolidated; (c) the same region after disorientation by heating; the pattern has changed to the dis-oriented β -keratin type; (d) the α -keratin pattern of the fully hardened, S-S-bonded hair above (c). Photographs from Mercer (1949a) provided by Dr. E. H. Mercer. See p. 277.
20. 1. Transverse section through the rostral region of *Trichonympha* showing sections of the flagella lying between two cytoplasmic plates. In these flagella the outer ring of nine fibrils is tangentially double. The nature of the cytoplasmic inclusions has not been established. Unpublished photograph provided by Dr. A. V. Grimstone (1956). See p. 271.
2. Slightly oblique transverse section through the triple row of kinetosomes (basal granules or bodies) associated with the cilia of a single membranelle from the adoral zone of *Stentor polymorphus* (Ciliata, Spirotricha, Heterotricha). Sections of the basal bodies in the upper part of the photograph are more distal, those below more proximal, in level. A distinct central particle (p) is visible in some of the former; on this the central filaments of the cilium terminate. The particle rests on a septum (s), visible in some of the sections. Below this, the kinetosome appears to consist of the outer filaments of the cilium. Photograph from Randall and S. F. Jackson (1958) provided by Professor J. T. Randall. See p. 273.
3. Section parallel to the plane of the scopula in *Campanella umbellaria* (Ciliata, Peritricha), passing through the array of kinetosomes (basal bodies), of which the peripheral members are arranged in regular concentric rows, while the central members are distributed at random. Each of the regularly arranged basal bodies gives rise to a cilium, c. 10 μ long, which appears to be surrounded by a fine tubule, the walls of which consist of filaments, 50 to 100 A in diameter. Each tubule seems to be a

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- prolongation of the surface membrane of a cilium. Photograph from Rouiller, Fauré-Fremiet, and Gauchery (1956) provided by Professor E. Fauré-Fremiet. See p. 273.
21. 1. Isolated fusiform cortical cells of wool. Photograph provided by the Textile Physics Laboratory of the University of Leeds. See p. 278.
2. Transverse section of portions of two cells from the cortex of the upper bulb region of a human hair, showing early filaments of keratin. Photograph from Birbeck and Mercer (1957a) provided by Dr. E. H. Mercer. See p. 278.
3. Transverse section of part of a cell from the upper follicle cortex of a human hair, showing late bundles of keratin filaments. Unpublished photograph provided by Dr. E. H. Mercer. See p. 278.
4. Gold-shadowed protofibrils of keratin obtained by enzymic disintegration of wool fibres, showing the protofibrils as strings of corpuscles, each corpuscle rather more than 100 Å wide. Photograph from Farrant, Rees, and Mercer (1947) provided by Dr. E. H. Mercer. See p. 278.
22. 1. X-ray diffraction pattern of α -keratin, fibre axis parallel to short edge of plate. See p. 283.
2. X-ray diffraction pattern of β -keratin, orientation as before. See p. 283.
3. So-called 'cross- β ' X-ray diffraction pattern of keratin, orientation of specimen as before, but the 'backbone' spacing appears on the meridian. See p. 280.
- Photographs 1, 2, and 3 provided by the Textile Physics Laboratory of the University of Leeds.
4. A single myofibril from a glycerol-extracted rabbit's psoas muscle, photographed under 'even-field' illumination in a Cooke-Dyson interference microscope, (*left*) before, (*right*) after extraction of myosin; together with densitometer tracings. Photographs from H. E. Huxley and Hanson (1957) provided by Dr. Jean Hanson. See p. 299.
5. Birefringence of the fresh axon of a fibre from a frog's sciatic nerve (*R. pipiens* or *R. catesbeiana*). The bare axon protrudes from the brilliantly luminous sheath, visible on the left. Photograph from Thornburg and de Robertis (1956) provided by Dr. W. Thornburg. See p. 286.
23. 1a. Longitudinal section of developing tergosternal muscle from a young pupa of *Tenebrio molitor*. The myofilaments occur in strands consisting of a few filaments only, relatively widely spaced, not accurately parallel, and without transverse striation.
- 1b. Longitudinal section of the same muscle from a somewhat older pupa. The strands now contain many more filaments in close parallel array but still without transverse striation.
- 1c. Longitudinal section of material from a late pupa showing striated myofibrils with strongly opaque Z-lines delimiting the sarcomeres.
- (a), (b), (c), unpublished photographs provided by Dr. D. S. Smith. See p. 294.
- 2a. Section through a single sarcomere of glycerinated psoas muscle from a 'rabbit parallel to the 1120 plane, showing primary filaments with large interfilament spacing (c. 500 Å) and pairs of secondary filaments between. Note the interruption of the secondary filaments at the H-zone, the cross bridges between primary and secondary filaments, the tapering of the primary filaments at the ends of the A-bands, and the thickening of the primary filaments in the H-zone. Photograph from H. E. Huxley (1957) provided by Dr. H. E. Huxley. See pp. 302, 304.
- 2b. Cross-section through myofibrils of the same material. In the sections to the left and above, the plane of section passes through the H-zone; in those to the right and below, through the A-region. In the latter the interpenetrating hexagonal arrays of primary and secondary filaments can be seen. Unpublished photograph provided by Dr. H. E. Huxley. See p. 299.