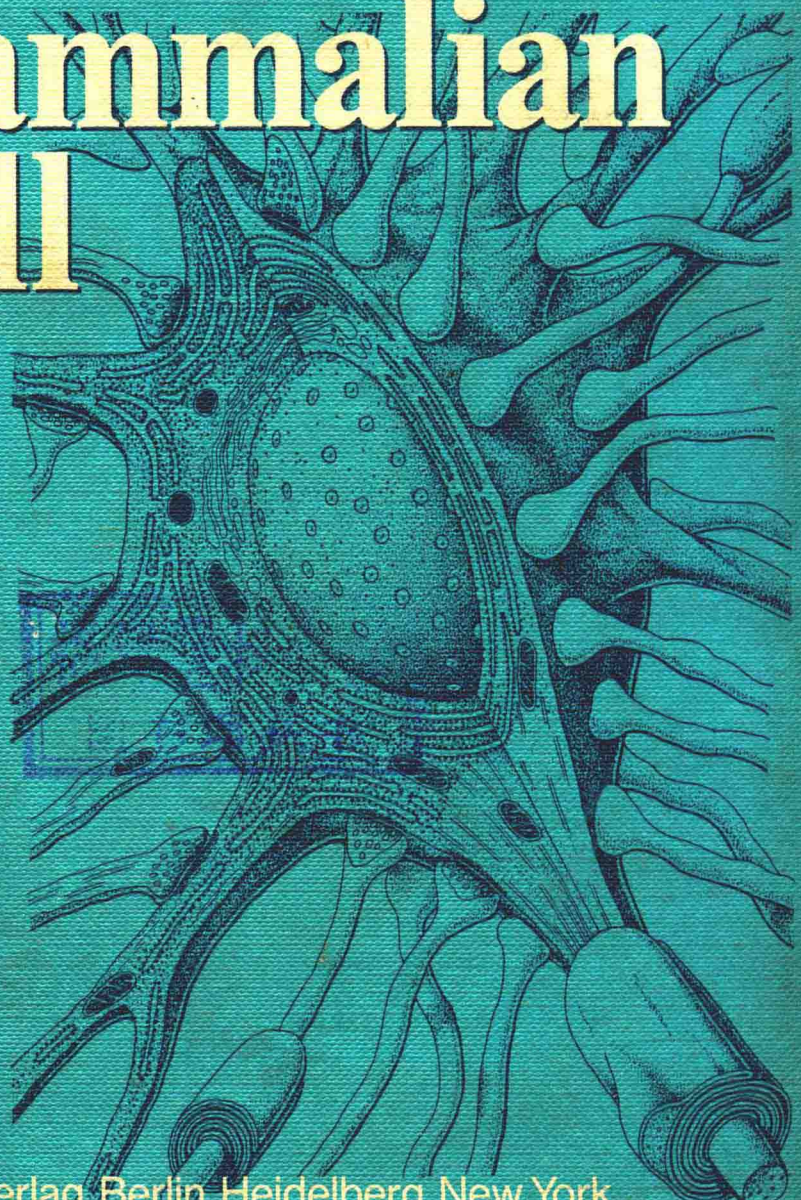
R. V. Krstić

Ultrastructure of the Mammalian Cell

An Atlas



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Ultrastructure of the Mammalian Cell

An Atlas

With a Foreword by W. Bargmann

Translated by
Arthur R. von Hochstetter

With 176 Plates Drawn by the Author

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Foreword to the German Edition

Ever since electron-microscopic research granted new insights into the ultrastructure of the cell and tissues, the analysis of electron micrographs has played a major role in the study of the fine structure of both the human and the animal organism. Thus, in an endeavor to arrive at a spatial and structural representation of the cell and its specializations, students of medicine and biology are confronted with the complexity of interpreting photographic outlines by means of morphological criteria. As every university teacher knows, the examination of even light-microscopic sections is steeped in difficulties when three-dimensional visualizations are attempted from structures presented in section.

It is, therefore, to be welcomed when an electron microscopist, as gifted artistically as he is experienced in teaching, assumes the task of recording representative elements of electron-microscopic biomorphology by clear two- as well as three-dimensional drawings. The atlas offers most appreciated help in the laboratory, in addition to being a most valuable supplement to textbooks, which it cannot replace and does not intend to replace. Moreover, it is hoped that it will stimulate future authors to grant didactically precious drawings more space than they generally receive. I sincerely wish Professor KRSTIĆ's book the wide popularity it deserves.

Kiel, Autumn 1975 W. BARGMANN

Preface to the English Edition

Two and a half years following the publication of the original German edition, the atlas is now presented in its English translation. Thanks to constructive criticism and advice expressed in book reviews of the original work, several mistakes could be corrected for the English edition, some plates modified, and the terminology brought up to date and adapted for Anglo-Saxon readers.

The most important additional feature, however, is the introduction of lists of special references. They accompany nearly every plate and are intended to help broaden the reader's understanding.

I wish to express at this point my deep gratitude to my friend, Dr. ARTHUR R. VON HOCHSTETTER, for his translation of my atlas. I am also most thankful to the editors of Springer for their constant attention to my desires.

Le Mont-sur-Lausanne,
July 1979

RADIVOJ V. KRSTIĆ

Preface to the German Edition

In view of the dominant role that photography plays today in the documentation of scientific domains such as cytology, an atlas composed of drawings may seem anachronistic. However, experience has taught us that a drawing may, by reason of its clarity, be more useful to the student than the best photograph, since it can be shaped to portray details in the third dimension. For this reason, I have drawn the most important cytologic structures, placing particular emphasis on concomitant two- and three-dimensional representations, in order to convey to the student a notion of the spatial configurations of the cell's structural elements. A didactic concept of this nature, however, invariably leads to repetitions.

The purpose of the atlas is to illustrate the characteristics of mammalian and human cytology. Consequently, the outline follows that of other textbooks of cytology and microscopic anatomy. In keeping with the book's character, the accompanying legends give a succint explanation of the important details of each particular structure. For more exhaustive information, a list at the back of the atlas indicates general reading references.

I wish to express at this point my most cordial gratitude to all who supported the conceptual and physical shaping of this book: to Prof. Dr. Otto Bucher, for his understanding and valuable stimulation; to Pierre-André Milliquet, for his excellent technical help in the preparation of the material used for most drawings; to Mrs. Helmtrud Bruder-Gerverdinck, for the correction of the original German text; to Mrs. Monique Devolz for her reliable skill with the typewriter; and not least to the editors of Springer for their obligingness in meeting my propositions and desires.

As I am aware that the following collection cannot claim perfection, I welcome any form of constructive criticism with sincere appreciation.

Lausanne, October 1975 Radivoj V. Krstić

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Numbers refer to plates

Introductory Technical Remarks

The drawings presented in this atlas are the product of numerous carefully evaluated electron micrographs taken of the biologic substrate. As the accompanying text gives indications now and then as to how the material was obtained, a few brief remarks on electron miscroscopy and its technique are called for.

1. Fixation. To be suitable for electron as for light microscopy, fresh tissue must be stabilized by bathing it in a solution of chemicals: fixation by immersion. Better results are obtained by injecting the fixative into the circulatory system during anesthesia: fixation by perfusion. Glutaraldehyde in a 1–6% solution has proved a particularly useful fixative. Tissue blocks are postfixed immediately afterward in 1–2% osmium tetroxide. The contrast necessary for the distinction of various cell and tissue structures is obtained through their unequal impregnation by a heavy metal (osmium). Any one particular structure is thus rendered more or less penetrable by the electron beam. Further contrast is achieved by treating thin sections (see below) with salts of heavy metals, such as lead, uranium, or tungsten. Contrasting in electron microscopy, then, is the result of the structures' altered densities and takes the place of differentiation by color, utilized in light microscopy.

2. Tissue Preparation for Electron Microscopy. The prerequisite for electron-microscopic examination of biologic material is the preparation of sections so thin that they are penetrable by an electron beam (transmission electron microscopy or TEM). Following the necessary preliminary steps, the fixed material needs to be embedded in a sectionable synthetic medium (Araldite, Durcupan, Epon, Maraglas, etc.). The synthetic embedding medium replaces, as it were, the paraffin of the light microscopist.

With the ultramicrotome, a specialized cutting apparatus, sections of an average thickness of 300–600 Å may be obtained. They are then transferred onto a very delicate metal grid, contrasted with heavy-metal salts, and placed inside the electron microscope. The areas overlying the grid spaces are now ready to be viewed and photographed at various magnifications. Small details may be made to appear by subsequent photographic enlargement of the negatives.

The electron microscope's resolving power is in the order of 3 Å. In other words, the observer is able to distinguish two points in the object that are separated by 3 Å. For technical reasons, however, the resolving power as it is used in the medical and biologic sciences is limited to 10–15 Å.

Discrete particles, e.g., viruses, or structural elements, e.g., collagen microfibrils, may be mounted on the grid and exposed under high vacuum to metallic vapors emanating from a point source at a chosen angle. The resulting shadow effect throws the structures into relief.

The freeze-etch technique plays an important part in the examination of surfaces, for instance of the cell membrane or various junctional devices. The object is submerged and instantly frozen in liquid nitrogen (−196 °C) and subsequently fractured under high vacuum at very low

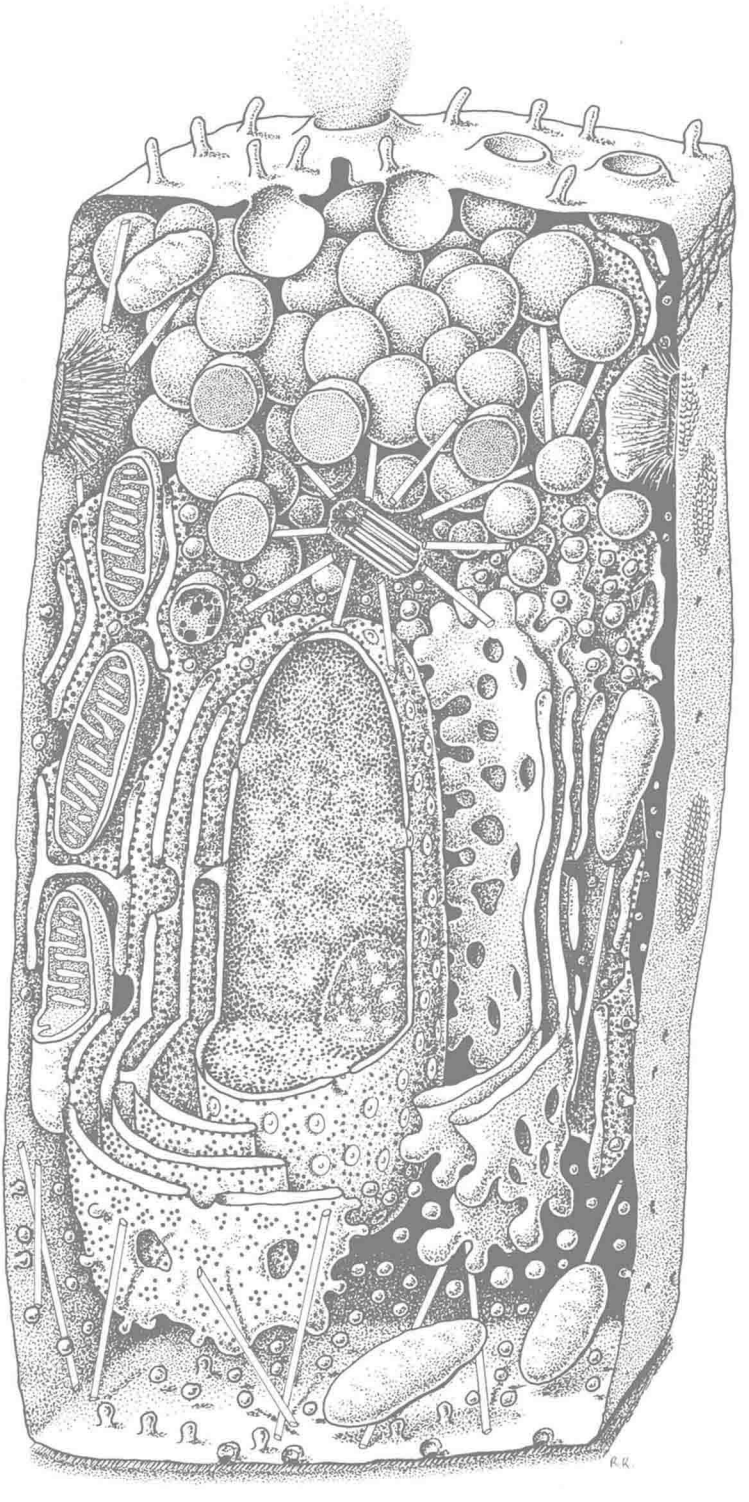
temperature (−100 °C). The fracture face now stands out in microrelief, which can be accentuated by the subsequent sublimation into the vacuum of surface ice, a process termed the etching phase. A layer of carbon and platinum is then evaporated over the frozen-fracture-etched surface. The resultant metal coat, an exact replica of the surface, may be freed from the tissue and examined by electron microscopy.

Three-dimensional images of structures usually seen only in profile in conventional sections are obtained by scanning electron microscopy (SEM). In SEM, an electron beam sweeps the tissue, previously dried and metal-coated, generating secondary electrons as it strikes the surface. These are collected and the information they carry is visualized and/or photographed by way of a television tube.

(For further details consult HAYAT, 1970–1976; KOEHLER, 1973; MILLONIG, 1976; General References.)

I. The Cell

General Description



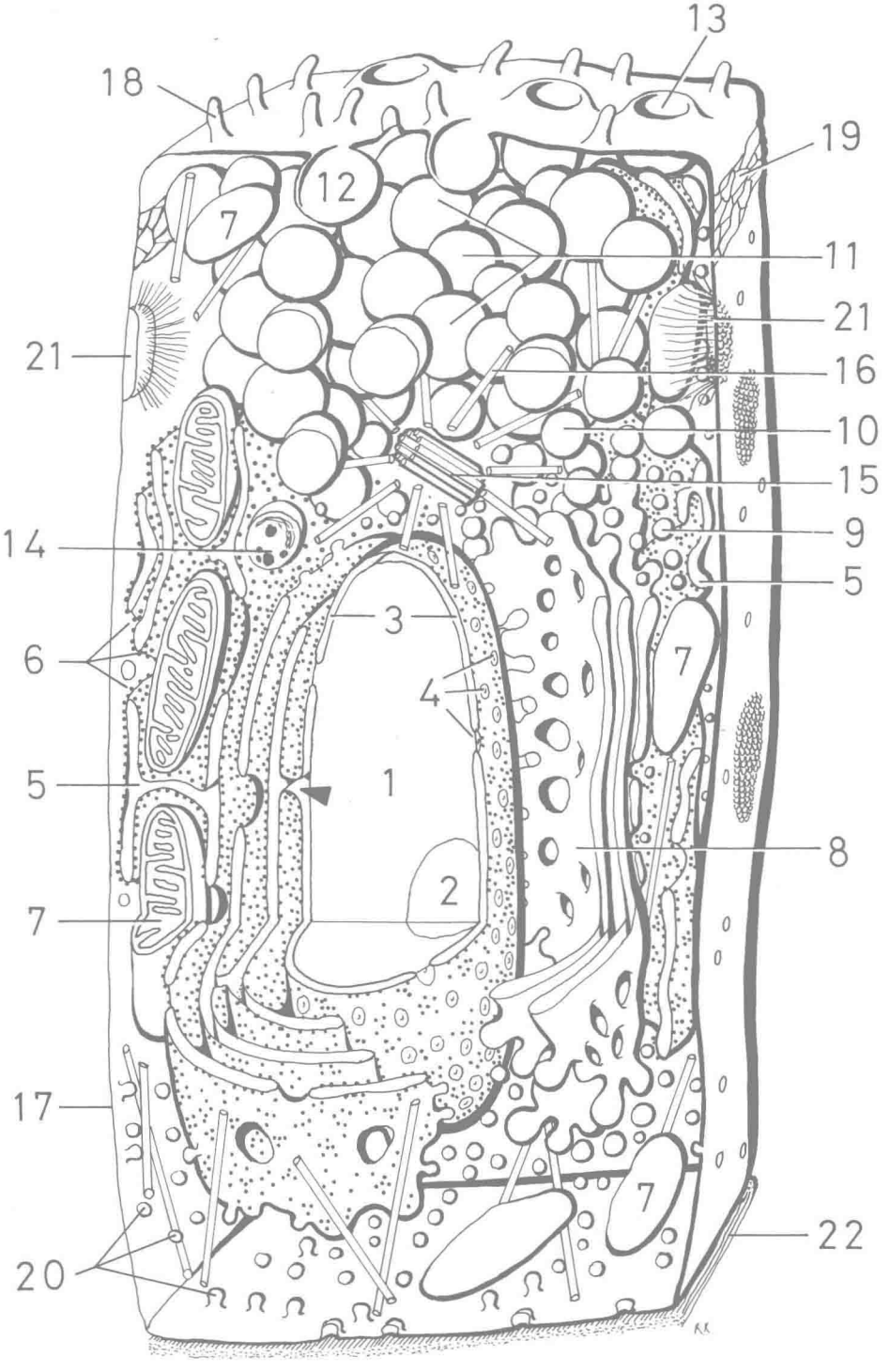

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Plate 1. Schematic Representation of a Secretory Epithelial Cell

Mammalian cells are of the eukaryotic type, i.e., they possess a morphologically discrete nucleus.

In the illustration, the nucleus (1) with its nucleolus (2) occupies the central portion of the cell body. It is surrounded by the perinuclear space (3) with numerous round nuclear pores (4).

To the left of the nucleus, the perinuclear space is continuous (arrowhead) with the rough endoplasmic reticulum (5), whose outer surface is studded with ribosomes (6). The rough endoplasmic reticulum (rough ER) forms a considerable labyrinth that envelops the nucleus and extends into the upper reaches of the cell. Between its cisternae and the cellular membrane to the left are three sectioned mitochondria (7). Other intact mitochondria, scattered throughout the cell, are easily distinguished by their oval shape.

To the right of the nucleus lies the Golgi apparatus (8) consisting mainly of parallel, flattened sacs. At their periphery numerous vesicles (9) and vacuoles (10) containing the secretory product are formed. Many of these secretory granules, some of which are cut revealing their finely granular contents of variable density, are seen above the nucleus (11). Two granules have fused with the plasma membrane of the apical portion of the cell and have already expelled their contents (12). Three openings, through which other secretory granules are in the process of doing the same, are seen on the upper surface of the cell (13).

A lysosome (14) with its heterogeneous contents lies just above and to the left of the nucleus.

Immediately above the nucleus is the centriole (15), in the midst of a star-shaped constellation of microtubules (16). Other microtubules are scattered throughout the cell body.

At the apical pole, the cell membrane (17) or plasmalemma, displays several outward projections or microvilli (18). It is also the site of the zonulae occludentes (19), which link the cells. In addition, the cell membrane forms numerous micropinocytic vesicles (20).

Desmosome halves (21) with tonofilaments radiating into the cytoplasmic matrix are shown on either side near the top of the drawing. The spaces between the cellular components are filled with a cell sap, the ground cytoplasm or hyaloplasm. The basal cell pole lies on a basal lamina (22).

Magnification: × 7500

(The magnification factors given in this atlas are intended to convey an approximate idea of scale: they are not necessarily precise.)

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(See also General References)

II. The Interior of the Cell

Plate 2. The Nucleus. Form and Structure. Example: Rat Hepatocyte

The most conspicuous of cellular structures, the nucleus, is present in all cells, except red blood corpuscles. It is mostly spherical or ovoid and surrounded by a membranous sac whose inner leaflet represents the nuclear membrane (1). The outer leaflet (2) is studded with ribosomes and is part of the rough ER (3). Together, these membranes make up the nuclear envelope, or karyotheca. Between them lies the perinuclear space (4), 150–300 Å wide, which is continuous with the rough ER (arrowheads) and is disrupted by several nuclear pores (5), as shown in Plate 1.

The nucleus houses the nucleolus (6) and chromatin. With appropriate fixation and contrasting procedures, two types of chromatin can be rendered visible. Heterochromatin (7), composed of osmiophilic granules 100–150 Å in diameter and filamets about 50 Å thick, is found usually close to the nuclear membrane and nucleolus. In the latter case it is called perinucleolar chromatin. Euchromatin, or interchromatin (8) lies between the clumps of heterochromatin. It is of low electron density and seems to be metabolically very active.

Nuclei contain deoxyribonucleic acid (DNA), the genetic material that determines the cell's activity (for details, consult textbooks of biochemistry and molecular biology). The ribonucleic acid (RNA) content of the nucleus is held within the nucleolus.

Note the numerous flattened cisternae of rough ER (3), mitochondria (9), peroxisomes (10), and very dense glycogen granules (11) near the nucleus.

Magnification: × 17000

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