

OUTLINES  
OF  
BIOCHEMISTRY

# OUTLINES OF BIOCHEMISTRY

By

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Third Edition

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## PREFACE TO THE THIRD EDITION

During the eleven years that have elapsed since this book was last revised, great strides have been made in nearly all phases of biochemistry. Of necessity, some of the chapters have had to be largely rewritten and many others have been extensively changed. New chapters dealing with protein denaturation, carbohydrate metabolism, and the metabolism of lipids have been added. Certain other chapters which appeared in the previous edition have been omitted from the present volume, but their subject matter has been partially reincorporated in logical fashion into existent chapters. Throughout this extensive revision, however, we have tried to keep the aims of the book and its approach to the subject matter as much as possible like those of the original author.

With so much new information at hand it was indeed difficult to keep the size of this new edition within reasonable limits. It was, of course, necessary to treat some sections more fully than in the past, but it was possible to make a roughly comparable reduction in certain other sections. In chapters dealing with subjects that are rather thoroughly dealt with in medical biochemistry textbooks, no attempt was made to cover the field extensively.

There have been rather prolonged, unavoidable delays in the preparation of this Third Edition of *Outlines*. World War II, coming at about the time that a new edition was being planned, held up preparation for several years. The post-war years placed unusually heavy teaching, research, and administrative responsibilities on the shoulders of those contributing to the present volume, with the result that several "deadlines" for receipt of manuscript had to be set. Thus, some parts of the manuscript were received well over a year before the last instalments were in. Despite many difficulties, we found the task inspiring and trust that the result is one of which the original author would be justly proud.

We are especially indebted to the following persons, each of whom handled the revision of one or more chapters: Drs. S. I. Aronovsky, P. D. Boyer, D. R. Briggs, H. B. Bull, G. O. Burr, W. F. Geddes, W. M. Sandstrom, and J. J. Willaman. We wish to thank Drs. Thomas Schoch and H. O. Halvorson for contributing material on starch and the bacterial metabolism of carbohydrates, respectively; Drs. M. G.

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ROSS A. GORTNER, JR.  
WILLIS A. GORTNER

*May, 1949*

## PREFACE TO THE FIRST EDITION

"When I have the honor of being consulted by a young man who has not yet found himself intellectually but who is filled with the desire to devote his life to some branch of medicine, be it clinical medicine, pathology, hygiene, bacteriology, physiology or pharmacology, my advice always is, 'Study chemistry at least three years. Try with all your power to master enough of this great science to start you on your career.'"

JOHN J. ABEL

It is rather generally agreed among the scientists that the actions and reactions of a biological organism are expressions of the energy relationships due to chemical and physicochemical processes taking place within the cells and tissues which comprise the organism.

The biological organism can be looked upon as a complex system of chemical constituents, composed mainly of proteins, carbohydrates, fats and lipids, mineral elements, and water, which are organized by the mysterious forces which we call "life," and the actions and reactions of this protoplasmic mass are in turn determined by the energy interchanges of molecular transformations and surface and interfacial forces.

In most of the universities of America the development of the field of biochemistry has been left very largely to the group interested in the medical aspects. Accordingly, in a very large measure the biochemistry of the American universities is not biochemistry in its strictest sense, but rather leans more and more toward the field of human pathology. Most medical school biochemistry could be more correctly designated as human pathological chemistry.

It is obvious that there should be strong departments of physiological chemistry associated with the medical schools. However, it should likewise be recognized that there is a necessity for a study of the fundamental reactions underlying the broader field of biology, the primary object of which is to study and investigate the chemical and physicochemical reactions which take place in the normal biological organism, whether that organism be animal or plant.

The greatest advance in the biological sciences can take place only when the chemists are fully aware of certain of the biological problems and the biological point of view, and only when the biologists appreciate the assistance which chemical knowledge and chemical technic can offer to the solution of the major problems.

When, in 1913, Professor R. W. Thatcher was called to the University

of Minnesota, he inaugurated a course of lectures on "phytochemistry" and taught the course until he became Dean of the Department of Agriculture in 1917, at which time Dr. C. A. Morrow assumed charge of the lecture work in "Phytochemistry" and supervision of the parallel laboratory course in "Biochemical Laboratory Methods."

Dr. Morrow remained in charge of both courses until his unfortunate illness in the spring of 1922, following which illness the responsibility for the lecture work was assumed by the present author, and upon resumption of active duties Dr. Morrow was left free to devote his entire energies to the development of the associated laboratory phases of the work. His success in this task is attested by the practical completion of the manuscript of the laboratory manual, *Biochemical Laboratory Methods*, which appeared posthumously from the press of John Wiley & Sons, Inc., in 1927.

The course of lectures upon which the present volume is based must not therefore be regarded as the product of a single individual, for it embodies primarily the efforts of three men who have actually taught the course, and in addition the advice, cooperation, and criticism of all other persons who from time to time have been members of the Staff of the Division of Agricultural Biochemistry.

During the year 1925-1926 the present author prepared a series of mimeographed lecture outlines as an aid to the students in the classroom. These outlines were somewhat revised in the summer of 1927 and issued to the students in bound mimeographed form. The present volume follows, in general, the topics as presented in these outlines, although the scope of the field has been greatly expanded.

All of the reactions and interactions which we call life take place in a colloid system, and the author believes that much of the "vital energy" can in the last analysis be traced back to energies characteristic of surface films and interfaces. This belief is the justification for the detailed consideration of colloid systems which forms the first section of the volume.

In the subsequent sections dealing with proteins, carbohydrates, fats, etc., those organic compounds characteristic of living tissues, particular attention has been paid to structural organic chemistry and organic and physicochemical reactions. No attempt has been made to produce a "handbook" of biochemical compounds or a "descriptive biochemistry" detailing the chemical properties, crystal structure, etc., of the various compounds. There are already many volumes covering these fields, and no good purpose would be served by adding to the list.

The purpose of the present volume is that those students who are interested in biological phenomena may have an insight into the roles which organic chemistry and physical chemistry play in living processes.

It may be regarded as an attempt to interpret some of the reactions characteristic of the normal cell. Although a great many of the illustrations have been drawn from plant material, it must be remembered that in the last analysis the chemistry of the cell is essentially the same both for plants and for animals. There is no sharp distinction between "phytochemistry" and "zoochemistry." The same general reactions of protoplasm apply to both. If the student interested in some pure or applied field of biology or of chemistry is assisted, ever so little, in the clarification of the problems in his special field, then the object of the author will have been attained.

Toward this end the exact titles have been included in the literature citations. With but few exceptions (and those are noted in the text) the citations have been checked back against the original publication so as to preclude bibliographic errors. A sincere attempt has been made to give to other investigators the proper credit for data or for ideas which have been utilized. On the other hand, the text does not pretend to be an exhaustive treatment of the subjects, nor is the literature cited necessarily in an historical sequence. It is recognized that in many instances the references cited are not the first publications on the subject, but it is felt that the references which are cited contain something which should be called to the attention of the reader. The author may perhaps be pardoned for the numerous references to work done in his own laboratories, for obviously he is most familiar with the details of such work and the conditions under which it was carried out.

In conclusion, the author wishes to thank his colleagues, Dr. J. J. Willaman and Dr. Leroy S. Palmer, who have contributed Chapters XXVII and XXXIV, respectively; The Williams & Wilkins Company, and Prof. W. Mansfield Clark; the editors of the *Journal of Biological Chemistry*; The Chemical Catalog Company, Prof. Harry N. Holmes, Prof. O. L. Sponsler, and Prof. W. H. Dore; The Carnegie Institution of Washington, and Dr. D. T. MacDougal; Carl Zeiss, Inc.; Dr. Karl Mez; Prof. John J. Abel; Prof. E. F. Burton; Jerome Alexander; Prof. Francis Lloyd; Dr. Robert Newton; Dr. G. E. Holm; Dr. P. V. Wells; Dr. William Robinson, and others for permission to use copyrighted material or for photographs or data.

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And lastly I wish to express my deepest appreciation of Miss Rachel Rude for invaluable assistance in the task of preparing the final manuscript and in proofreading.

ROSS AIKEN GORTNER



# CONTENTS

## I. COLLOIDS

1. THE COLLOID STATE OF MATTER . . . . .	3
2. METHODS OF PREPARATION . . . . .	12
3. CERTAIN PHYSICAL PROPERTIES CHARACTERISTIC OF COLLOID SYSTEMS . . . . .	38
4. HYDROGEN-ION CONCENTRATION . . . . .	63
5. OXIDATION-REDUCTION . . . . .	90
6. ELECTROKINETIC PHENOMENA . . . . .	104
7. SURFACE TENSION, INTERFACIAL TENSION, SURFACE ENERGY, AND ADSORPTION . . . . .	138
8. ELECTROLYTES AND COLLOID SYSTEMS . . . . .	201
9. GELS AND THE WATER RELATIONSHIPS OF THE HYDROPHILIC COLLOIDS . . . . .	227
10. THE GIBBS-DONNAN EQUILIBRIUM . . . . .	264

## II. PROTEINS

11. THE AMINO ACIDS, THE PRIMARY DECOMPOSITION PRODUCTS OF PROTEINS . . . . .	277
12. POLYPEPTIDES . . . . .	301
13. ANALYSIS OF PROTEINS . . . . .	315
14. PROTEIN CLASSIFICATION . . . . .	347
15. PROTEIN STRUCTURE AND THE POSSIBILITIES OF PROTEIN ISOMERISM . . . . .	360
16. CHARACTERISTIC PROPERTIES OF PROTEIN SYSTEMS . . . . .	379
17. REACTIONS OF PROTEINS WITH ACIDS AND BASES . . . . .	425
18. PROTEIN DENATURATION . . . . .	439
19. METABOLISM OF PROTEINS . . . . .	448
20. BIOLOGICAL REACTIONS OF THE PROTEINS . . . . .	469
21. NITROGEN BASES . . . . .	488

## III. CARBOHYDRATES AND RELATED SUBSTANCES

22. INTRODUCTION TO THE CHEMISTRY OF THE CARBOHYDRATES . . . . .	517
23. THE MONOSACCHARIDES . . . . .	540
24. THE OLIGOSACCHARIDES—COMPLEX OR COMPOUND SUGARS . . . . .	602

25. THE POLYSACCHARIDES . . . . .	624
26. METABOLISM OF CARBOHYDRATES . . . . .	675
27. THE GLYCOSIDES AND SAPONINS . . . . .	712
28. THE PECTIC SUBSTANCES . . . . .	724
29. LIGNIN AND THE TANNINS . . . . .	737

#### IV. THE LIPIDS AND ESSENTIAL OILS

30. THE SIMPLE LIPIDS: THE FATTY ACIDS, GLYCERIDES, WAXES, STEROLS, AND BILE ACIDS . . . . .	765
31. THE COMPOUND LIPIDS . . . . .	807
32. METABOLISM OF THE LIPIDS . . . . .	818
33. ESSENTIAL OILS . . . . .	833

#### V. PLANT PIGMENTS

34. CHLOROPHYLL AND THE CAROTENOIDS . . . . .	845
35. THE FLAVONES, XANTHONES, AND ANTHOCYANINS . . . . .	869

#### VI. BIOCHEMICAL REGULATORS

36. VITAMINS . . . . .	885
37. THE HORMONES . . . . .	946
38. ENZYMES . . . . .	982
AUTHOR INDEX . . . . .	1017
SUBJECT INDEX . . . . .	1047

# I

## COLLOIDS

*The colloidal is, in fact, the dynamical state of matter; crystalloidal being the statical condition. The colloid possesses ENERGIA. It may be looked upon as the probable primary source of the force appearing in the phenomena of vitality.*

THOMAS GRAHAM (1861)

*The colloid field today presents the most promising realm in medical research.*

W. G. MAYO (1928)

*If the colloid structures did not display highly specialized molecular structures at their surface, no reactions would occur; for here catalysis occurs. Were it not equipped with catalysts, every living unit would be a static system.*

SIR FREDERICK GOWLAND HOPKINS (1933)

*Progress in our attack against disease, in our better understanding of the human body, of bacteria, viruses, and other vectors of disease, and of their interaction with each other depends on a better understanding of intermolecular forces and interactions.*

*Usually specific physiological properties are determined not by strong intramolecular forces but by the weak forces—van der Waals forces, hydrogen bonds, and so on—which operate between molecules. Physiological activity seems related to size, shape and structure of the interacting molecules.*

LINUS PAULING (1946)



## CHAPTER 1

### The Colloid State of Matter

It seems appropriate to begin the study of biochemistry with a consideration of the colloid state of matter, because in the last analysis many of the reactions of biological systems are dependent on the colloidal phenomena operating in such systems. There are a number of useful text and reference books on colloid chemistry. Among these may be mentioned those of Hauser,<sup>1</sup> Weiser,<sup>2</sup> Hartman,<sup>3</sup> Alexander,<sup>4</sup> and Freundlich.<sup>5</sup>

We often hear the statement that such and such a material is a colloid. A statement of this kind is not strictly correct. Colloid phenomena deal with a *state* of matter, not a kind of matter. Early workers in this field published many papers indicating that certain materials could under certain specific conditions of manipulation be brought into the colloidal state. We now know that, if the proper technic is used, any material can be brought into the colloidal state. Consequently there is no sharp line of demarcation between substances which can be regarded as colloids and substances which are generally non-colloids.

The first real work in the field of colloid chemistry was due to the activities of Thomas Graham (1805-1869). All of Graham's forty-six research papers dealt with the single phenomenon of diffusion.<sup>6</sup> Graham<sup>7</sup> published important summaries in 1861 and 1864, and in these introduced many new terms. Thus, speaking of the properties of colloids, Graham states, "Their peculiar physical aggregation with the chemical indifference referred to appears to be required in substances that can intervene in the organic processes of life. The plastic elements of the animal body are found in this class. As gelatine appears to be

<sup>1</sup> E. A. Hauser, *Colloidal Phenomena*, McGraw-Hill Book Co., New York, 1939.

<sup>2</sup> H. B. Weiser, *Colloid Chemistry*, 2nd ed., John Wiley & Sons, New York, 1949.

<sup>3</sup> R. J. Hartman, *Colloid Chemistry*, Houghton Mifflin Co., Boston, 1939.

<sup>4</sup> J. Alexander, *Colloid Chemistry; Principles and Applications*, 4th ed., D. Van Nostrand Co., New York, 1937.

<sup>5</sup> H. Freundlich, *Kapillarchemie*, Bd. 1 and 2, Akademische Verlagsgesellschaft M.B.H., Leipzig, 1930, 1932.

<sup>6</sup> Cf. R. A. Gortner, *J. Chem. Educ.*, **11**, 279 (1934).

<sup>7</sup> Thomas Graham, *Phil. Trans.*, 1861, p. 183; *J. Chem. Soc.*, **17**, 318 (1864).

its type, it is proposed to designate substances of the class as *colloidal*<sup>8</sup> and to speak of their peculiar form of aggregation as the *colloidal condition of matter*. Opposed to the colloidal is the crystalline condition. Substances affecting the latter form will be classed as *crystalloids*. The discussion is no doubt one of intimate molecular constitution."

Graham recognized that there was no sharp discontinuity between colloids and crystalloids and that one and the same substance may under different sets of conditions be either colloidal or crystalloidal. Thus, he states (1861), "A departure from its normal condition appears to be presented by a colloid holding so high a place in its class as albumen. In the so-called blood-crystals of Funke, a soft and gelatinous albuminoid body is seen to assume a crystalline contour. Can any facts more strikingly illustrate the maxim that in nature there are no abrupt transitions, and that distinctions of class are never absolute?"

We now know that any substance, even including such substances as sodium chloride, can by proper technic and by the proper choice of medium be brought into the colloidal state. Some substances may be colloidal in one liquid medium and truly crystalloidal in another. Tannin dispersed in water gives rise to a colloidal system, whereas it dissolves in acetic acid to form a crystalloidal solution. Many other substances show similar behavior. *Only the physical properties of the resulting system will show whether or not a given material is colloidal or crystalloidal.*

A substance cannot be strictly spoken of as a colloid, because colloid implies (1) a state of matter and (2) at least two components or phases. Thus, we have not a colloid material but rather colloidal systems.

Water has three states: vapor, liquid, and solid. Each of these may exist in colloidal systems. Barnes<sup>9</sup> has discussed certain natural phenomena produced by colloidal water and colloidal ice, and we shall have occasion later to consider instances in which water vapor is involved.

Inasmuch as a colloid system is a heterogeneous system, it is necessary to distinguish between the substance which is dispersed and the medium in which the material is dispersed. Various terms have been employed by different writers. Some authors speak of the *disperse phase* and *dispersions medium*; others of the *discontinuous phase* and the *continuous phase*; others of the *internal phase* and the *external phase*; and still others of the *micelles* and the *intermicellar liquid*. The last group of terms appears to be coming more and more into general use and in some respects appears preferable.

<sup>8</sup> From the Greek, *κολλα*, *kolla*, meaning glue or gelatin, and *ειδος*, *eidōs*, meaning like.

<sup>9</sup> Howard T. Barnes, Colloid Symposium Monograph, Vol. III, p. 103, Chemical Catalog Co., New York, 1925.

In the older literature a distinction is drawn between colloids and crystalloids on the basis that colloids are amorphous. This distinction is to be discouraged as having little or no meaning; x-ray studies have shown that many colloidal particles have a crystalline structure. The only satisfactory way to define a colloid is on the basis of particle size. This has been done arbitrarily as shown in the following diagram.

Molecules and Ions	Colloids	Matter in Mass
Not Visible in Ultramicroscope	Visible in Ultramicroscope 1 m $\mu$	Visible in Microscope 0.1 $\mu$

It will be noted that a boundary has been placed at 1 m $\mu$  (0.000001 mm.) diameter, defining the lower limit of the colloid realm, and another boundary at approximately 0.1  $\mu$  (0.0001 mm.), defining the upper limit of the colloid realm. All particles within this range of dimensions are known as colloidal whether they are molecularly dispersed or not. It cannot be too strongly emphasized that *these are arbitrary boundaries*. However, they seem to have been rather wisely chosen. Most compounds which are crystalline in the solid state and which yield monodisperse solutions of molecules or ions do not contain molecules which exceed 1 m $\mu$  in diameter. On the other hand, monomolecular solutions of proteins fall within this size range and exhibit properties of colloidal systems.

The upper limit of the colloid realm, 0.1  $\mu$  in diameter, was chosen because this represents the extreme range of the ordinary microscope, with an oil-immersion objective. The colloid realm is thus concerned with systems containing subdivisions of matter lying between the limits of visibility of the usual laboratory microscope and those solutions which are strictly crystalloidal. It must be understood at the outset that the properties of the colloidal systems do not strictly coincide with these arbitrary boundaries but that *there is a continual gradation in properties from truly crystalloidal systems to coarsely divided suspensions, and that the optimum zone of colloidal lies somewhere near the center of the colloid realm, as noted in the diagram above*. In other words a coarsely divided suspension will show to a minor degree certain of the phenomena characteristic of the colloidal state, and in the same way certain of the phenomena of the colloidal state reflect in a minor degree the characteristics of true solutions.

Siedentopf and Zsigmondy classify the three states of matter noted in the above diagram as *microns* visible in the microscope, *submicrons* or *ultramicros* visible in the ultramicroscope, and *amicros* not visible in the ultramicroscope. According to their terminology all systems

showing characteristic colloidal properties contain submicrons. We are probably nearer the truth when we place the lower limit of colloid systems at  $1\text{ m}\mu$  than when we place the upper limit at  $0.1\text{ }\mu$ , and there has been a general tendency in recent years to raise the upper limit to

perhaps  $0.5\text{ }\mu$ , inasmuch as fine suspensions possess to a large degree certain characteristic properties of colloidal systems.

Perhaps everyone has viewed a red blood corpuscle under the microscope and accordingly has some idea of the relative size of a red blood corpuscle as compared with other familiar objects. Figure 1 illustrates the size relationships of some rather common materials as compared with the size of colloidal particles. It should be noted, however, that the smallest colloidal particle noted at (f) is ten times the diameter of the particles which fix the lower limit of the colloidal realm. Hackh<sup>10</sup> has tabulated some very interesting data comparing size, time, mass, velocity, and temperature relationships for common objects and systems. A study of these tabulations will greatly assist the student in orienting himself in the field of natural phenomena.

According to Wo. Ostwald one can conveniently classify colloid systems into eight great groups:

**Solid-in-Solid.** Examples are the ruby glass of the cathedral windows which is a colloid system of metallic gold dispersed in glass; blue rock salt, a colloid system of sodium dispersed in sodium chloride; the black diamond, which is carbon dispersed in crystalline carbon. The colors of many precious stones are examples of solid-in-solid colloidal systems. This type of system is important in metallurgy, but from the biological standpoint it is relatively unimportant.

**Solid-in-Liquid.** Faraday, in 1857, exhibited before the Royal Society a brilliant red liquid which he had prepared by reducing an aqueous solution of auric chloride. Inasmuch as this liquid showed a beautiful red color by transmitted light and a golden sheen by reflected light, he suggested that the color might be due to particles of solid gold suspended

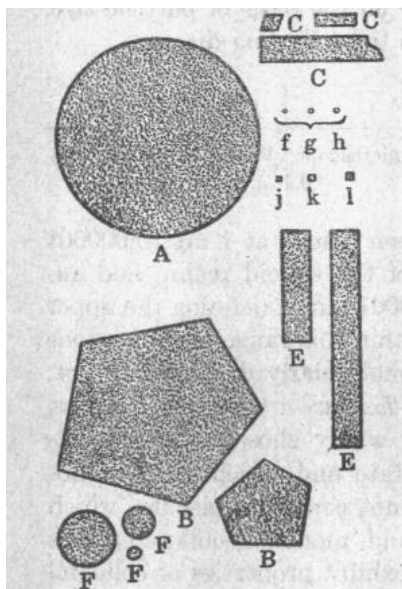


FIG. 1. A = red blood cells; B = starch grains; C = clay particles; E = *Anthrax bacilli*; F = *Cocci*; fgh = colloidal gold (f =  $10\text{ m}\mu$ ); jkl = gold coagula. (After Zsigmondy. By permission from Alexander's *Colloid Chemistry*, 1924.)

<sup>10</sup> I. W. D. Hackh, *Sci. Monthly*, 36, 55 (1933).



in the liquid. This experiment was forgotten for many years, but we now know that Faraday had prepared one of the first examples of a solid-in-liquid colloidal system.

However, the definition of "a solid-in-liquid" does not at all times tell the whole story. In the gold-in-water systems we have a *lyophobic* (solvent-hating) system in which *the disperse phase is insoluble in the dispersions medium and the dispersions medium does not dissolve in the disperse phase*. Thus, we may have systems of gold and water, sulfur and water, rubber and water, sodium chloride and alcohol, etc. This type of system is of rather general importance in biochemical studies, and certain of its characteristics will be considered in greater detail in the following pages.

On the other hand, when gelatin is dispersed in water a *lyophilic* (solvent-loving) system results. This is defined by Martin Fischer as "*a system in which the disperse phase and the dispersions medium are mutually more or less soluble one in the other.*" This indicates that *hydration* (when water is the dispersions medium) or *solvation* (a term which applies to any dispersions medium) takes place. Gelatin swells in water; some of the gelatin disperses in the water, and a considerable amount of the water "dissolves" in the gelatin. The gelatin is *hydrated*. Gelatin in alcohol or benzine is a lyophobic system. Rubber in alcohol or benzine is a lyophilic system, in water a lyophobic system. In biological problems the lyophilic colloids constitute by far the most important class.

**Solid-in-Gas.** In this system we are dealing with such phenomena as the smoke-vapors of ammonia and hydrochloric acid, the "blue haze" of the forest fire areas that hangs for weeks in the air without settling, and the "blue" smoke of the cigarette. The darker colored smokes usually contain the more coarsely divided suspensions of carbon. When these larger particles have settled out, the blue colloidal haze still persists and forms a very stable system. From the military standpoint such systems constitute a rather important field of study involving smoke screens, etc., for the reason that one desires the maximum density of smoke which can be formed from the minimum amount of original material, the degree of subdivision thus playing a very important role. Bacterial and fungus spores present in spray from coughing and sneezing may be considered examples of solid-in-gas systems which are of importance from the biological and medical standpoint.

**Liquid-in-Solid.** The principal examples of this system are found in minerals and gems. The opal is a system of silicon dioxide and water, the pearl a system of calcium carbonate and water. An opal rather readily loses its "fire" and the pearl its "life" or luster if kept for a con-