Proceedings of the

FIFTH INTERNATIONAL CONGRESS OF

BIOCHEMISTRY

Moscow, 1961

Proceedings of the

FIFTH INTERNATIONAL CONGRESS

OF

BIOCHEMISTRY

Moscow, 10-16 August 1961

GENERAL EDITOR

N. M. SISSAKIAN, Moscow, U.S.S.R.

Secretary-General of the Congress

VOLUME III

EVOLUTIONARY BIOCHEMISTRY

Edited by
A. I. OPARIN, Moscow

SYMPOSIUM PUBLICATIONS DIVISION PERGAMON PRESS

NEW YORK · OXFORD · LONDON · PARIS

PWN-POLISH SCIENTIFIC PUBLISHERS

WARSAW

1963

PERGAMON PRESS LTD.

Headington Hill Hall, Oxford

4 and 5 Fitzrov Square, London W.1

PERGAMON PRESS INC.

122 East 55th Street, New York 22, N.Y.

GAUTHIER-VILLARS ED. 55, Quai des Grands-Augustins, Paris 6

PERGAMON PRESS G.m.b.H.

Kaiserstrasse 75, Frankfurt am Main

Distributed in the Western Hemisphere by MACMILLAN COMPANY · NEW YORK pursuant to a special arrangement with PERGAMON PRESS LTD.

Oxford, England

Copyright © 1963 Pergamon Press Ltd.

Library of Congress Card Number 59-8791

LIST OF AUTHORS

ABELSON, P. H.	Geophysical Laboratory, Carnegie Institution of Washington, Washington, D.C., U.S.A.
AIL, S. J.	Research Laboratories, Albert Einstein Medical Center, Philadelphia, Pennsylvania, U.S.A.
Belozersky, A. N.	Biological Faculty, State University of Moscow, U.S.S.R.
BERNAL, J.	Birbeck College, University of London, England
Brown, G. W., Jr.	Department of Physiological Chemistry, University of Wisconsin, Madison, Wisconsin, U.S.A.
Bücher, T.	Physiologisch-Chemisches Institut der Philipps- Universität, Marburg/Lahn, Germany
BUEDING, E.	Department of Pathobiology, School of Hygiene and Public Health, The Johns Hopkins University, Baltimore, Maryland, U.S.A.
BURRIS, R. H.	Department of Biochemistry, University of Wisconsin, Madison, Wisconsin, U.S.A.
COHEN, P. P.	Department of Physiological Chemistry, University of Wisconsin, Madison, Wisconsin, U.S.A.
COHEN, S. S.	Department of Biochemistry, University of Pennsylvania, School of Medicine, Philadelphia, Pennsylvania, U.S.A.
Eagle, H.	National Institutes of Health, Bethesda, Maryland, U.S.A.
EGAMI, F.	Department of Biophysics and Biochemistry, Faculty of Sciences, University of Tokyo, Japan

FLORKIN, M. Laboratoires des Biochemie, Université de Liège, Belgique

Fraenkel-Conrat, H. Virus Laboratory, University of California, Berkeley, California, U.S.A.

GAFFRON, H. Department of Biological Science (Fels Fund), Florida State University, Tallahassee, Florida, U.S.A.

GIERER, A. Max-Planck-Institut für Virusforschung, Tübingen, Germany

GOODWIN, T. W. Department of Agricultural Biochemistry, University College of Wales, Aberystwyth, U.K.

HANDLER, P. Department of Biochemistry, Duke University School of Medicine, Durham, North Carolina, U.S.A.

HELLER, J. Institute of Biochemistry and Biophysics, Polish Academy of Sciences, Warsaw, Poland

HORECKER, B. L. New York University School of Medicine, New York, U.S.A.

HOTCHKISS, R. D. The Rockefeller Institute, New York City, U.S.A.

IMSHENETSKII, A. A. Institute of Microbiology, U.S.S.R. Academy of Sciences, Moscow

ISHIMOTO, M. Department of Biophysics and Biochemistry, Faculty of Science, University of Tokyo, Japan

ITAHASHI, M. Department of Biophysics and Biochemistry, Faculty of Science, University of Tokyo, Japan

KALCKAR, H. M. McCollum-Pratt Institute and Department of Biology, the Johns Hopkins University, Baltimore, Maryland, U.S.A.

KAMEN, M. D. Graduate Department of Biochemistry, Brandeis University, Waltham, Massachusetts, U.S.A.

KAPLAN, N.O. Graduate Department of Biochemistry, Brandeis University, Waltham, Massachusetts, U.S.A. Department of Microbiology, New York Uni-MAAS, W. K. versity School of Medicine, New York, U.S.A. McElroy, W. D. Department of Biology and McCollum-Pratt Institute, The Johns Hopkins University, Baltimore, Md., U.S.A. NIEMIERKO, W. Department of Biochemistry, Nencki Institute. Warsaw, Poland OPARIN, A. I. Institute of Biochemistry, U.S.S.R. Academy of Sciences, Moscow OTTOLENGHI, E. The Rockefeller Institute, New York, U.S.A. PAPPENHEIMER, A. M., Biological Laboratories, Harvard University. JR. Cambridge, Massachusetts, U.S.A. PETTE, D. Physiologisch-Chemisches Institut der Philipps-Universität, Marburg/Lahn, Germany REEVES, H. C. Research Laboratories, Albert Einstein Medical Center, Philadelphia, Pennsylvania, U.S.A. ROCHE, J. Laboratoire de Biochimie Générale et Comparée. Collège de France, Paris, France Seliger, H. H. Department of Biology and McCollum-Pratt Institute, The Johns Hopkins University, Baltimore, Md., U.S.A.

SHAPOSHNIKOV, V. N. Institute of Microbiology, U.S.S.R. Academy of Sciences, Moscow

SOROKIN, YU. I. Biological Station "Borok", U.S.S.R. Academy of Sciences

TATUM, E. L. The Rockefeller Institute, New York, N.Y., U.S.A.

Tsugita, A. Virus Laboratory, University of California, Berkeley, California, U.S.A.

Research Laboratories, Veterans Administration VAN WAGTENDONK. W. J.

Hospital, and the Department of Biochemistry. University of Miami Medical School, Coral Gables,

Florida, U.S.A.

Vogel, H. J. Institute of Microbiology, Rutgers, The State

University, New Brunswick, New Jersey, U.S.A.

WALD, G. Biological Laboratories of Harvard University,

Cambridge, Mass., U.S.A.

Department of Plant Biochemistry, Faculty of YEVREINOVA, T. N.

Fundamental Biology of the Moscow University,

U.S.S.R.

CONTENTS

List of Authors	Page
	ix
A. I. OPARIN Opening Address	1
J. Bernal	
Cosmic Aspects of the Origin of Life	3
G. WALD	
Phylogeny and Ontogeny at the Molecular Level	12
P. H. ABELSON	
Paleobiochemistry	52
A. I. Oparin	-
Origin and Evolution of Metabolism	69
	85
B. L. HORECKER	
Alternative Pathways of Carbohydrate Metabolism in Relation to Evolutionary Development	86
	80
S. J. AIL and H. C. REEVES	
Pathways of C ₂ Metabolism	94
M. FLORKIN	
Fossil Conchiolins of Mother of Pearl	96
N. O. Kaplan	
Studies on Molecular Evolution with Pyridine Coenzyme Analogs	97
V. N. Shaposhnikov	
Significance and Modes of Formation of Pyruvic Acid on Anaerobic Fermentation of Carbohydrates	102

T. N. YEVREINOVA Distribution of Nucleic Acids in Coacervate Drops	110
H. GAFFRON Evolution of Photosynthesis	114
P. P. Cohen and G. W. Brown, Jr. Evolution of Nitrogen Metabolism	129
A. A. IMSHENETSKII Evolution of the Biological Fixation of Nitrogen	139
P. HANDLER Evolution of the Coenzymes	149
W. D. McElroy and H. H. Seliger Origin and Evolution of Bioluminescence	158
DISCUSSION	167
H. EAGLE Metabolic Activities of Cultured Mammalian Cells	169
Yu. I. Sorokin Assimilation of CO ₂ by Heterotrophic Organisms and the Evolution of Photo- and Chemosynthesis	171
R. H. Burris Discussion of Evolution of Biological Nitrogen Fixation	173
E. L. TATUM Biochemical Genetics and Evolution	178
DISCUSSION	187
A. GIERER Chemical Basis of Mutation	189
A. N. Belozersky The Species-specificity of Nucleic Acids	198
R. D. HOTCHKISS and ELENA OTTOLENGHI Genetic Transformation as a Basis for Evolution in Bacteria	215
DISCUSSION	221

S. S. Cohen	
Virus-induced Synthesis of Enzymes and Other Proteins in Bacteria	223
DISCUSSION	239
H. Fraenkel-Conrat and A. Tsugita Biological and Protein-structural Effects of Chemical Mutagenesis of TMV-RNA	242
H. M. KALCKAR Interrelation of Enzyme Syntheses in the "Galactose Sequence"	245
W. K. MAAS Differences in the Arrangement of Genes Controlling Biosynthetic Pathways in Bacteria	248
M. FLORKIN L'évolution biochimique et la radiation physiologique des systèmes biochimiques, chez les animaux	250
T. BÜCHER and D. PETTE Comparable and Specific Relations in the Patterns of Enzymic Activities of the Main Pathways of Energy-producing Metabolism	271
E. BUEDING Comparative Biochemistry of Parasitic Helminths	280
J. Heller Biochemistry of Insects	291
T. W. GOODWIN Comparative Biochemistry of Carotenoids	300
J. ROCHE Biochimie des hormones thyroidiennes et évolution	313
F. EGAMI, M. ISHIMOTO and M. ITAHASHI Some Aspects of Comparative Biochemistry of Sulfate Metabolism	327
M. D. KAMEN Remarks on the Role of Tetrapyrrolic Iron and Magnesium Chelates in Evolutionary Biochemistry	335

		•		
v	ı	1	1	

CONTENTS

W. Niemierko	
Comparative Study on Some Aspects of Digestion and Absorption of Lipids	337
A. M. PAPPENHEIMER, JR.	
Comparative Biochemistry of Respiratory Pigments	339
H. J. Vogel	
Lysine Pathways as "Biochemical Fossils"	341
W. J. van Wagtendonk	
Comparative Biochemistry of Protozoa	343
Index	347

OPENING ADDRESS

by A. I. OPARIN

LADIES AND GENTLEMEN, DEAR FRIENDS:

I extend a warm welcome to all of you gathered here at the Symposium on Evolutionary Biochemistry and express my regret that the leader of our symposium Professor Ochoa has not been able to be present at our Congress. The programme for the present symposium was largely drawn up by Professor Ochoa who took no little trouble in arranging it. We must also express our deep gratitude to Professors Obel, Bolduan, Florkin and Egami for assistance in this work.

Arranging our symposium was no easy matter, since this discussion of biochemical problems along evolutionary lines is the first to be held at an International Congress of Biochemistry. The topicality of this discussion is now perfectly obvious since in the world literature on the subject a wealth of factual material has been gathered requiring interpretation and discussion; an essential for further progressive development of biochemistry.

Aristotle in his time wrote that only he can penetrate the essence of things who understands their origin and development and these words so full of meaning are of course fully applicable both to an understanding of the essence of life in general, and to understanding of metabolism, the basis of knowledge in biochemistry.

The modern biochemist witnesses the ever further unrolling of the variegated tapestry of diverse combinations of metabolic chains and cycles peculiar to individual representatives of animate nature. But, just as the anatomist studying and comparing the structure of the organs in animals reconstructs a picture of their evolutionary development, so the biochemist on the basis of comparative study of substances, separate links in metabolism and their combinations is able to visualize the sequential course of the biochemical evolution of the animate world. The main difficulty here is that evolution of metabolism has not taken a straight pathway: the twists and turns are many and confused.

However, the close relation between the organization of metabolism and the chemical mechanisms underlying it and which run throughout the diversity of the present-day animate world enables us to single out certain combinations of biochemical reactions which are strikingly universal and which must, therefore, have arisen even before the branching of the tree of life

From this, we can even now conceive to a certain degree the sequential course of events and the picture of gradual complication and perfection of metabolism. Of course, by no means everything within this picture commands general aproval and assent. This is still even more true of our judgements on the driving forces in the evolutionary development of metabolism. In this respect there are as we know different views and opinions, discussion of which in this symposium will undoubtedly be useful even if we fail to find agreement on them at this our first meeting.

Allow me to express my warm wishes for the success of our symposium.

COSMIC ASPECTS OF THE ORIGIN OF LIFE

by J. BERNAL

Birkbeck College, University of London, England

DISCOVERIES made in the last few years have furnished a solution to many of the very difficult problems that have appeared earlier in considering the very first stages of the origin of life. What I shall have to say in this introductory talk is to discuss what might be called the preliminary or introductory chapter to Oparin's great theory, a chapter nought, as you might say, of the origin. But this new chapter is necessarily one far more removed from life as we know it than any of the subsequent changes. If we consider the logical prerequisites of any living system, that is the materials and the energy supplies required for life, then we find great difficulties if these, in the first place are limited, as they have been hitherto, to considering that the whole of life, beginning with atoms, originated in the early phases of the earth as we know it now.

In the discussions which took place at Moscow two years ago one of the problems, and a major one at that, was to find the form of the carbon compounds which went to make up life on the primitive earth. There were many points of view put forward on that occasion. The reduced forms, such as methane and ammonia, originally put forward by Oparin and Haldane, still seemed appropriate to most present. However, some adduced arguments based on stability and chemical equilibrium that made it improbable that such reduced forms would be actually those which would appear on an evolving globe. If, however, we postulate, as I did myself, that CO₂ rather than CH₄ was the primary carbon-containing compound, then one has to face the opposite difficulty of accounting for the energy source.

Qualitatively there is no great difficulty in picturing paths of evolution from simple to complex carbon and nitrogen compounds. The experiments which had already been done up to that date by Mueller and others of Urey's school, have demonstrated quite clearly that it was perfectly possible to form the various more elaborate compounds, such as amino acids,

vegetable acids and so forth, from the simple carbon compounds of almost any constitution, provided enough energy could be drawn in from outside. But quantitatively, as you are to see later, there are serious difficulties of accounting for the necessary source of free energy if it be limited to the finite surface of the planet.

In the meanwhile an entirely new source, or a new possible source, for such compounds and the necessary energy has come into consideration. Apart from the old doctrine of Panspermia which Arrhenius had put forward at the beginning of the century, the contribution of outer space to the origin of life has not been seriously considered up to almost a year ago. It came into prominence again not so much by the discovery of radically new facts, but by re-evaluation of some facts already available to the students of the development of the solar system and of its odd constituents, particularly the meteorites. It seemed worth-while to look once again to outer space rather than to the rather limited surface of a planet to discover the form of primary carbon and nitrogen compounds.

Now, it may seem an odd fact that the constitution of the astral bodies, the stars and cosmic clouds is by and large almost identical to the constitution of life. Leaving on one side the inert gases such as helium, neon and argon, the main elements which are found in all stars, and are evidently the nuclearly determined major constituent elements of the universe, are the same seven elements which are, with one very notable exception, silicon, extremely common in life. These are, beginning with the most common, hydrogen—oxygen, carbon, nitrogen, magnesium, silicon and iron. All other elements are present in relatively small proportions and their role in life process is clearly an auxiliary one. But what are the intermediate stages? What are the stages before the selection of those elements which occur in the evolution of life took place?

Now, as it happens, we have been presented with specimens which may very well be these intermediate stages themselves, or very closely related to them. These are the so-called carbonaceous meteorites which constitute a very small and anomalous group. Because they are rare and of unusual composition, the official view has been that they can be neglected, whereas the history of science should have taught us that this is precisely why we should pay attention to them.

The first step in the recent appreciation of the importance of these meteorites came with the observation by Mason in New York, (1) that the carbonaceous meteorites, though they have some analogies to the stony meteorites, contained, in their silicate phase, anything up to 10 per cent of water in the form of hydroxyl. As the water contained in a hydrosilicate

would be expelled by heating at comparatively low temperatures, of some 400°C, it follows that these meteorites have never been exposed since their formation to the kind of temperature necessary to melt the other silicate components forming the so-called chondrites which make up the major part of the stony meteorites. Further, the carbonaceous composition, as studied by Mueller⁽²⁾ and others, shows even greater volatility, loss of organically held water at temperatures below 200°C, and also the considerable decomposition and expulsion of carbon compounds to structures which have been through any kind of heating process.

Mason has put forward the hypothesis that the carbonaceous meteorites were virtual samples of the most primitive forms of condensation of dust in the solar system at the very time of the formation of the planets themselves. The actual meteorites that come to us may have had an intermediate stage on the surface of some asteroid, but they have not, as most of the stony and all the iron meteorites, been subjected, through pressure or radiation, to any really high temperatures. Mason suggests that with primary condensation it might be in the form of an amorphous hydrous magnesium silicate and later this may have crystallized to the various serpentinic or other platy and fibrous silicate materials which are found. It is notable that some electron microscope studies in the laboratory in London have indicated that a number of silicates occurred in these meteorites which have not been recorded so far on earth, disposing, incidentally, of the suggestion that the silicates in these meteorites are artefacts arising after their fall to earth.

Detailed studies of one carbonaceous meteorite, the so-called Kaba meteorite, by Sztrokay⁽³⁾ shows that the problem may be somewhat more complicated than Mason anticipated, because here carbonaceous material appears around and filling cracks in what are definitely high-temperature silicates, while the remaining material, as Mason has shown, contains low-temperature hydrosilicates.

It is possible to push Mason's speculations further to account for the origin of the carbonaceous part of the meteorite amounting to some 10 per cent of its total weight. If in the original dust cloud surrounding the sun we can start condensation at relatively high temperatures with the formation of amorphous anhydrous silicates, the resulting dust would have a very considerable opacity if it was of the order of particle size of 1μ . This opacity in a disc covering the present area of the solar system would induce the formation on these particles as nuclei of the layers of ice, solid ammonia and methane from the surrounding gases. They would, in a sense, become cosmic snowflakes and such snowflakes might have an indefinite

life and possibly do, in the outer regions of the solar system today where the comets are formed, but as in the nearer and denser regions they aggregated together by accidental collision the opacity would diminish exposing them to solar heating. Beginning with the sun outwards they would begin to heat up and lose their main bulk of accumulated ice and gas, reducing them once again to the state of silicate particles.

However, this cannot be the whole story, because the particles all the time had been exposed to cosmic radiation and to some of the more penetrating solar radiations as well. The effect of such radiation on a condensed carbonaceous gas would be to form free radicals, and we have indeed evidence of the formation of these free radicals in the observations of Duchesne⁽⁴⁾ in Liège that free radicals are detectable by magnetic resonance methods in actual carbonaceous meteorites. On evaporation of the main bulk of the hydrocarbons the free radical material would tend to polymerize and form a thin skin on the particles. The existence of this thin skin is brought out by an observation of Mueller's in attempting to analyse the cold Bokkeveldt meteorite, namely that it was not, in the first instance, soluble in boiling hydrofluoric acid, indicating that the silicates which should instantly dissolve in this acid must be protected by thin layers of carbonaceous material.

However, we do not depend in this question on speculations as to the origin of the carbonaceous material, that material is there and can be analysed. The analysis has given rise to many interesting features and somewhere there is great divergence of opinion. Mueller's original and rather crude analysis indicated that the material from the cold Bokkeveldt meteorite contained some 45 per cent of oxygen, and in general was of the nature of a hydrated substance of the type on earth of ordinary black humus, mostly covered with acid carboxyl groups associated with organically bound iron. (The presence of a large amount of organic chlorine may have been associated with the use of chloroform as a solvent.) This year some further analyses have been carried out by other methods. Calvin. (5) for instance, has studied the effects of the infra-red spectra and discovered lines which might correspond to those given by aromatic or purine bodies. Later, Nagy, Meinschein and Hennessy, (6) by the use of mass spectroscopy. maintained that the materials from the particularly unstable Orgeuil meteorite gave on heating hydrocarbon residues corresponding to the normal sequence of saturated fatty acids found in organic bodies and in recent sediments. These conclusions have been queried, but they are no means at present disproved. If they are true, anything said so far about the origin of the carbonaceous meteorites would have to be put backwards about