ELEMENTS

 \mathbf{OF}

PHYSICAL BIOLOGY

BY

ALFRED J. LOTKA, M.A., D.Sc.

"Voilà un homme qui a fait son mieux pour ennuyer deux ou trois cents de ses concitoyens; mais son intention était bonne: il n'y a pas de quoi détruire Persépolis."

— Voltaire



BALTIMORE
WILLIAMS & WILKINS COMPANY
1925

Copyright 1925 WILLIAMS & WILKINS COMPANY

Made in United States of America

Published February, 1925

ALL RIGHTS RESERVED

Composed and Printed at the
WAVERLY PRESS
BY THE WILLIAMS & WILKINS COMPANY
Baltimore, Md., U. S. A.

$\begin{array}{c} {\bf ELEMENTS} \\ {\bf OF} \\ {\bf PHYSICAL~BIOLOGY} \end{array}$

DEDICATED TO THE MEMORY OF JOHN HENRY POYNTING

PREFACE

The preface is that part of a book which is written last, placed first, and read least. As I approach my concluding task I am moved to reflect why a preface should be written at all. This question, if followed into all the intricacies of which it holds potentiality, should apparently result in a composition new in literature, a Preface to the Such precedent should not be lightly established, for it suggests a vista of future degenerations after the pattern of Josiah Royce's infinite succession of maps, each containing within itself its own replica on a reduced scale. But without going to such lengths as this, the philosophy of the preface may perhaps briefly be summarized to this effect, that it is the author's subjective introduction to the more objective matter that should follow. Here he may, if this is deemed of any interest, say something regarding the circumstances that gave origin to the work, and the conditions under which it came into being. He may express his feelings as to its alleged purpose, and may follow custom by giving voice to pious wishes as to the function which the product of his presumptive mind may fulfill in an Universe in which no event, however trivial—be it no more than the addition of one more book to the groaning library shelves—is without distant reverberations.

As to origin, the first plan of the work was laid about 1902, in the author's student days in Leipzig. The development of the topic is recorded, in outline, in various publications, of which the first appeared in 1907 in the American Journal of Science. Reference to this and to its various sequels will be found in pertinent places in the text that follows. The last stage of the work, arrangement of the matter in collected form, and filling in the flesh about the skeleton framework elaborated in the journal literature, was carried out at the Johns Hopkins University upon the invitation of the Department of Biometry and Vital Statistics. For the courtesies so extended to him the author wishes here to express his thanks, as well as for the interest shown in the progress of the work by Dr. Raymond Pearl and the members of the Department, notably Drs. W. T. Howard, L. J. Reed and J. R. Miner. Outside the walls of

viii PREFACE

this University I think with very particular appreciation of the never-failing succor in times of mathematical trouble, which I found at the hands of Prof. F. R. Sharpe of Cornell University; also of the patient assistance, upon more than one occasion, from Prof. W. B. Fite of Columbia University. And I gratefully recall encouragement received from Dr. G. K. Burgess, Director of the Bureau of Standards, especially in the earlier stages of the work, when encouragement was most needed.

Acknowledgment has been made in the text for numerous quotations. The somewhat extended excerpts from certain articles published in the Scientific Monthly call for special notice here, and I wish to express my thanks both to the author, Prof. G. W. Martin, and to the Editor of the Monthly, for permission to quote thus at length from its pages. I am similarly indebted to the Editor of Harpers Magazine for permission to reproduce here certain portions of an article from my pen, entitled "Biassed Evolution", which originally appeared in the May issue (1924) of that publication.

Toward the publishers, Messrs. Williams and Wilkins and in particular Mr. C. C. Thomas, I have every occasion to entertain feelings of the most cordial appreciation. Through their courteous attentions the business of bookmaking was made a pleasure.

My greatest debt is acknowledged in the dedication. Whatever merits this book possesses may well be credited to the influence and teaching of Poynting. There is little danger that its faults shall be charged to his account.

As to the topic of the work it seems unnecessary to say many words here, inasmuch as a delineation of this has been made the subject of a special chapter on *The Program of Physical Biology*. Only this explanation it may be well to offer here, that, as proposed in Chapter V, the term *Physical Biology* has been employed to denote the broad application of physical principles and methods in the contemplation of biological *systems*, whereas *Biophysics*, in common parlance, relates rather to the special field of certain physical aspects of the life processes of the *individual*. With this terminology, Physical Biology would comprehend Biophysics within its scope.

The writer cannot in reason expect to have produced a work without blemish. Even an approach to such absolute perfection is the rare privilege of a few. He would, however, be unjustified in addressing the reading public at all if he did not entertain the hope

PREFACE

that, despite shortcomings, these pages may bring to the reader new assets, here and there a new piece for his mental furniture, now and again a new perspective, a new comprehensive outlook over a body of facts and relations in themselves perhaps familiar.

The work has been largely one of systematization, and of development of method. Factual material has been introduced essentially for the purpose of illustrating the point of view to be set forth. There seems therefore hardly any occasion for apologetic explanations that anything of the nature of completeness in the presentation of pertinent facts was in nowise aimed at. Indeed, it must be obvious upon most casual reflection that such completeness, in a subject of the amplitude of that here taken in view, could be achieved only in a cyclopedic work of several tiers of volumes.

Considerable care has been taken to cite in detail the sources consulted. It was felt that, on account of the wide dispersal of these citations over a broad field of scientific literature, few readers could be expected to be familiar with all the branches of pertinent library lore, and for this reason a collation of such references should have a value of its own, even apart from the text. At the same time the compilation of anything like a complete bibliography could not be undertaken on the present occasion.

It is hoped that the mathematical mien of certain pages will not deter biologists and others, who may be disposed to look askance at symbols of the art, from acquiring an interest in other portions of the book. Biometricians will, presumably, not shrink on this score; to them, and to physicists, (whom I should greatly wish to number among my readers) I may perhaps confess that I have striven to infuse the mathematical spirit also into those pages on which symbols do not present themselves to the eye. For this I offer no apology.

For the sake of space economy recapitulary paragraphs have, as a rule, not been given a place in the text. An exception has however been made in Chapters XX, XXXIII and XXIV, the last of which, in particular resumes and amplifies somewhat certain phases of the topics discussed in earlier chapters. The reader who may wish briefly to review the substance of his reading as he proceeds, should find suitable assistance in the rather detailed Analytical Synopsis of Chapters that has been placed immediately after the Table of Contents. And finally, a bird's eye survey of the general

X PREFACE

field covered in this work can be obtained by consulting the Tabular Synopsis at the end.

Here, then, I make my exit from the prefatory stage and commend my work to the tender mercies of the reader; not without some trepidation, for I recall how Voltaire said of one: "Il fit une philosophie comme on fait un bon roman; tout parut vraisemblable, et rien ne fut vrai;" and there comes to mind the language still plainer of du Maupassant—"Depuis qu'ils ont appris à lire et à écrire, la bêtise latente se dégage." I trust that the reader's response to these pages may not be too fervent an Amen to the prayer of The Sceptical Chymist "It is to be hoped that these men, finding that they can not longer write impertinently and absurdly will be reduced either to write nothing, or books that may teach us something . . . ; and so, ceasing to trouble the world with riddles or impertinencies, we shall either by their books receive an advantage, or by their silence escape an inconvenience."

Alfred J. Lotka.

Johns Hopkins University, May, 1924.

ANALYTICAL SYNOPSIS OF CHAPTERS

PART I. GENERAL PRINCIPLE

Chapter I. Regarding Definitions. Definitions are arbitrary, 3-But are governed by considerations of expediency, 3—The problem of expediency in framing definitions is not always a simple one, 3-Pseudo-problems arising from failure to recognize the arbitrary character of definitions: Hunting the Jabberwock, 4-Subjective discontinuities introduced by the senses, 5-Examples: Colors, e.g. blue, green; light and heat waves; distinction between animals and plants; between biological species; between living and non-living matter, 5-To such abrupt subjective divisions there may correspond no objective discontinuity in nature, 5-Definitions in Biology, 5-Vitalism versus Mechanism; merely a question of terms, 7—Herbert Spencer's "proximate definition" of life, 7-Inadequacy of Spencer's definition, 7-Sir Edward Schaefer's standpoint, 8—Line of division recedes with increasing knowledge 8-Alleged characteristics of living matter: Growth from within 8-Chemical growth as distinguished from physical growth of crystals, 10—Growth from unsaturated solution, as distinguished from growth of crystals from supersaturated solution, 10-"Selective" growth, 10-Reproduction, 11-Vital Force, 13—Physical chemistry of structured systems, 13—Geometrical element lacking in physical chemistry of today, 13-Systems ordinarily considered are either structureless or of simple structure, 14-This absence of structural features in physico-chemical systems is due to subjective, not objective reasons, 14—Due in part to convenient arbitrary restrictions, 15—Relation between growth, environment and structure, 15-The laws of chemical dynamics in structured systems will be the laws that govern the evolution of a system comprising living organisms, 16-Application to Biology: The organism as a structured physico-chemical system, 16—The travelling environment, milieu intérieur, 17—Increasing independence of organism of its remote environment, 18—The policy of resignation: Abandoning the attempt to define life, 18-Parallels in the history of science: Abandonment of the attempt to prove Euclid's twelfth postulate led to new systems of geometry, 18—Abandonment of attempts to build perpetual motion machines was equivalent to recognizing the law of conservation of energy, 18-Abandonment of the attempt to detect the earth's motion through the ether is the foundation of the modern theory of relativity, 18—The ideal definition is quantitative, 19— Desirability of establishing a quantitative definition and conception of evolution, 19.

Chapter II. Evolution Defined. Definition should conform as far as possible to common usage of the term, 20—Analysis of common conception of evolution, 20—Evolution is history, but not all history is evolution, 20—Systems in purely periodic motion would not be said to evolve. They repeat in endless

succession the same series of events. In an evolving system each day is unlike any other day, 21-Evolution not a mere changeful sequence, 21-Abortive attempts to formulate the direction of evolution, 21-These attempt definition in terms of a single component, 22-Such definitions are foredoomed to failure, a successful definition must be framed in terms of the evolving system as a whole, 22—Evolution is the history of a system in the course of irreversible transformation, 24-Scope of this definition: What it excludes; what it includes 24-The line of division depends on the nature and extent of our knowledge regarding the system, 25-This is in harmony with the fact that problems of evolution are largely problems of probability, 25-All real transformations are irreversible, hence all real history is evolution, 26-What then is gained by the definition? 26-It indicates the direction of evolution as the direction of irreversible transformations, the direction of increasing entropy, 26-Example of pendulum. Irreversible feature introduced by frictional force, 27—Inertia-free or completely damped systems, 28—Accelerations vanish with velocities, 29-Velocities are single-valued functions of configuration, 29.

Chapter III. The Statistical Meaning of Irreversibility. Apparent irreversibility (progressiveness in time) of certain theoretically periodic processes, 30—Their periodicity, with eventual return to initial state, never observed in practice, 30-Explanation of this discrepancy: Macroscopic model illustrative of irreversibility of gaseous diffusion, 30—Return to initial state possible, but exceedingly rare (highly improbable), 31—The model is competent to illustrate also the highly improbable event of return to initial state, 32-Dynamical theory indicates not only occasional but periodic return to initial state, 32—A second model illustrates this also, 32—Evolution as passage from less probable to more probable states, 35-Inadequacy of this "principle": it is indefinite in failing to specify the characteristic with respect to which probability is reckoned; and it is incomplete in failing to draw attention to certain energy relations, 35—Irreversibility is relative, depending upon the means naturally available or arbitrarily permitted to operate upon the system, 35-Significance of this in organic world: Macroscopic irreversibility of diffusion processes in nature, 36-Need of a method of mathematical analysis to deal with cases intermediate, in specified degree, between the following two extremes: (a) Wholly indiscriminate (pure chance) operation upon material in bulk. (b) Wholly determinate operation, with nothing left to chance, upon materials discriminated and acted upon in detail, piece by piece, and circumstance by circumstance, 36—This method must take account of degree of perfection of the mechanical and psychic equipment by which each organism reacts upon its environment, 37—Senses as a means of overcoming chance, 37—Physical significance of our subjective sense of forward direction in time, which finds no expression in the differential equations of pure dynamics, 37—This subjective time sense may be related to the influence of initial conditions in dynamics, 38-But the direction of evolution seems related rather to that directedness in time which is characteristic of aperiodic or seemingly aperiodic processes, 38-Inadequacy of thermodynamic method, 39—The linking of evolution with the

concepts of thermodynamics and statistical mechanics is instructive as suggesting a conception of the direction of evolution, the direction of increasing entropy, increasing probability, 39—This point of view, however, is inadequate for application to concrete cases of organic evolution, because data are furnished in terms unsuited to the methods of thermodynamics, 39—Neither are existing methods of statistical mechanics, as applied to molecules and the like, helpful; the instrument is ill adapted to the scale of the object, 39—New method needed, that shall accept its problems in terms of biological data, as thermodynamics accepts its problems in terms of physical data; a General Theory of State, an "Allgemeine Zustandslehre" 39.

Chapter IV. Evolution Conceived as a Redistribution. Evolution viewed as a redistribution of matter among the components of a system, 41-System described by statement of mass of each component, and indication of value of certain parameters, 41—Analytical expression of history of system given by relations or equations established between the variables and parameters defining the state of the system, 41—Fundamental equations usually simplest in form of differential equations, 42—Particular form of equations of evolving systems, 42—General form of equations of evolving system, 43—Equations as applied to life-bearing system, 43—Definition of the components arbitrary but conclusions relate to the components as defined, 44—Relation of evolution, as here conceived, to the problem of the origin of species, 44—Inter-group and intra-group evolution, 44—Analytical indication of intra-group evolution, 45—Fundamental equations resemble in form the equations for an inertia-free or completely damped system, 47—Fundamental equations, as here given, may not cover all cases, but are at any rate of very wide scope, 47—Equations interpreted to include possible lag or lead effects, 47-Singular implications of lag and lead effects; possible relation to phenomena of memory and will, 48-Appearance of lag and lead effects in equations may, however, be spurious, 48.

Chapter V. The Program of Physical Biology. Systematization and division of subject, 49—General mechanics of evolution, 49—Macro-mechanics and micro-mechanics, 50—Statistical mechanics as the connecting link, 50—Stoichiometry, the study of mass relations (material transformations), 50—Energetics or Dynamics, the study of the energy transformations, 50—Kinetics and Statics, 51—Equilibrium and steady states, 51—Moving equilibria, 51—Displacement of equilibrium; Le Chatelier's principle, 52—Sociological analogues of forces and "quasi-dynamics" (economics), 52—The term *Physical Biology* to be used to cover the territory indicated in this chapter, 52—Methods of obtaining data, 52—Chart of Program of Physical Biology, 53—Methods of elaborating data, 54.

PART II. KINETICS

Chapter VI. The Fundamental Equations of Kinetics of Evolving Systems. General case, 57—Some implications of the fundamental equations in their general form, 57—Equations of constraint, 58—Elimination of variables. Introduction of constants A, 58—Evolution with parameters P, Q and A constant, 58—Equilibria or steady states, 59—Number and character of

equilibria. Example: Fly population, 59—Fundamental equations transformed by introduction of excess of actual masses over equilibrium masses in place of the former, 60—Expansion in Taylor's series, and solution in exponential series, 60—Characteristic equation for exponential coefficients, 60—Significance of sign and character of roots λ of characteristic equation, 61—Stability of equilibrium, 61—Mode of approach to equilibrium: Aperiodic and periodic (oscillatory) type, 61—Analytical confirmation and extension of a passage in Herbert Spencer's First Principles, 61—Zero or negative roots of the equilibrium equation: Unfit species, 62.

Chapter VII. Fundamental Equations of Kinetics (Continued). Special Case: Single Dependent Variable. Law of population growth, 64—Population of United States, 66—Stability of equilibrium, 67—Experimental populations, 69—Diminishing population, 70—Growth of individual organism, 71—Autocatakinesis, 76.

Chapter VIII. Fundamental Equations of Kinetics (Continued). Special Cases: Two and Three Dependent Variables. Interdependence of species, 77—Several types of interdependence, 77—Analytical characteristics of those types, 78—Effect of these characteristics upon the nature of the solution of the equation of Kinetics for two variables, 79—Concrete examples, 5—Martini's equation for immunizing diseases, 79—A special case noted by Watson, 81—The Ross malaria equations, 81—Example in parasitology, 83—Thompson's treatment of the case, 83—Objections to this, 87—Treatment of case by general equation of kinetics, 88—Nature of the solution: it represents a periodic or oscillatory process, 90—Comparison with observed facts according to L. O. Howard, 90—Annihilation of one species by another, 92—Case of three dependent variables, 94—Relation of this to a practical problem in sea fisheries, 95—Replaceable and irreplaceable components, 95—Limiting factors, 97—Liebig's law, 97—Chart of types of interdependence of biological species, 98.

Chapter IX. Analysis of the Growth Function. The form of the function F, 100—Growth of aggregates, 100—Demographic functions, 101—Survival curve data, 107—Influence of age distribution upon rate of growth of population, 109—The stable or "normal" age distribution, 110—Demographic relations in "normal" population, 115—Rate of increase per generation, 118—Effect of selective slaughtering, 119—Intelligence as a discriminating agency, 120. Intra-group evolution (with Mendelian inheritance, according to J. B. S. Haldane), 122.

Chapter X. Further Analysis of the Growth Function. Adjustment of the birth rate to optimum, 128—Births do not in themselves add to the mass of the aggregate, but only furnish new mouths for the assimilation of mass, 129—Aggregates of constant units, 129—Aggregates of variable units, 130—The stream of substance through the form of the organism, 130—Two types of organism: economic and wasteful of births, 131—Domestic animals kept for produce, 132—Evolution does not favor either the economic or the wasteful type of organism; both persist side by side, 135—Interdependence of these two types as example that direction of evolution can not be defined in terms of a single species, 11—Domestic species as producers of human food: wastefulness

from standpoint of domestic species is high efficiency from human standpoint, 135—Network of chains of interrelated species, 136—Transformation factors and their economic significance, 137.

PART III. STATICS

Chapter XI. General Principles of Equilibrium. Equilibria and stationary states, 143—Scope of Statics, 143—Kinetic, dynamic, and energetic definition of equilibrium, 143—Our chief interest here in stationary states not true equilibria, 145—General equilibrium condition, 145—Different types of equilibria, 146—Illustration: Malaria equilibrium according to Ross, 147—Metastable equilibrium, 151—Exceptional cases, 151.

Chapter XII. Chemical Equilibrium, as an Example of Evolution under a Known Law. Case of simple balanced reaction, 152—Relation between "birth" rate and "death" rate of molecules, 153—The survival factor p (a) and life curve of molecules, 153—Reaction constant as a a force of mortality, 154—Chemical reaction as a case of survival of the fittest, 154—Analogy of chemical reaction to course of events in population of mixed biological species, 155—Presumptive mechanism of chemical reaction (Baly), 155—The fugaceous transitional state intermediate between chemical compounds (Schönbein), 156—Laws of thermodynamics, as determinants of the end state in an equilibrium reaction, are, in this case, the Law of Evolution of the system, 157—Natural laws conveniently expressed as maximum or minimum principles, 157—Law of organic evolution may be expected to take this form, 158—Law of chemical evolution is framed in terms of the system as a whole; law of organic evolution must undoubtedly also be thus framed, 158—Law of equilibrium expressed in form of a minimum principle, 158.

Chapter XIII. Inter-Species Equilibrium. Equilibrium condition in more particular form, 161—Numerical illustration, 162—Economic relationship of coefficients appearing in equilibrium condition, 163—Sources of information regarding biological equilibrium: Biological surveys, 164—Analysis of stomach, contents, 166—Intra-species equilibrium (with Mendelian inheritance), 170.

Chapter XIV. Inter-species Equilibrium: Aquatic Life. Special occasion for demological studies of aquatic population, 171—Fishes as natural dragnets, 171—Aquatic food chains in relation to human food, 2—Importance of aquiculture for the future, 172—Loss of fertilizer through modern methods of sewage disposal, 172—Partial restoration of such material to human food supply through fisheries, 173—Different methods of census of marine population: dragnet; bottom samplers; recatching of marked catches; centrifuge; dilution culture, 173—The nannoplankton, 173—Work of Petersen in Kattegatt, 174—Quantitative estimates of principal groups of the marine population of Kattegatt, and their interrelation, 175—Summary of methods of marine biological census (Table), 176—Food chains, 176—Necessity of occupying ourselves with the more remote links of our food chain, 177—"Feeding our foods," a species of symbiosis, 180—Agriculture and aquiculture, as mining and as manufacturing industries, 180—Resources but recently tapped, and others still untouched, 180—Food chains in aquatic species, 180—Wastefulness of long food chains,

181—Economic value of shell fisheries owing to simple food chain coverting vegetation directly into human food (oysters, etc.), 181—Primary, secondary and tertiary foods, 171—Cycles and the circulation of the elements in Nature, 183.

Chapter XV. The Stage of the Life Drama. The tripartite world, 185—Atmosphere, 185—How the earth holds her atmosphere, 185—Cosmic losses from the atmosphere negligible, 188—Cosmic accessions to the atmosphere, 192—Hydrosphere, 192—Aquatic atmosphere, 193—Lithosphere, 193—Cosmic accessions to lithosphere, 195—Composition of earth's crust, 195—Relation to composition of organism, 197—Similarity in composition of sea water and blood serum, 201—Significance of this as regards aquatic origin of terrestrial fauna, 202—Chemical correlation in soil and in organism, 204—Accessibility of valuable earth constituents, 206—Accessibility not in any direct relation to abundance, 206—H. S. Washington's classification of petrogenic (rock-forming) and metallogenic (ore-forming) elements of the periodic table, 207—Dissipating and concentrating processes in Nature, 208.

Chapter XVI. The Circulation of the Elements: The Water Cycle. Circulation of elements vaguely realized by ancients, 209—Water requirements of human body, 210—Water requirements of plants; rainfall as limiting factor, 211—Sources of supply, 213—Quantitative estimates of several items in water cycle, 213—Water cycle diagram, 215—Fraction of total water circulation taking part in life cycle, 216.

Chapter XVII. The Carbon Dioxide Cycle. Combustion as an essential feature of the life process, 218—Analogy of flame arising from spark and life arising from germ, 218-Rarity of ignition except from pre-existing flame analogous to apparent impossibility of life originating except from preexisting life, 218—Oxygen as an inorganic food, 219—Plant nature of man in his attitude toward this inorganic food, 219—The carbon cycle, 220—Carbon as the organic element, 220—Source and gate of entry into the organic carbon cycle, 220— Some estimates of quantities involved in the carbon cycle, 220—Interrelation of green plants and animals, 221—Carbonization of dead vegetable matter and its significance for the industrial civilization of the present era, 221—The present an atypical epoch: man living on his capital, 222—Attempts to establish the balance sheet of the earth's carbon economy, 222—Absorption of CO₂ in weathering of rocks, 223—Formation of CO₂ by burning of coal, 224—The ocean as an equalizer regulating the CO₂ content of the air, 224—Uncertainty as to net loss or gain of total CO₂ in atmosphere, 225—The oxygen cycle, 225—Origin of atmospheric carbon dioxide and oxygen, 225—Carbon cycle diagram, 226— Loss of oxygen from the atmosphere, 228.

Chapter XVIII. The Nitrogen Cycle. Natural demand and supply, 229—Seeming abundance of nitrogen illusory, 229—Nitrogen cycle diagram, 230—Gate of entry into nitrogen cycle, 232—Leak of nitrogen out of circulation, 232—Loss of nitrogen in combustion, distillation and coking of coal, 233—Significance and rapid increase of by-product recovery type of coke ovens, 233—Other losses of combined nitrogen, 234—Accessory sources of combined nitrogen; volcanic effluvia, 234—Human interference in nitrogen cycle, 236—Exploitation of guano deposits, 236—Chilean nitre beds, 236—Consumption of

saltpeter as fertilizer and otherwise, 237—Origin of nitre beds, 238—Industrial nitrogen fixation processes, 239—Birkeland and Eyde nitric acid process. Cyanamide process. Haber ammonia process. Bücher cyanide process, 239—Combination of Haber process with Solvay soda process, 239—Ostwald oxidation process, 241—Meteoric rise of nitrogen fixation industry, 241—Its ethnological significance, 241—Economic and energetic significance of concentration, e.g. of supply of combined nitrogen, 243—Localized sources of concentrated supplies as centers of attraction in man's economic activities, 244—Total circulation tends to increase, 245.

Chapter XIX. The Phosphorus Cycle. Immobile elements, 246—Natural phosphorus supply of soils, 246—Phosphorus cycle diagram, 247—Leakage of phosphorus from circulation, 248—Phosphate rock and the migration of phosphorus, 248—The rôle of fish and birds in the phosphorus cycle, 249—Soil losses of phosphorus, 250—Phosphate slag as fertilizer, 251.

Chapter XX. Cycles: Conclusion and Summary. Circulation of chlorine and the alkalis, 252—The sea and the sun as a Soxhlet extractor, 252—Sodium chloride cycle diagram, 254—Differential behavior of sodium and potassium in the process of extraction, 255—Comparative rarity of potash in soils, 255—Effect of World War on potash market, 256—Circulation of sulphur, 256—Circulation of iron, 256—Summary of cycles, 257—Supply of plant food in soil, 257—Rate of participation of elements in cycles of nature, 258.

Chapter XXI. Moving Equilibria. Principle of continuity, 259—Equation of slowly moving equilibrium; first approximation, 259—Higher approximations, 260—Special case: pace set by slowest member in a chain, 261—Radioactive equilibrium, 261—Equilibrium polygon, 266—Extinction of unadapted species, 266—Example of inaccuracy of first approximation, 268—Radioactive chains as cosmic clocks, 268—Geological time table, 269—Origin of elements and ultimate genesis of organisms, 269—Relative abundance of the elements, 271—Terminal stages of the earth's evolution: Geophysics and geochemistry, 273—Joly's theory of periodic melting of the earth's crust, 275—Organic moving equilibria, 276—Equilibrium polygon, 277.

Chapter XXII. Displacement of Equilibrium. Perfectly general case of influence of change in parameters will not here be considered, 280—Principle of Le Chatelier, 281—Some common misstatements of the principle, 282—Early essayed application to biology, 283—Conditions of validity of the principle, 284—Extension of scope of rigorous applicability, 286—Area and rent, 288—Discussion of displacement of equilibrium independently of Le Chatelier's principle, 289—Case I: Displacement of equilibrium between food and feeding species, 289—Case II: Change of circulation through moving cycles, 292—Some significant cases of instability, 294—Vicious circles, 294—Cumulative cycles simulating orthogenesis, 296—Benign cycles, 297.

Chapter XXIII. The Parameters of State. Topographic parameters, 300—Intensity factor of energy, 303—Simpliest examples of topographic parameters: volume, area, 301—Complexity of topography in organic evolution, 301—Simplification of problem by "substituting ideal upon which it is possible to operate, for intractable reality", 302—Empirical study of biogeography and ecology, 302—Conjugate parameters, 303—The intensity law in organic and

economic systems, 303—Rent as a measure or index of population pressure 304—But population pressure exists independently of rent, e.g., in species other than man, 304—Distant analogy of law of population pressure to gas law, 305—Law of urban concentration, 306—Biological background of population pressure, 307—Influence of population density on rate of reproduction (Pearl and Parker), 308—Influence of population density on duration of life (Pearl and Parker), 309—Topographic parameters during period of diffusion, 311—Willis' theory of Age and Area, 311—Climatic parameters, 317—Their laboratory investigation (Pearl and Parker), 319—Parameters of state and the analytical condition for equilibrium, 319—Thermodynamic analogy, 320—Inversion of typical problem of thermodynamics, 321—Systems of Quasi-Dynamics, 321.

PART IV. DYNAMICS

Chapter XXIV. The Energy Transformers of Nature. The fundamental equations of Kinetics do not exhibit any explicit reference to dynamical or energetic relations, 325—But certain of the components S are energy transformers, 325—Fundamental characteristics of energy transformers, 325—Cyclic working; output and efficiency, 326—Thermodynamic law of maximum output, 326—Reversible and irreversible processes, 327—Composite and coupled transformers, 327—Accumulators, 328—Chemical accumulators, 328—Growth, 328—Law of growth, 328—Anabions and catabions, 329—Systems of transformers, 329—Plant and animal as coupled transformer, 330—The World Engine, 331—Share of sun's energy that falls to different constituents of world, 331—Share falling to organic circulation, 331—Relation of transformer cycle to circulation of the elements, 334—Influence of limiting factors upon working of world engine, 334—Evolution of the World Engine, 335.

Chapter XXV. Relation of the Transformer to Available Sources. Distributed and localized sources of energy, 336—Random and aimed collisions, 337 -Negative correlation, 337-The correlating apparatus, 338-Component elements of correlating apparatus: Depictors, Receptors, Elaborators, Adjustors, 339-Receptor-effector circuit begins and ends in environment, 340-Significance of this, 340—Correlating apparatus not peculiar to living organisms, 340—Mechanical imitations of living beings (automatons) 341—Chess as a conventional model of the battlefield of life, 343—The biological contest considered in the light of the chess analogy, 343—Topographic map, centers of mobility and centers of influence as the elements of the game, 343—Zones of influence, 344—Collisions or encounters, 344—Zones of mobility, 345—Analytical statement of problem of organic conflict, 345—The behavior schedule, 346—Specific productivity, 347—Effect of change in zone pattern, (Intraspecies evolution), 348—Biologic relation of economic value, 350—Effect of change in behavior schedule, 350-Rigid or automaton type and elastic or free-choice type of behavior schedule, 350—Relation between ideal and actual organism, 352—Effect of small departure from perfect adjustment. 353—Relation of economic value to physical energy, 354—Economic conversion factors of energy, 355—General or aggregate effect of individual

struggles for energy capture, 356—The law of evolution adumbrated as a law of maximum energy flux, 357—Statistical mechanics of a system of organisms, 358—Mean free path, 358—Frequency of collision and capture, 359—Influence of size of organism, 359—Curves of pursuit, 360—Random motion under a bias, 360—Use of models, 360.

Chapter XXVI. The Correlating Apparatus, 362—Receptors, 363—Artificial receptors, 364—Significance of these in evolution of modern man, 364—Effectors, 366—Artificial effectors; industrial evolution, 367—Singular effects of industrial evolution, 368.

Chapter XXVII. Extension of the Sensuous World Picture. The Elaborators, 371—The scientific world picture: Systems of coordinates, 372—The ego as a coordinate reference frame, 372—The ego immaterial, 373—Interpenetration of the egos, 374—Where is Mind?, 375—Fundamental premises and implicit assumptions, 376—Difficulty of shaking off preconceived premises, 377—Obstacle which this raises to understanding, 377—The communicators, 378—Orthogenesis in human evolution, 378—Orthogenesis does not suspend selection, 380—Importance of curiosity in evolution, 380.

Chapter XXVIII. The Adjustors. Mechanistic and teleological interpretation of adjustors, 381—Significance of the future in the operation of adjustors, 382—The future that may be and the future that will be, 382—The doubtful cases, 383—Final causes or purposes not usually postulated when sufficient account can be given of events in terms of efficient causes (e.g., in terms of mechanistic explanation), 384—Adaptive adjustment of tastes, 385—Spencer's hedonistic principle, 386—Genuine utility for social service, 386.

Chapter XXIX. Consciousness. Relation of consciousness to physical conditions, 388—Conditional relations, 388—A fundamental hypothesis admitted, 389—Consciousness is closely bound up with life processes and structures, 390—Consciousness dependent on metabolism. The personal element, 391—Consciousness possibly a general property of matter, 392.

Chapter XXX. The Function of Consciousness. The contents of consciousness determined by past and present bodily states, 394—Operative relations of consciousness to physical conditions, 394—Not only knowledge but motive required in the working of the human organism, 394—Motivation in lower organisms appears fatalistic (simple tropisms), 395—Purposive action, 395—Dynamic psychology, instinctive drives to action, 396—Individual traits. Instinct of workmanship and self-expression, 396—Influence of special aptitudes, 399—The industrial and the personal problem of satisfying instincts, 400.

Chapter XXXI. The Origin of Consciousness in Living Organisms. Why has nature resorted to consciousness as means for effecting adaptive reactions of organisms? 402—The problem of psycho-physical parallelism, 402—The double aspect theory of consciousness, 403—Physical analogies, 403—Physico-chemical theory of consciousness as a state related to the transitional state of molecules in chemical reaction, 403—Argument of simplicity of structure may be invoked in favor of this theory, 404—Origin of consciousness, 404—Some elementary forms of consciousness perhaps a general property of all matter, 404—In that case not consciousness has been evolved, but only a particular type of consciousness, a consciousness integrated around an ego, 404.