

Series in Population Biology



McGRAW-HILL PUBLICATIONS
IN THE BIOLOGICAL SCIENCES

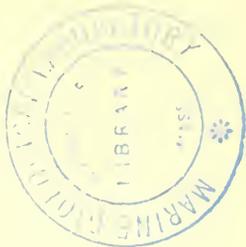
Marine Biological Laboratory Library
Woods Hole, Massachusetts



MBL/WHOI



0 0301 001161 3



the process of evolution

**Recent McGraw-Hill Publications
in the Biological Sciences**

Series in Population Biology

Ehrlich and Holm The Process of Evolution

Series in Organism Biology

Mazia and Tyler The General Physiology of Cell Specialization



This symbol of the cephalopod Nautilus appears on all McGraw-Hill Publications in the Biological Sciences. It was chosen to represent the just proportion of living structures and to suggest the harmonious workings and balanced arrangement of the parts and elements of living things. The color of the binding represents the Biological Series in which this book is published.

CH 222
E 17

the process of evolution



PAUL R. EHRLICH | RICHARD W. HOLM

Department of Biological Sciences

Stanford University

Illustrated by ANNE H. EHRLICH

McGRAW-HILL BOOK COMPANY, INC.

New York

San Francisco

Toronto

London

The Process of Evolution

*Copyright © 1963 by the McGraw-Hill Book Company, Inc. All Rights Reserved.
Printed in the United States of America. This book, or parts thereof, may not
be reproduced in any form without permission of the publishers.
Library of Congress Catalog Card Number 63-15891*

19130

56789101112 HD MM 7543210698

To Edgar Anderson
Joseph H. Camin
Herbert L. Mason
Charles D. Michener
Robert B. Sokal
and Robert E. Woodson

preface

Modern evolutionary theory is the great unifying concept of biology. It represents the major theoretical triumph of the biological sciences—an all-embracing theory which attempts to explain the manifold complexities of biological phenomena. The biochemist attempting to understand the genetic code, the neurophysiologist probing the complex mechanisms of the mind, the embryologist seeking to understand how one tissue affects the development of another, indeed, all biologists, are working on problems whose *theoretical* significance can be measured only by their contribution to our understanding of evolutionary phenomena. The biochemist may be able eventually to cure cancer, the neurophysiologist to understand mental disorders, and the embryologist to discover how the genetic code is translated into an organism. But, without a theory that interrelates all these phenomena, their work would have only applied significance.

The central position of evolution in biology has long been recognized. Nevertheless, most laymen and many biologists are largely ignorant of modern evolutionary theory. This book is an attempt to supply a reasonably concise volume dealing with organic evolution. It has been written for the reader concerned more with the *process* of evolution than with its products per se. There are no pictures of dinosaurs, no taxonomic descriptions of organic diversity, and no discourses on the history of evolutionary thought.

We have assumed that our readers have reached at least that level of biological sophistication attained in a rigorous university course in biology. We hope that the book will serve as a challenging text for an undergraduate course in evolutionary theory, as a basic text to be supplemented with outside reading for a graduate course, and as general reading for biologists in other fields who may wish a brief review of what is known of the process of evolution. Most of the material presented has been used in either the undergraduate course in evolutionary processes or the course in advanced topics in evolution at Stanford University.

An attempt has been made to present evolutionary theory as a unified whole. Because we are assuming some familiarity, at least on a casual level, with phenomena such as selection and mitosis, we have felt free to make passing reference to them before they are treated in detail. Life, meiosis, genetic systems, culture, and the like have not been taken for granted. Rather we have attempted to show how these phenomena are themselves the result of evolutionary processes. Necessarily this involves speculation, which we

feel to be rewarding and stimulating. It is, however, important that it be recognized as speculation. In some areas, other evolutionists certainly will find our treatment heterodox. In particular, we have deemphasized taxonomic ideas such as species and subspecies, which we feel have channeled the thinking of biologists about evolutionary problems. The term adaptation has been given the relatively inconspicuous role that we feel it deserves. Our reasons are discussed in the final chapter.

We have tried to make our descriptions and discussions as rigorous as possible, except where it becomes absurdly pedantic to avoid taxonomic concepts or the casual use of words such as selection and adaptation. Lapses into what may be termed teleology we regard as teleonomy. We hope the reader will agree that a somewhat more unified and logical treatment of evolutionary phenomena is possible if a rigid taxonomic framework is not followed. Scientific names used in this book connote kinds of organisms and carry no implications of genetic attributes or phylogeny.

At the end of each chapter is a list of references chosen, in part, because of their currency and extensive bibliographies. Each reference is briefly annotated. Reference without a direct citation often is made to scientists closely associated with a particular concept or experiment; direct citations can be found in the bibliographies of general papers listed. A rather extensive glossary also has been included.

Our intellectual indebtedness to a very large number of evolutionists will be obvious. We must specifically acknowledge the writings of Edgar Anderson, C. D. Darlington, Theodosius Dobzhansky, Herbert L. Mason, Ernst Mayr, George Gaylord Simpson, G. Ledyard Stebbins, and Sewall Wright which have had a profound influence in interesting us in evolutionary problems and in shaping our thoughts about them.

We should like to thank the following persons who have helped us in many ways in the task of preparing this book: Joseph H. Camin, Verne Grant, P. H. Greenwood, N. K. Johnson, Alan E. Leviton, George S. Myers, C. L. Remington, R. G. Schmieder, and Robert C. Stebbins.

One or more chapters of the manuscript were read by Kenneth B. Armitage, William K. Baker, D. L. Bilderback, Marsden S. Blois, Winslow R. Briggs, Howell V. Daly, Ruth R. Ehrlich, M. M. Green, Robert W. Hull, Joan Johnston, Donald Kennedy, Charles D. Michener, Ashley Montagu, Robert M. Page, John F. Pelton, David D. Perkins, Timothy Prout, Peter H. Raven, David C. Regnery, G. G. Simpson, Robert R. Sokal, Michael E. Soulé, John H. Thomas,

Robert P. Wagner, Norman K. Wessells, and Charles Yanofsky. Theodosius Dobzhansky read and criticized the entire book. This generous donation of time and effort on the part of all these individuals is deeply appreciated. Many of the subjects considered here have been discussed in detail with colleagues and students in our Population Biology Seminar. The authors accept full responsibility for all errors of fact and interpretation, as they have not always been able to adopt the suggestions of the reviewers.

Paul R. Ehrlich
Richard W. Holm

contents

**PART 1 | ORGANISMS:
ORIGIN AND FUNCTION**

Chapter 1 | The Origin of Life 4

The Early Stages	6
Origin of Self-replicating Systems	8
Energy Sources	9
Origin of Structure	12
Origin of the Genetic Code	13
Reading the Code	17
Summary	19
References	21

Chapter 2 | Units of Replication 22

Structure of Cells	23
Cell Division: Mitosis	27
Cell Division: Meiosis	31
Summary	35
References	35

Chapter 3 | Genetics 36

Variation and Mendelian Genetics	37
The Units of Heredity	38
Mendel's Laws	39
Recombination	40
The Expression of Genes	42
Mutation	44
Evolution of Dominance	45
Chromosomal Mechanisms	46
Sex Chromosomes	47
Alterations of the Chromosomes	48
Deletions and Duplications	48
Inversions and Translocations	49

Continuous Variation 52
Summary 54
References 55

Chapter 4 | Development 56

Growth and Homeostasis 57
Life Cycles 61
Differentiation and Morphogenesis 62
Modification of the Developmental System 66
Summary 67
References 68

**PART 2 | POPULATIONS:
PROPERTIES**

Chapter 5 | Populations 72

Individuals and Colonies 73
Spatial Distribution 75
Ecological Distribution 76
Structure 79
Numbers of Individuals 80
Environment 82
Communities 86
Summary 87
References 88

Chapter 6 | The Theory of Population Genetics 90

Mendelian Populations 91
 Panmixis 91
 Gene Pool and Gene Frequency 92
 Hardy-Weinberg Law 93
Population Size 95
 Effective Breeding Size 96
 Genetic Drift 97
 Decay of Variability 98
 Loss of Mutations 100
Mutation 101

Selection	102
Fitness or Adaptive Value	104
Types of Selection	104
Homozygous Recessives Completely Unsuccessful	105
Homozygous Recessives Relatively Unsuccessful	108
Homozygotes Inferior to Heterozygotes	109
Balanced Polymorphism and the Retention of Variability	110
Genetic Load	112
Heterozygotes Inferior to Homozygotes	114
Migration and Population Structure	114
Joint Pressures	116
Adaptation and Gene Combinations	120
Summary	122
References	123

Chapter 7 | Changes in Populations 124

Examples from Nature	125
Differential Mortality in Sparrows	125
Industrial Melanism	125
Microevolution in British Lepidoptera	131
Polymorphic Land Snails	133
Island Water Snakes	137
Chromosomal Polymorphism in <i>Drosophila</i>	139
Examples from Man	145
Pasture Plants	146
Mimicry of Flax	147
Disruptive Selection in Mimetic Butterflies	147
Resistance to Antibiotics and Insecticides	148
Laboratory Populations	150
Genetic Homeostasis	153
Genetic Assimilation	154
Adjustment to the Environment	157
Summary	158
References	158

Chapter 8 | Genetic Systems I 160

Genetic Systems in Microorganisms	161
Transformation	161
Recombination in Viruses	162
Transduction	163

Sexual Recombination in Bacteria	163
Microbial Genetics and Evolution	164
Genetic Systems of Other Organisms	165
Sexuality and Diploidy	166
Diploid Life Cycles and Alternation of Generations	167
Recombination and Genetic Systems	169
Reduction of Recombination	169
Mating Systems and Recombination	170
Inbreeding Systems	171
Outbreeding Systems	172
Summary	172

Chapter 9 | Genetic Systems II 174

Meiotic Drive	175
Changes in Chromosome Structure	176
Inversions	176
Reciprocal Translocations	177
Changes in Chromosome Size and Shape	182
Changes in Chromosome Number	183
Polyploidy	183
Aneuployploidy	184
Euployploidy	189
Apomixis	196
Summary	207
References	207

**PART 3 | POPULATIONS:
DIFFERENTIATION**

Chapter 10 | The Differentiation of Populations 210

Examples of Differentiation	212
Continuous Geographic Variation	212
Color, Pattern, and Size Variation in Animals	212
Ecotypic Variation in Plants	213
Clinal Variation in Plants	214
Clinal Variation in Animals	215
The First Stages of Genetic Isolation	218
Closely Related Isolates	220

Species Swarms in Fishes	220
Sibling Species of Alpine Butterflies	220
The Galápagos Finches	224
Host Preference in Parasitic Organisms	229
Discussion of Observed Patterns	230
Geographic Variation in Selection Pressures	230
Exchange of Genetic Information	234
Cessation of Gene Exchange	236
Isolation	237
Fusion of Populations	238
Meeting with No Gene Exchange	238
Limited Gene Exchange	240
Selection against Hybrids	242
Patterns of Differentiation	243
The Galápagos Finches and African Cichlids	243
Sibling Butterfly Species	244
Differentiation of Parasites	245
Allopatric Speciation	247
Sympatric Speciation	247
Summary	248
References	249

Chapter 11 | Major Patterns of Variation 250

Extinction and Biogeographic Provincialism	251
Extinction	251
Biogeographic Provincialism	256
Reticulate Variation	258
The Fossil Record	258
Modes of Evolution	259
Rates of Evolution	261
Major Evolutionary Patterns	264
Adaptive Radiation	264
Differing Rates of Evolution and Adaptive Zones	266
Competition	270
Convergence	270
Higher Categories	272
Evolutionary Trends	274
Increase in Size	274
Increase in Complexity	275
Summary	276
References	277

**PART 4 | HUMAN EVOLUTION:
PHYSICAL AND CULTURAL**

Chapter 12 | The Evolution of Man 280

Man's Evolutionary History	281
Culture	285
Summary	292
References	293

Chapter 13 | The Theory of Evolution 294

Anthropocentrism	295
Cultural Bias	296
Scientific Bias	298
Evolutionary Biology	308
Epilogue	312
References	314

Glossary	316
Index	332

101-112

the process of evolution

1

organisms: origin and function

The Process of Evolution is divided into four major sections. These deal with (1) the origin and functioning of organisms, (2) the properties of populations of organisms, (3) the ways in which differentiation of populations occurs and results in major patterns of variation, and (4) the evolution of man and his culture (which includes evolutionary theory).

This initial section deals to a large extent with subjects that often are taken for granted in discussions of evolution. The basic properties of life are themselves products of an evolutionary process. In these first four chapters, certain of the properties of living systems critical to the study of evolution are outlined. Emphasis is given to the ways in which a continuity of information is maintained in the cyclic stream of life and to ways in which this information is elaborated. Where possible, intelligent speculation about ways and means of ancient transformations and origins of ubiquitous mechanisms is included. Such speculation, no matter how inaccurate it may turn out to be, serves to remind us that such things as photosynthesis, DNA, meiosis, dominance, and cellular differentiation did not always exist in their present forms. No attempt has been made to give an encyclopedic account of these major areas of biological thought; rather we have tried to set the stage for the consideration of the process of evolution in organisms as we know them today.

1

the origin of life

One is so accustomed to the axiom that all life originates from pre-existing life that he seldom considers the question of how life began in the first place. The ancients solved the problem with the idea of the spontaneous generation of such complex organisms as flies and mice from nonliving matter. But these, as well as more sophisticated ideas, were laid to rest by the experiments of Redi and Pasteur. As a result, however, the basic question, How did life originate?, was brought into focus. Without some type of spontaneous generation, how can the origin of the myriad entities which are called "alive" be explained? Often this problem has been confused by the tendency to equate life with the properties of highly complex organisms. The contrast between a bird and a rock or between a bacterium and an iron filing is self-evident. Indeed, it is so striking that the difference between the living and the nonliving could be misconstrued as one of kind rather than one of degree.

The great majority of biologists believe that there is no significant discontinuity between the living and the nonliving, even though they may not agree on a definition of "life" or even upon the "properties" of life. Many obstacles may be avoided merely by viewing life as a special property of matter at a certain stage of complexity and not attempting a rigorous definition. At least it can be said that living systems handle energy in a regulative manner so as to establish an energy potential between the organism and its environment; certainly one of the most fundamental properties of life is the continuous and directed movement of electrons among the complex molecules of which living organisms are made. It is important to note that these energy transformations are precisely controlled. The regulated release of an amount of energy, which uncontrolled would cause a mild explosion, results in what is thought of as life. In addition, living systems have the property of reproducing themselves. Thus when the problem of the origin of life is considered, answers must be sought to the questions of how the systems that extract and utilize energy from the environment could arise and how they could replicate. There seems to be a sort of twilight zone between the extremes of living and nonliving, an area in which these terms may not be applicable. In this zone of viruses, nucleic acids, and specialized sorts of colloids some of the answers to our questions may be found.

It does not seem likely that the spontaneous origination of life can be observed at the present time. If new life did appear spontaneously, it would probably quickly be eliminated by modern hetero-

trophic organisms even if the environment were favorable. The situation was quite different under the conditions that were probable on the earth billions of years ago.

THE EARLY STAGES

The *sine qua non* of the production of life as we know it is the development of certain organic compounds—compounds built around carbon and consisting, in the main, of this element joined in diverse configurations with nitrogen, oxygen, hydrogen, phosphorus, and sulfur. The early stages in the chemical evolution of the earth's surface must have been characterized by the presence of much simpler inorganic molecules. The questions that immediately arise are how these were combined to produce the more complex compounds found in living systems, and what the source of energy for such transformations may have been.

There is considerable evidence to support the thesis of Oparin that the atmosphere of the early earth was reducing in character, being made up principally of methane, water vapor, ammonia, and hydrogen. The behavior of these substances under a variety of conditions has been studied. For example, Miller placed mixtures of these gases in an apparatus (Fig. 1.1) in which they could be exposed to electrical discharges. Circulation was produced by boiling water on one side of the apparatus and condensing it on the other. Chromatographic analysis at the end of the experiments revealed the presence of amino, hydroxy, and aliphatic acids—three basic types of organic molecules, including the unit of protein structure. The amino acids included glycine and alanine (the most common amino acids in proteins), aspartic acid, and glutamic acid. It is interesting to note that α -alanine predominated over β -alanine in these experiments; modern proteins contain only α -amino acids. (α -amino acids have the NH_2 and COOH groups both attached to the same carbon atom.) Miller argues that the same types of compounds would have been produced under the influence of ultraviolet light and electrical discharges if the primitive earth had had a reducing atmosphere. He further contends that organic compounds would not be produced if oxidizing conditions were present and points out that, if amino acids (and other organic compounds) are necessary for life, the presence of life on earth is evidence for a primitive reducing atmosphere.

The theory that the early atmosphere was reducing in character now seems widely accepted. Free oxygen, which first appeared some 800 million to 2 billion or more years ago and which gives the

present atmosphere its oxidizing character, came from two sources: Part had a photochemical origin (from water undergoing photolysis in the upper atmosphere, with the hydrogen escaping into space); the rest was produced photosynthetically by living organisms (the main source today).

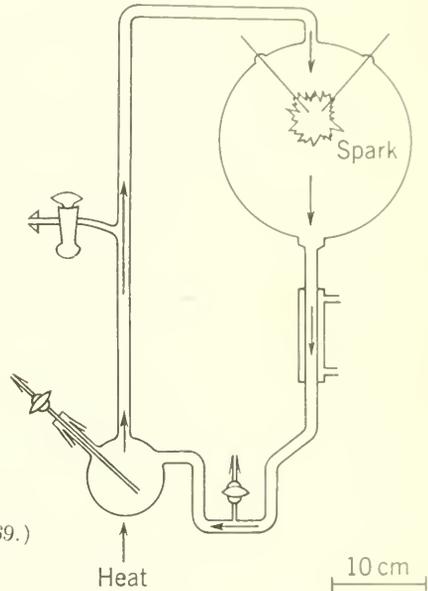


Fig. 1.1 | Spark-discharge apparatus.
(After Miller, 1957, *Ann. N.Y. Acad. Sci.* 69.)

In addition to the abiogenic formation of organic compounds as outlined above, simple organic compounds are formed by the interaction of water vapor with carbides in magma brought to the surface by volcanic activity ($3\text{Fe}_m\text{C}_n + 4m\text{H}_2\text{O} = \text{Fe}_3\text{O}_4 + \text{C}_{3n}\text{H}_{3m}$). Calvin and others have shown in experiments with ionizing radiations (of the sort that would be produced by radioactive materials or by cosmic rays) that, in the presence of molecular hydrogen, partial reduction of carbon dioxide can occur. Further irradiation of aqueous solutions of the substances produced (formic acid, formaldehyde) leads to the formation of compounds such as oxalic acid or acetic acid. Eventually molecules of two-carbon compounds (acetic acid) may combine to produce a four-carbon compound (succinic acid). In these experiments amino acids also are produced.

In other experiments, Fox has shown that heating dry amino acid mixtures results in the formation of synthetic polypeptides (pro-

teinoids). Proteinoids in water tend to form spherules of varying size and shape, depending upon their interaction with substances mixed with them. These spherules, in some respects, resemble coacervates and other cell models. Among other things, the proteinoid spherules retain their integrity for rather long periods and are not destroyed by high-speed centrifugation.

ORIGIN OF SELF-REPLICATING SYSTEMS

Thus it can be seen that there were diverse ways in which organic compounds may have been produced on the primitive earth. It is not unreasonable to assume, therefore, that the primitive ocean was comparable to a thin soup of organic materials. There is little agreement as to how the first self-replicating systems developed in this "soup." Obviously, what was first required was the selective construction of molecules. Calvin has pointed out that the phenomenon of autocatalysis has the nature of a selective process. Autocatalysis occurs whenever the product of a chemical reaction has the property of influencing catalytically the rate of its *own* formation. There follows a progressive build-up of products in a sequence of increasingly complex compounds formed from simpler ones. An early selection of this nature (for complexity) must have gone on in the organic soup.

Autocatalytic reactions are only partly analogous to a self-replicating living system. No presently known substance, when isolated, will replicate itself. Only systems have the ability to replicate. The living systems familiar to us are composed of proteins and nucleic acids, together with some means of energy mobilization. Polypeptide chains, the backbones of protein molecules, are formed by the linkage of amino acids in linear series. The linkage is accompanied by the elimination of water as the amino acid chain lengthens. The bonds between the amino acid units are known as peptide bonds. The spontaneous formation of even a small protein in a solution of amino acids requires outside energy and is a very improbable event. But in the absence of free oxygen and predatory organisms, the life of an amino acid "soup" could be extremely long, long enough to turn the improbable into the probable. (The chance of being struck by lightning in a 70-year life span is very slight, but if one lives for 700 million years it becomes almost a certainty.)

However, as Wald points out, the spontaneous generation of protein molecules is opposed by their tendency toward spontaneous dissolution. Indeed, the equilibrium point in the reversible, spon-

taneous protein-generation reaction lies on the side of dissolution rather than synthesis. Wald suggests, nevertheless, that molecules seem to be able to resist dissolution both through large size and through aggregation with other molecules. Proteins may be an unstable mid-point, subject either to dissolution into their component amino acids or to the formation of more stable aggregates. The first "organisms" may well have been the result of the formation of larger and larger aggregates.

ENERGY SOURCES

Ultraviolet light usually is considered the chief source of energy for early synthetic processes. With simple molecules, only very short wavelengths are absorbed, but as more complex molecules appear, absorption of longer ultraviolet wavelengths takes place. As the earth evolved its thick atmospheric layers, ultraviolet of short wavelengths no longer could penetrate to the earth's surface to be used as an energy source. The appearance of colored pigments (e.g., porphyrins mentioned below) made possible the absorption of energy in the visible spectrum. However, whatever the source of energy, there is a considerable gap between the absorption of a quantum of energy and its mobilization for use in biological processes.

The problems of utilizing energy for protein synthesis and the conditions under which it may occur are particularly vexing ones. In present-day biological systems the enzymes responsible for the mobilization of energy and for the synthesis itself *are* proteins. Thus if one is to postulate the functioning of such systems in the formation of the first proteins, he becomes embroiled in a "chicken or egg" dilemma. It has been suggested that, in the absence of proteins, other substances (e.g., clays) may have served as catalysts, since many of the known enzymatic phenomena are fundamentally molecule-surface reactions. This raises the question of how proteins subsequently came to assume this function. At least it can be said that the surface phenomena of clays and surface configurations of proteins have certain aspects in common.

Chemical energy for synthesis in modern biological systems involves organophosphate bonds that yield exceptionally high energies upon cleavage. The energy released upon cleavage or transfer of these bonds is regulated by a complex system of catalysts (enzymes plus their coenzymes); the characteristics of these sets of reactions are unique to living systems. They change velocity in response to changes in concentration of product; are dependent upon physical

conditions (temperature, pressure) in a fashion distinct from non-living reactions; and demonstrate a degree of conservation of energy not often equaled in inorganic reactions. Such reactions in living systems are referred to as *biological oxidations*. The energy needed by the heterotrophic organism is almost universally mediated by a single type of organophosphate bond, that in the energy-rich compound called adenosine triphosphate (ATP). When ATP releases energy in a biological reaction, it releases one phosphate and becomes adenosine diphosphate (ADP). The latter still includes one energy-rich phosphate bond and is particularly susceptible to being rephosphorylated into ATP. But the rephosphorylation (called oxidative phosphorylation) is mediated by the system of enzymes referred to above. These enzymes in their turn depend upon energy from the cleavage of ATP bonds, but the important point is that, for each ATP bond that releases its energy for these enzymes to function, more than one ATP bond is formed. The extra energy is derived from the energy stored in the glucose (or other) molecule upon which the enzymes are acting directly. By this interlocked series of reactions, chemical energy supplied to the organism as molecules of carbohydrate, lipid, or protein (which the organism cannot use, as such) is transformed into ATP-bond energy that the organism can use.

In nonliving systems, energy transfer by molecular degradation yields smaller molecules plus much heat. In living systems, the products are high-energy organophosphate bonds, smaller molecules, and surprisingly little heat. In fact, one of the salient features of the living energetic machinery is the closeness of the coupling between energy-yielding and energy-storing reactions and the resultant conservation of energy. Of course the ultimate source of energy in existing organisms (except chemosynthetic bacteria) is that of the sun trapped by photosynthetic organisms and eventually stored in phosphate bonds by a related process involving photophosphorylation in the photosynthetic organism or by synthesis into carbohydrate with phosphorylation. Many important enzymes or catalysts in both photosynthesis and biological oxidations are colored compounds involving metal ions (Fe, Mg) and the organic substances known as porphyrins. Calvin has diagrammed (Fig. 1.2) how such important biological materials might have arisen in the course of chemical selection involving autocatalysis. In the sequence from simpler to more complex molecules, later stages are catalysts for succeeding stages. Since the use of porphyrins by nonphotosynthetic organisms is widespread, Calvin feels that the presumably random

variation involving small changes in the porphyrins led eventually to the construction of chlorophyll and the invention of photosynthesis. In addition, Granick believes that all the colored compounds in the sequence that leads to chlorophyll might have had the same function as chlorophyll. In the early stages, metallic ions, present as constituents of minerals, might have served to catalyze the same reactions that they now catalyze as metalloenzymes.

Photosynthesis is the result of a complex series of reactions. Some of these can take place in the dark, whereas others can occur only with illumination. Most of the many reactions usually included under the rubric photosynthesis, in the broad sense, are actually dark reactions, involving the addition of CO_2 to —C—C—C— chains. These dark reactions can be carried out by most cells. It seems likely that many of these reactions evolved independently, perhaps earlier than

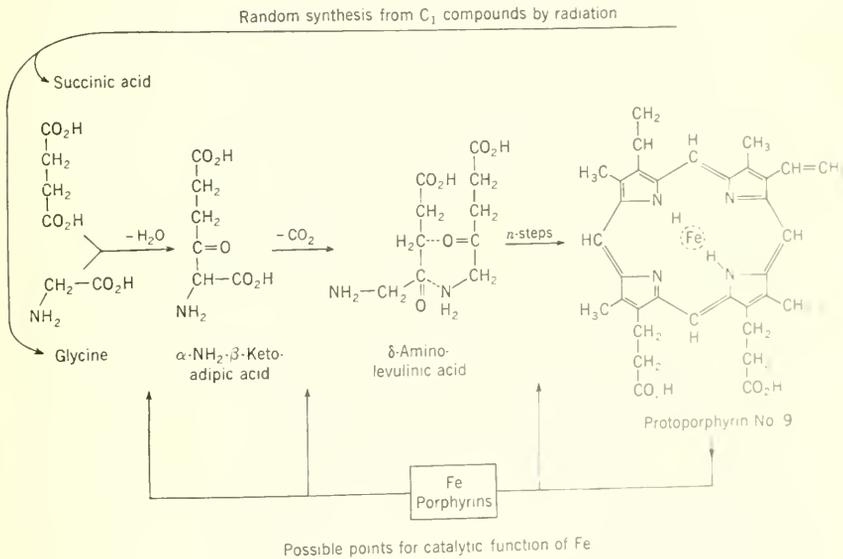


Fig. 1.2 | Possible steps in the synthesis of porphyrin compounds from molecules produced randomly under the influence of radiation. Iron may act as a catalyst at the points marked by arrows but is a much better catalyst when combined with porphyrin. Thus the production of protoporphyrin 9 is facilitated by the presence of protoporphyrin 9. (From Calvin, 1959, *Evolution* 13.)

strictly photosynthetic reactions. The light reaction leads to the production of a reducing agent and some type of high-energy phosphate, probably adenosine triphosphate (ATP). The reducing agent usually is hydrogen but occasionally is a phosphorus compound. These substances then operate the carbon reduction cycle, and hexose sugar molecules are produced. This energy is mobilized, in ways which are imperfectly understood, so that excited chlorophyll transforms other molecules to produce the reducing agent and the ATP. Thus, typically, photosynthesis involves photophosphorylation, i.e., the transformation of light into the "energy currency" of phosphate bonds.

It probably never will be possible to say with certainty whether or not the coupling of colored compounds with biosynthetic processes took place before or after the appearance of what today would be called living organisms. Calvin believes that the final step in the development of modern photosynthesis, the production of oxygen, did not take place until relatively late in the sequence of events. Therefore reactions like those of some modern organisms, which are photosynthetic but do not emit oxygen, were prior.

ORIGIN OF STRUCTURE

In the light of the above discussion, it is not overwhelmingly difficult to imagine how the substances required for the processes we think of as metabolism could have arisen. However, living systems are not fluid structureless entities. Generally they have a characteristic and complex organization of the matter comprising this energy-conversion mechanism. Now the factors involved in the evolution of structure as well as of function must be considered. In the sea the original molecules probably were dispersed as a rather uniform colloidal suspension. However, in colloids of different substances, semiliquid colloidal gels or coacervates are formed, and it might be expected that these may have arisen as the organic soup became increasingly complex. From the work of physical chemists, much is known about the behavior of coacervates. They often do not form as a continuous layer but rather separate out of the equilibrium liquid (thus left colloid-poor) in the form of discrete droplets. These droplets not only concentrate organic molecules of high molecular weight but also possess a definite internal structure as well as a highly developed surface separating them from the equilibrium liquid. In the coacervate droplet one can see the first distinct separation of a structural complex of organic material from its environment.

Oparin suggests that, in a sense, coacervate droplets competed with each other for materials—that some, which by chance had a favorable composition or internal configuration, grew more rapidly than others. These successful droplets were then first to reach a size at which they became unstable and broke apart into smaller particles. These then enlarged, subsequently divided, and thus continued the sequence. One can also imagine that accidental fusion of droplets might have carried them beyond the stability point, causing breakdown into smaller units. Should the droplets have different compositions, a sort of protosexual recombination process would occur. Thus one can see in coacervates many properties that would qualify them as links in a chain leading to the structure of life as now known, and, since the matter carries on the function, to living systems of the familiar sort. They are clearly separated from their environment, have internal structuring, absorb matter from their environment, and have sufficient multiplication and “recombination” to permit the operation of natural selection.

It seems clear that, in the vast stretches of geologic time, mechanisms such as those outlined above (and others as yet undiscovered) produced the ancestors of the living systems we know today. Indeed, when one pictures the vast oceans, lakes, and hot springs rich in organic compounds and presenting a wide variety of conditions of temperature, light, salt concentration, and physical substrate (crystals, clays), it is difficult not to believe that living systems developed more than once. It is not unlikely that modern organisms are the descendants of the victor in a fierce energy war among the early “organisms.”

ORIGIN OF THE GENETIC CODE

The level of complexity of the hypothetical ancestral organism discussed to this point does not involve a system by means of which the entity could be replicated as a unit. Splitting by fission may or may not result in the formation of equal parts; in fact, it might be imagined that occasionally one of the parts would lack a component essential for the maintenance of life. At this stage there was no system of heredity, no genetics, which would ensure the continued production of functional entities. The first principle of genetics is “like begets like.” This is not the result of a great immutable “law of nature” but rather the functioning of a complex system for transmitting genetic “information,” the information needed to construct a new organism. Without such a system, it seems certain that life would not have evolved beyond the level of coacervate droplets.

The efficiency of the transmission apparatus has been a major factor in determining the limits of intricacy of living entities.

In the 2 or 3 billion years of chemical evolution that preceded the evolution of life, many systems of transmitting information may have been tried and discarded in a selectional process. It is clear that the hereditary system must have been coupled to the synthetic and energy-converting systems; therefore it is no surprise to note that the substances involved in the hereditary system, the nucleic acids, have adenosine phosphate as a building block. The system found in most cellular organisms is based on coding information in two macromolecular nucleic acids, ribonucleic acid (RNA) and deoxyribonucleic acid (DNA).

The assumption usually drawn is that the giant ordered molecules of which living systems are composed are the evolutionary end result of some process of aggregation of smaller molecules and that selective forces controlled the process. With the spontaneous random occurrence of a sequence of ordered molecular subunits of nucleic acid, for example, a template against which further sequences are replicated becomes possible. This leaves essentially unanswered and unanswerable the question of how the original sequence arose.

This is not the only possible interpretation, however, as Pattee has pointed out. He suggests that the precursors of biological macromolecules were not random sequences but naturally ordered crystal structures. These result from various restrictions found in crystallization processes in general. In the growth of polymers the configuration at a particular stage may determine which subunits are added. Thus there may be feedback control of the growth of macromolecules. By using a computer model (Fig. 1.3), Pattee has shown that, with feedback, simple configurations can be assembled to produce elaborate, repeating, and well-ordered sequences. It is not necessary to postulate, as most authors have done, a statistically highly improbable preexisting sequence that must be copied. In Pattee's view, the present genetic mechanisms themselves are the evolutionary result of the natural occurrence of ordered macromolecular sequences.

The exact functioning of genetic mechanisms has not been elucidated entirely, but in general outlines it is as follows: The units of information, known as genes, are coded into the structure of giant self-replicating molecules of DNA. These molecules, reproduced and passed from generation to generation, are the master blueprints from which all living organisms are produced; they maintain the continuity of life. Slight changes in these blueprints are also repro-

duced and are responsible for the variation that permits evolution. DNA molecules are chains made up of four nucleotide units: deoxyguanylic acid, deoxycytidylic acid, deoxyadenylic acid, and deoxythymidylic acid. Similarly, RNA molecules are made up of four nucleotides: guanylic, cytidylic, adenylic, and uridylic acids. Each nucleotide group consists of a pentose sugar molecule with an attached base and an attached phosphate group. The backbones of the DNA and RNA molecules are made up of the pentose sugars linked by the phosphate groups. Attached to each sugar residue in

Fig. 1.3 | Mechanical computer model for the production (by feedback) of ordered sequences. The beam of the balance operates the gate permitting an A ball to enter when the pans are balanced and a B ball to enter when the pans are unbalanced. A balls are heavier than B balls. (From Pattee, 1961, *Biophysical Journal* 1.)

Sequence generated by the balance mechanism

B B A B A A B A B B A A A B B A B B B B A B B A B A B B B A A B B A A B A A B
 A A A B B B A A A A B A B B B B B A A B A B A B B B A A B B A B A A A B A
 A B B B B A A A B A B A A A A B B A A A A A B B A A A A B B B B B B B A
 B A B A B A A B B A A B B B A B B B A B A A B B A A A B B A A B B B B A
 B B A B A B B A B B A A B A A B A A A A B B B A A A A B B B B B A A B A
 B A B B B A A B B A B A A B A A B B B B A A B A B A A A A B B A A A A
 A B A A A A A A B B B B B B B A B A B A B A A B B A A B B B A B B B A B A

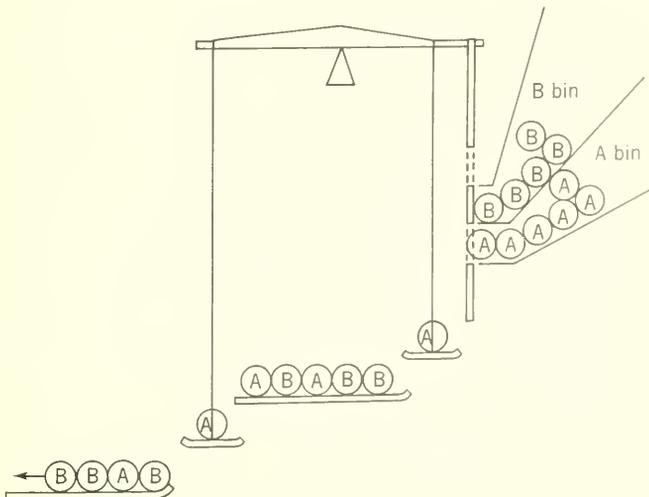
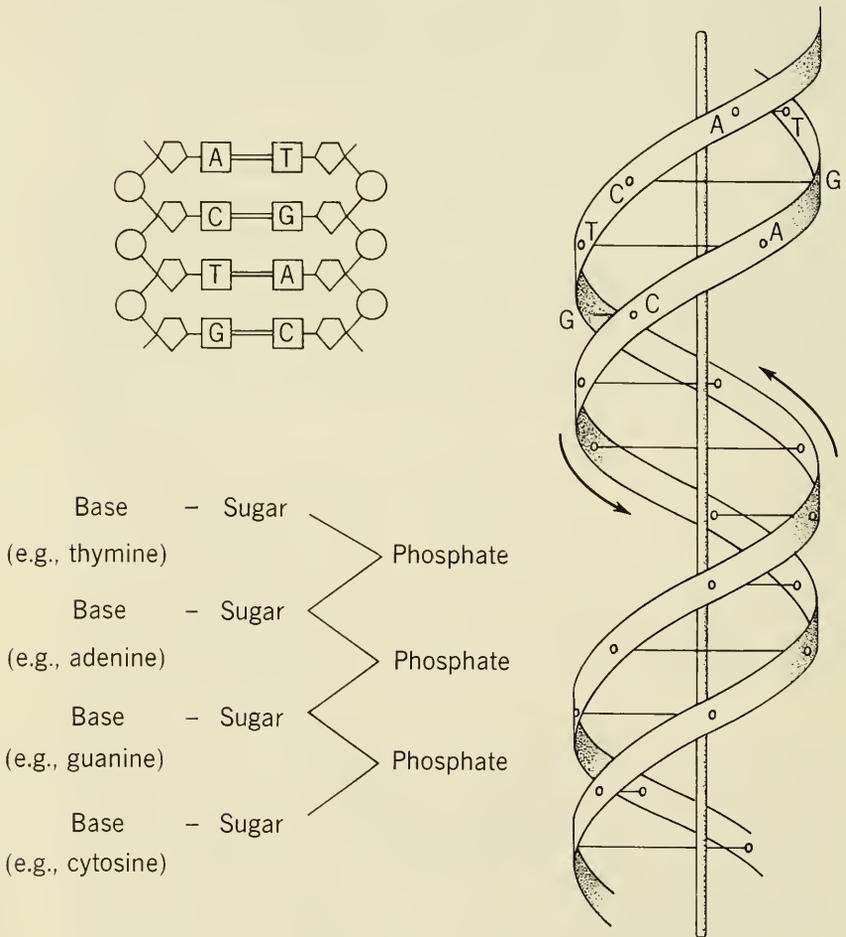


Fig. 1.4 | The structure of DNA. Upper left, complementary chains of nucleotides. Letters, bases; five-sided figures, pentose sugars; circles, phosphate groups; double lines, hydrogen bonds. Lower left, detail of segment of one strand. Right, model of double helix in which the nucleotide chains are arranged. Ribbons, phosphate-sugar backbone; bars, paired bases joining backbones. This double-helix configuration is known as the Watson-Crick model. (After Sinnott, Dunn, and Dobzhansky, 1958, *Principles of Genetics*, McGraw-Hill.)



this regular chain is one of five bases: either a purine (adenine, guanine) or a pyrimidine (cytosine, thymine in DNA, or uracil in RNA). The configuration of the DNA molecule appears to be a double helix of the sugar-phosphate backbones held together with cross-linkages of paired bases (Fig. 1.4). Because of their chemical properties, these bases line up the following pairs: adenine with thymine and cytosine with guanine. This helical structure best explains the results of X-ray diffraction and other studies to determine the physical properties of the molecule.

When chromosome duplication takes place in preparation for cell division, the complementary helices probably "unwind," and each helix forms a chemical template on which DNA precursors attach to re-form the complementary strand and reestablish the double helix. This is the mechanism by which the genetic code is passed from cell to cell and (through the gametes) from organism to organism. The genetic code has been shown to be the actual sequence of nucleotides in the DNA strand.

READING THE CODE

Protein synthesis takes place largely in the ribosomes (microsomes) of the cell—cytoplasmic structures physically separated from the nuclear DNA. The ribosomes contain the vast majority of the RNA in the cell. DNA serves as a template against which can be assembled another identical strand of DNA or a strand of RNA. Thus the code may be transferred to "messenger" RNA molecules which presumably carry it to the ribosomes where protein formation occurs. (It is not known how the cell "tells" the DNA whether to make more DNA or RNA.)

There are several possible explanations of how the DNA master blueprint and the RNA messengers control the assembly of various proteins. It is necessary for the code, transferred from the DNA to the RNA, to be able unambiguously to control the sequential positions of 20 common amino acids which may go into the composition of proteins. One suggestion was based on the mathematical demonstration that 20, and only 20, different sequences that will not be subject to the confusion of overlapping can be constructed by taking the four nucleotide units three at a time. For example, if the nucleotides are numbered 1, 2, 3, and 4, the sequences 131 and 312 would be overlapping; if they were placed adjacent to each other, the sequence might be 141131312, in which 131 occurs in two overlapping positions. The nonoverlapping triplets would be 112, 212,

131, 132, 133, 231, 232, 233, 141, 142, 143, 144, 241, 242, 243, 244, 341, 342, 343, 344.

Recently several groups of workers have been able to show that the RNA code consists of nonoverlapping triplets, each of which determines the position of an amino acid. At this writing, codes for 19 of the 20 amino acids have been partially worked out. For instance, the amino acid alanine is coded as some sequence of uracil, cytosine, and guanine, and the amino acid serine as a triplet containing two uracils and a cytosine.

It now appears likely that the nonoverlapping nature of the code is determined not by the structure of the triplets themselves but rather by the existence of some device for designating starting points for "reading" the code. For instance, in the sample sequence above (141131312) there is no ambiguity if the left end is designated the starting point and the code exists only as triplets; it becomes clearly 141-131-312. If the code works in this manner, there are then $4^3 = 64$ different possible sequences, a plethora for determining only 20 items. It is quite possible that each amino acid can be coded by more than one triplet combination and that certain combinations indicate "capital" triplets (those starting a sequence). Work on the decoding problem is now proceeding so rapidly that it seems inevitable that some of these questions will be settled before these words are published. Whatever the answers, they will surely contain fascinating hints as to the evolution of the code itself.

Now, how do the amino acids "read" the messenger RNA sequence code so that they condense into proteins containing the proper order of amino acid residues? Amino acids become bound to relatively small soluble RNA molecules (*transfer RNA*) *before* the acids are linked together into proteins. Further data are very suggestive of the following pattern of protein construction. There is a separate transfer RNA molecule for each amino acid. In one part of the molecule is a sequence of nucleotides that determines with which amino acid it may react, and in another part is the sequence (a triplet?) that determines the position on the RNA template to be assumed by the transfer RNA unit. The compounds of RNA and amino acids are formed with energy supplied by ATP. This enzyme-mediated reaction is diagrammed in Fig. 1.5. The transfer RNA-amino acid units then find their places on the long RNA template, presumably pairing with complementary sequences on the template. The amino acids are still in an activated state; when they are brought into close proximity in the manner outlined above, they condense (probably with the aid of an enzyme) to form a protein with the proper sequence of amino acid residues.

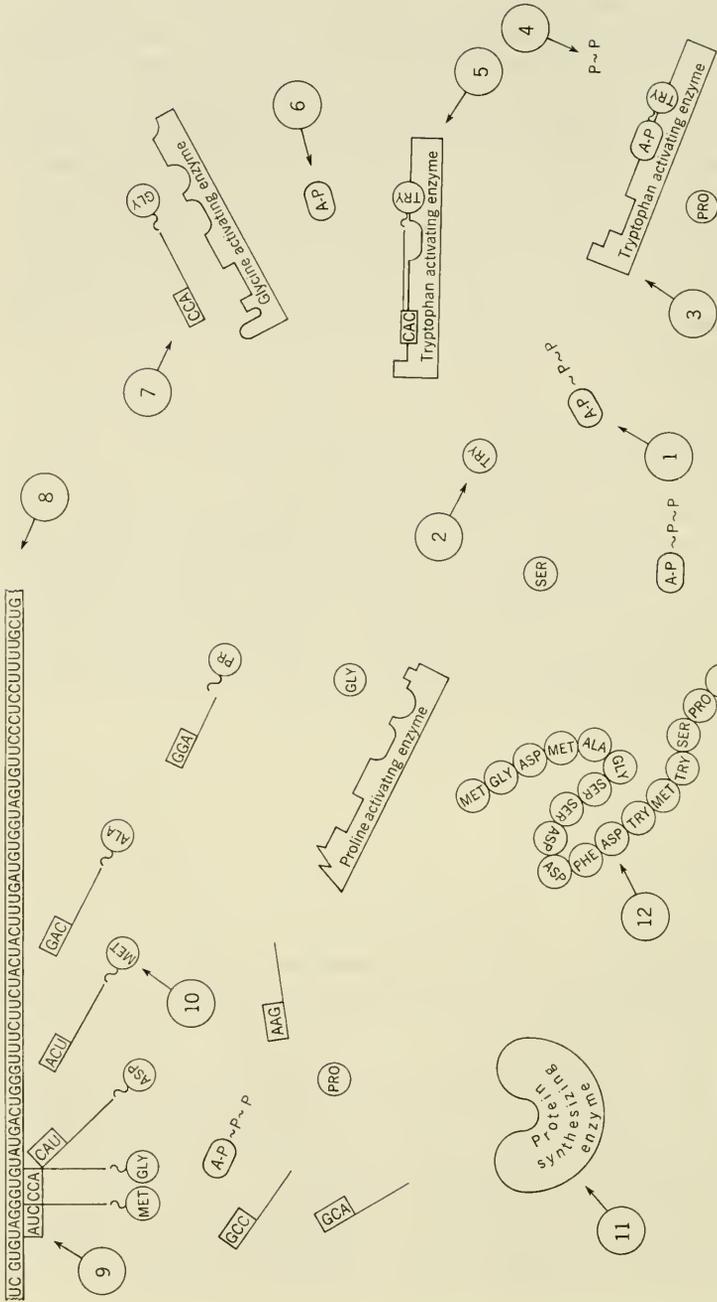
One can well imagine that this system is a far cry from the first system of transmitting genetic information. For example, its sophistication may be seen in the fact that the DNA remains as a master template, reducing the possibilities for error that would be inherent in a system in which copies are made from copies. Similarly, the short transfer RNA molecules are highly specialized to accomplish the proper positioning of the protein precursors. The manifold interactions of DNA and RNA in the organism are not confined to processes concerning transmission of genetic information and protein synthesis. There is speculation that RNA functions in those higher-organism systems that involve training and memory. The mental properties of primates may eventually be described in terms of fundamental chemical properties recognizable in the simplest cells and organisms.

In viewing the complexities of function found in the cells of present-day organisms—the highly specialized organelles, the very efficient system for utilizing high-energy phosphate bonds, the precise mechanisms for distribution of genetic information and for cell division—one may find it hard to believe that such complexity ever arose from the coacervate stage previously described. It is like looking at a unicellular organism and a man and trying to imagine one as the ancestor of the other without knowledge of any intermediates. It should be remembered that the time available for the evolution of the coacervate into the complex cell was of the same magnitude as that available for the journey from protistan to man.

SUMMARY

Life is a complex energy-matter nexus whose origin can be explained logically in general terms. Important events in the origination of life certainly were the development of organic compounds, their segregation into structural entities, the origin of energy-mobilizing cycles, and the development of systems for self-replication. These events presumably must have been partially synchronous and were controlled by a sort of protoselection. The present system for self-replication utilizes information coded in macromolecules of nucleic acids that control protein synthesis.

Life may be considered to be an aspect of the matter-energy continuum characterized by incessant replication. Perfect replication is impossible, and therefore natural selection is inevitable.



REFERENCES

- Calvin, M. 1959. Round trip from space. *Evolution* 13: 362–377. A good brief discussion of the problem of the origin of life.
- Miller, S. L. 1951. The formation of organic compounds on the primitive earth. *Ann. N.Y. Acad. Sci.* 59: 260–275. See this for details on the atmosphere experiment. This article is in a number entitled *Modern Ideas on Spontaneous Generation* which contains several interesting papers.
- Needham, A. E. 1959. The origination of life. *Quart. Rev. Biol.* 34: 189–209. A stimulating discussion in very broad terms.
- Oparin, A. I., A. E. Braunshtein, A. G. Pasynskii, and T. E. Pavlovskaya [eds.]. 1959. *The Origin of Life on the Earth*. Pergamon Press, New York. This symposium volume contains a large number of important papers, most of which are highly technical.
- Oparin, A. I. 1961. *Life: Its Nature, Origin and Development*. Academic, New York. The latest revision of the classic work on the origin of life.
- Sagan, Carl. 1961. On the origin and planetary distribution of life. *Radiation Res.* 15: 174–192. A recent summary paper with extensive bibliography.

Fig. 1.5 | (see opposite page) Diagrammatic theoretical representation of the process of protein synthesis under the control of messenger RNA. (1) ATP molecule. (2) Amino acid (tryptophan). (3) Enzyme mediating high-energy bonding of tryptophan residue with adenylic acid (AMP). (4) Phosphate groups previously bonded with AMP dropping away from enzyme substrate. (5) Same enzyme mediating transfer of tryptophan residue and high-energy bond from AMP to proper transfer RNA molecule. (6) AMP molecule dropping away from enzyme. (7) Glycine-charged transfer RNA unit dropping away from glycine-activating enzyme. (8) Messenger RNA template. (9) Start of synthesis of protein strand. “Capital” methionine-charged transfer RNA unit aligned with “capital” methionine triplet (UAG) on RNA template. (10) “Lowercase” methionine-charged transfer RNA unit approaching “lowercase” methionine triplet (UGA) on template. (11) Enzyme “zipper” which assembles amino acid residues into protein. (12) Newly formed protein that has dropped away from template, freeing the transfer RNA units involved in its synthesis. Only a small sample of presumably many simultaneous reactions is shown in this diagram.

2 | **units of replication**

One of the most dramatic results of modern scientific technology and of the development of the electron microscope has been the revival of interest in cytology. The increased resolution of the electron microscope has revealed structures of amazing complexity where none was known to exist and, indeed, virtually has brought form and function together at the level of macromolecules and their aggregates. From our point of view, these results are particularly interesting; from them we can hypothesize that the membrane systems of which cells are largely composed may have been the inevitable result of the mixture of large and complex molecules, such as lipids and proteins, before the origin of life itself, as suggested in Chap. 1. These macromolecular structures, originating by chance, may be similar to the membranes seen to be combined in cells in a variety of ways. The basic cellular constituents are common to plants and animals, providing a structural ground plan for all life except in the most highly specialized cells or organisms. A brief review of cell structure is given below to provide background for the later discussion of the evolution of genetic mechanisms and systems.

Whatever may have been the origin of cells, both plant and animal cells show such striking similarity in structure as to suggest that either there is a common ancestral type or, with life as we know it, only one basic type of structure (Fig. 2.1) is compatible with function. The chemical composition of cells is relatively easy to determine, and many physical properties of cells and their constituents can be measured. However, it is in the organization of these chemicals that the unique property of life and the cellular state is achieved. The chief structural units of cells are large molecules of proteins, carbohydrates, and lipids. Interspersed among, and sometimes actually associated with, the physical framework that results from the aggregation of these molecules are the myriad types of smaller molecules: soluble proteins, amino acids, vitamins, inorganic constituents, etc.

STRUCTURE OF CELLS

Both plant and animal cells appear to be bounded by a membrane, called the plasma membrane, which has the important property of being differentially permeable. Physical, chemical, and biological studies of this membrane indicate that it is a complex structure composed of protein and lipid molecules associated in layers. The bipolar lipid molecules are arranged in two layers, with their hydrophobic

tails together and their hydrophilic heads pointed toward the hydrated protein strands, which have their long axis at right angles to that of the lipid molecules. Particularly in free-living cells and cells in culture, the property of pinocytosis may be seen: By the rapid and constant extrusion and withdrawal of minute pseudopod-like extensions of their surface, the cells may ingest water and other molecules.

Free cells and cells in tissues seem always to have additional layers outside the plasma membrane. In the animal cell, these layers are composed largely of molecules of proteins and sugars, and their integrity depends upon the calcium balance of the cell environment. Plant cells are rather different in two respects. First of all, the outer layers (or cell wall) of plants are composed mainly of carbohydrate molecules. Glucose residues arranged in long chains form the most important constituent, cellulose. Other carbohydrates, as well as fatty acid substances (suberin, cutin, etc.), also are associated with this wall. Contiguous cells in tissues are cemented together by a middle lamella, which is pectate in nature and also dependent upon calcium for rigidity. The second important difference between plant and animal cells is that cells in plant tissues are in organic connection through strands of cytoplasm called plasmodesmata. By means of electron micrographs, most instances of so-called plasmodesmata in animals have been shown not to involve continuity of protoplasm. That is, across the strands that look like

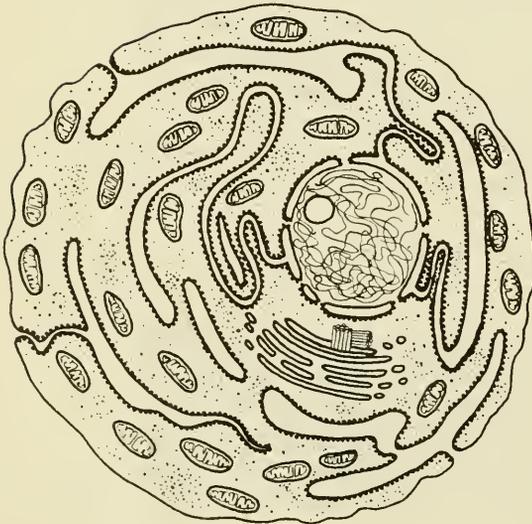


Fig. 2.1 | Diagram of a generalized cell with parts as seen under the electron microscope (some components enlarged or simplified).

plasmodesmata, there is a pair of plasma membranes. It is as if the tissues of Metazoa were composed of cells stuck together, whereas those of plants result from the more or less incomplete partition of "protoplasm." The boundary between animal cells may be exceedingly complex. Structural and chemical properties of the intercellular region suggest that specialization of the periphery of the cell may play an important role in cellular differentiation.

The most conspicuous structure within most cells is, of course, the nucleus. Recent electron micrographs show that the nucleus is bounded by a pair of membranes; the term nuclear envelope may be used to refer to both. The inner membrane appears to surround the nuclear contents like a sack. The outer membrane, however, is clearly continuous with a membrane system that permeates the cytoplasm to a greater or lesser extent. Thus the cell appears to be penetrated by a system of tubes, canals, vesicles, and cisternae (the amount and type depending upon the nature of the cell and its state of activity) called the endoplasmic reticulum. In a sense, the nuclear contents are outside the cell, for the cytoplasmic membranes are continuous also with the plasma membrane. The inner and outer membranes of the nuclear envelope are connected, however, since they are both perforated by pores distributed rather regularly over the surface of the envelope. These pores lead to the cytoplasm surrounding the endoplasmic reticulum.

Electron micrographs of the cytoplasm around the endoplasmic reticulum show it to be far from homogeneous. The tubes of which the reticulum is composed are associated with small dense granules in synthetically active cells. These are absent where the tubes are continuous with the plasma membrane. Occasionally these granules, which are rich in ribonucleo-protein, are found in the intervening cytoplasm. They are known as ribosomes and, as mentioned in Chap. 1, are thought to be concerned with protein synthesis. Particles known as microsomes which have been studied by physiologists appear to be artifacts: aggregations of ribosomes and endoplasmic reticulum that appear when the cell is fractionated. Ribosomes do not occur where the endoplasmic reticulum is continuous, with more or less flattened, concentrically arranged cisternae making up the Golgi material of both plant and animal cells. The Golgi complex is difficult to isolate from the other cell organelles, and its precise function is not yet known.

Scattered among the tubes and vesicles comprising the endoplasmic reticulum are found the mitochondria of plant and animal cells. These spherical or tube-shaped structures also have a double-membrane boundary, the inner membrane being thrown into a series

of convolutions forming lamellae or villae. The mitochondria are the site of most of the reactions involved in cellular respiration, including the formation of adenosine triphosphate (ATP). There is some evidence also that mitochondria may play a role in cytoplasmic inheritance in the sense that they may be self-replicating.

Closely related to the mitochondria structurally, but found only in plant cells, are the plastids. Like the mitochondria, they are the site of important reactions providing energy for the cell (indeed for nearly all life). Plastids have a lamellar structure, and upon the alternating layers of lipid and protein molecules are found layers of special pigments such as the various types of chlorophyll, carotenoids, and others (depending upon the plant group studied). Light energy absorbed by the plastid is converted to chemical energy; in a series of steps, energy from oxidation is utilized to phosphorylate ADP to ATP. This photophosphorylation obviously is related to the phosphorylation carried out by the mitochondria. The functional units of chloroplasts in higher plants are minute particles called grana. In the green bacteria and blue-green algae the grana are not organized into plastids.

The cytoplasm of most animal and many plant cells has a structure, known as the centrosome, adjacent to the nucleus. Within this relatively clear area of cytoplasm there are one or two granules, the centrioles. These organelles are important in the origin and function of flagella and cilia and in nuclear and cell division. The nine strands making up the outer portion of a flagellum or cilium are continuous with nine tubelike or filamentlike structural components of the centriole or basal granule. This remarkable similarity of centrioles, basal granules, and cilia (which is preserved even in such highly specialized cells as retinal photoreceptors) is found throughout the animal kingdom. The centriole and obviously related structures (such as basal granules) apparently have properties that lead to the organization of fibrous protein molecules in special ways, for example, in the formation of the spindle tubules (fibers) during mitosis.

The genetic information in the cell is located mostly in the chromosomes within the nucleus. The precise state of the material is not known. In the so-called resting or metabolic stage, chromosome material in the nucleus usually is difficult to view. In some instances, portions of chromosomes that have not undergone the usual transformations accompanying mitosis may be seen. Often one or more of these chromosome regions are associated with the nucleolus, a usually conspicuous feature of the metabolically active nucleus. Presumably during the metabolic stage, material is exchanged be-

tween the cytoplasm and the nucleus, and the role of messenger and transfer RNA in translating the DNA code into protein structure is carried on. The mechanism of this exchange is not understood, however. Evidence clearly indicates movement of nucleic acid from nucleus to cytoplasm. Actual particles usually have not been found in the pores of the nuclear envelope, as seen in the electron microscope. Cytologists have reported that portions of the nuclear envelope may pinch or bud off into the cytoplasm, where the pieces have the appearance of endoplasmic reticulum or mitochondria.

CELL DIVISION: MITOSIS

When cells divide (Fig. 2.2), the first conspicuous change usually is in the appearance of the nucleus. The chromosomes become visible within the nuclear envelope in living or stained cells and, usually concomitantly, the nucleolus decreases in size. This first of the arbitrarily designated stages of mitosis or nuclear division is prophase. Toward the end of this stage, it can be seen in the cells of many organisms that the chromosomes are double, each consisting of two half chromosomes (chromatids). In most organisms the disappearance of the nuclear envelope marks the beginning of prometaphase. During this period, or somewhat prior to it, a spindle-shaped bundle of fibers (now known to be microtubules) is organized in the cytoplasm. Toward the end of prometaphase the chromosomes become arranged in a group at the equator of this structure.

The spindle in those organisms in which it can be isolated and studied chemically is composed of fibrous protein molecules containing many sulfhydryl linkages and apparently oriented by the centrioles at either end. In animals (and in some plants) the centrioles also are surrounded by a pompon of fibers, the aster. In the somatic cells of most plants no asters or centrioles are visible, but they may be conspicuous in the reproductive cells. During the brief stage called metaphase, the chromosomes are arranged across the equator of the spindle with at least their spindle attachment points or centromeres in essentially a plane at right angles to the long axis of the spindle. Very shortly thereafter the centromeres appear to divide (they may actually have split at an earlier period) and the chromatids—now daughter chromosomes—move to the poles.

The phase of chromosome movement is called anaphase, and its mechanism is still not understood. None of the current theories satisfactorily explains the behavior of chromosomes and cells in all organisms. In some animals, for example, certain chromosomes behave

with remarkable autonomy. Sex chromosomes may appear as precocious or tardy in comparison with the autosomes. Specialized chromosomes may be confined to the germ line and become eliminated in later divisions. In the fungus gnat *Sciara* a monopolar spindle is formed at one division, and one group of chromosomes moves to the "nonpolar" end. Occasionally in animals the nuclear envelope does not disappear, and chromosome division takes place within the membrane, which eventually is pinched in two. As more work is carried out on the little-known invertebrates, algae, and fungi, other examples of unusual behavior undoubtedly will be found. Indeed, when proper perspective is reached as a result of systematic study, the higher plant-vertebrate mechanisms may seem unusual.

When the chromosomes have reached the poles of the spindle, a new nuclear envelope, which may arise from one of the membrane systems of the cytoplasm, is formed about each group of daughters. During this stage, telophase, animal cells usually divide by furrowing and plant cells by cell-plate formation. (A new cell wall partitions the old cell.) With this formation of two daughter cells, the process of cell division ends. Thus two cells, each with the same genotype, have been produced as a result of equational division of the chromosomes (mitosis) and division of the cytoplasm, during which the cytoplasmic organelles are apportioned roughly equally.

During the course of mitosis, the chromosomes (Fig. 2.3) go through an interesting and important series of changes. If a prophase chromosome is compared with an anaphase chromosome, striking differences are seen. The anaphase chromosome is not only easily visible and stainable but fatter and much shorter. By use of appropriate treatments, it can be shown that the anaphase chromosome is in the form of a tight spiral, the gyres (turns of the coil) of which behave as if they were invested with a stainable substance usually called matrix. The basic thread or chromonema of an anaphase chromosome often can be seen to be coiled in a fine series of gyres called minor coils. The easily seen major coils are imposed upon these by whatever process causes the shortening of the chromosomes. When there is more than one chromatid, as in metaphase, these may be twisted about one another.

Mitosis provides for the equational division of the chromosomes so that, barring a mutational event, each daughter cell receives the same genetic information. In many instances, as cells become specialized in form and function, division of the chromosomes may occur without division of the nucleus or of the cell. The result is cells with more than one nucleus or nuclei with more than the zygotic

Fig. 2.2 | Mitosis. A, early prophase; B, late prophase; C, prometaphase; D, metaphase; E, early anaphase; F, early telophase; G, late telophase; H, daughter nuclei. (Adapted from De Robertis, Nowinski, and Saez, 1954, *General Cytology*, 2d ed., W. B. Saunders Company.)

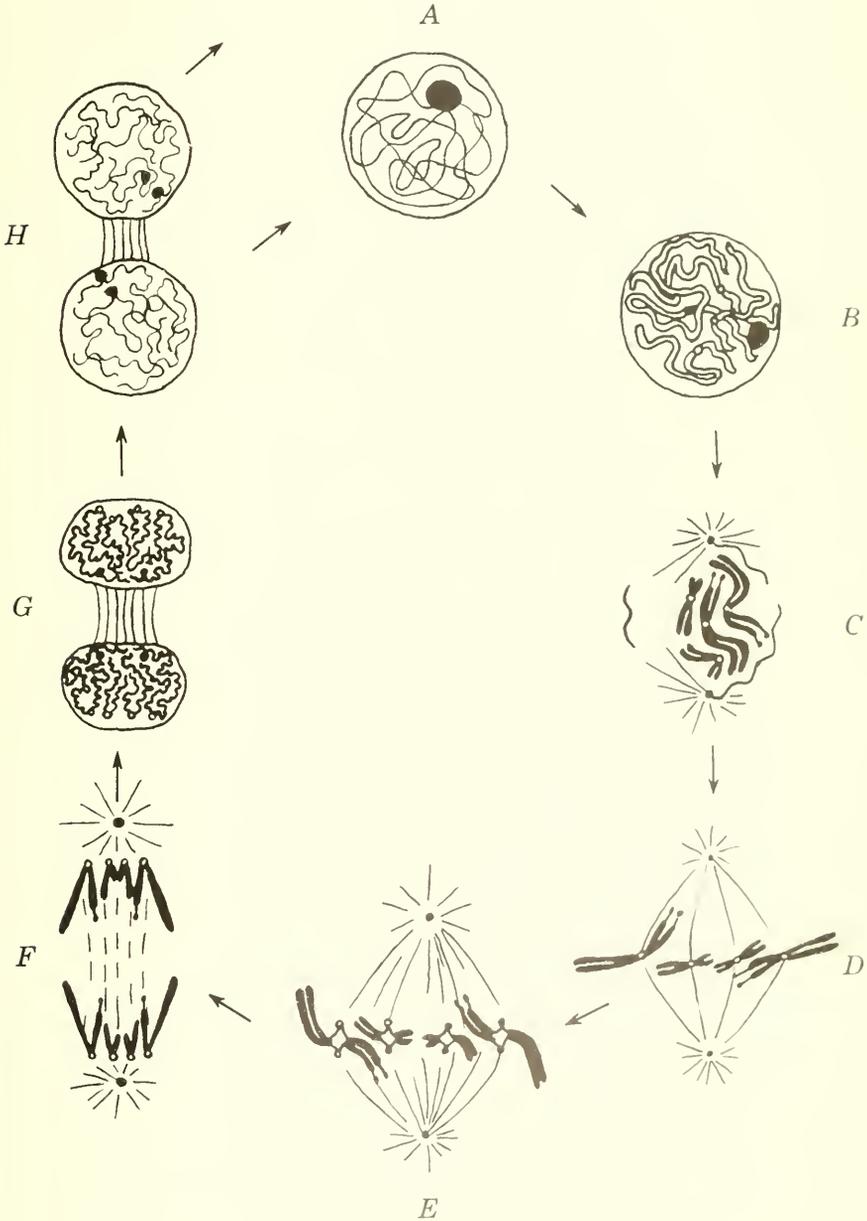
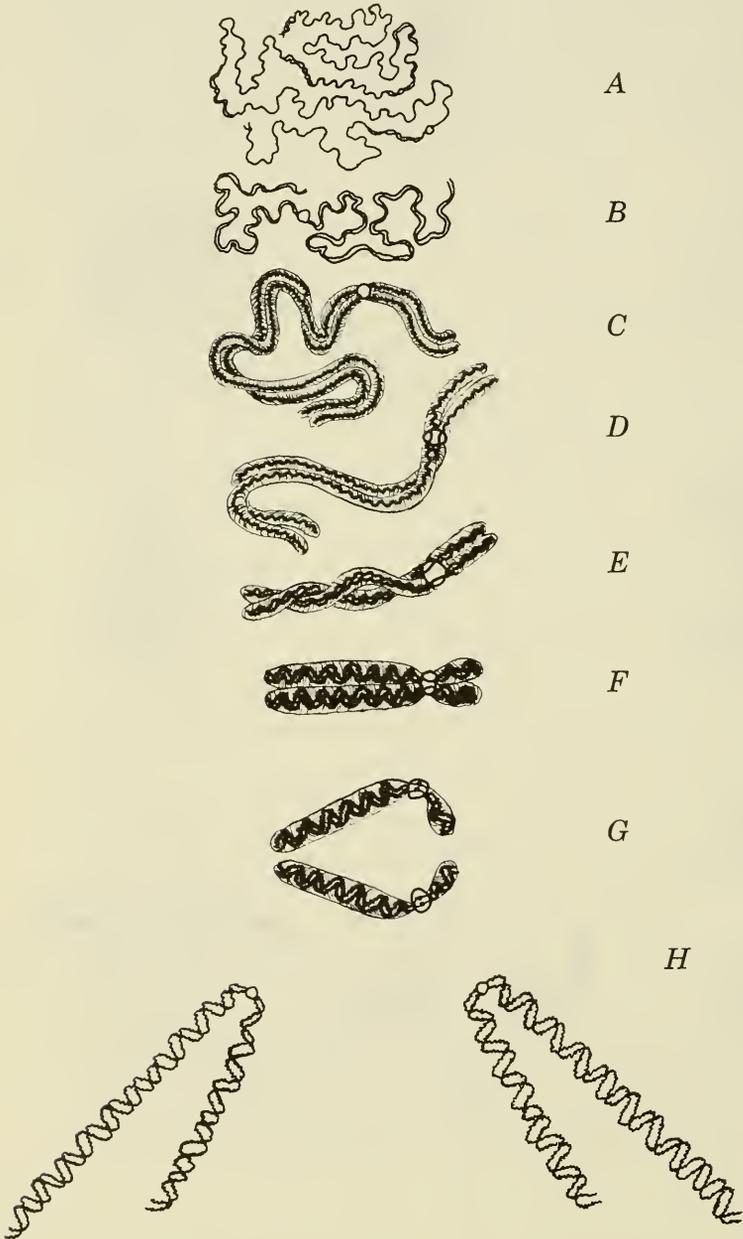


Fig. 2.3. | Spiralization cycle of the chromosomes. *A*, interphase; *B*, *C*, *D*, prophase changes, appearance of matrix; *E*, prometaphase, chromatids visibly double; *F*, metaphase; *G*, anaphase; *H*, telophase changes beginning in daughter chromosomes, disappearance of matrix. (Adapted from De Robertis, Nowinski, and Saez, 1954, *General Cytology*, 2d ed., W. B. Saunders Company.)



number of chromosomes. The latter appears to be the more common; it is referred to as endopolyploidy. In some organisms (e.g., insects) each tissue has its own characteristic degree of polyploidy. In the salivary glands of water striders (*Gerris*) the highly specialized cells may be 2,048-ploid. Tissues of other organisms contain a population of cells of varying degrees of ploidy (usually with a norm at a level above diploidy, e.g., at the tetraploid or octaploid level). This is the situation in the human liver, for example, or in tissues in the roots and stems of the flowering plants.

The significance of the phenomenon of endopolyploidy is not well understood. Certainly it correlates with secretory activities of the cells, and it may play a role in development as well as in differentiation. It should be emphasized, however, that no qualitative changes in the genetic material have been demonstrated. Germ-line cells in animals and cells producing spores in plants usually do not become endopolyploid. Reproductive cells therefore retain the zygotic or gametic number of chromosomes, while somatic cells may experience successive increases. If vegetative reproduction in plants takes place by means of budding or suckering from somatic tissue, offspring with increased chromosome number may arise. Such situations are discussed in Chap. 9.

CELL DIVISION: MEIOSIS

In addition to these mechanisms of preserving the existing chromosome number or of increasing it, organisms obviously must have a mechanism for reducing it. Mechanisms for reducing high endopolyploid numbers are poorly understood, but they have been reported in insects (*Culex*) and plants (*Allium*). The great majority of organisms share the mechanism for reducing the zygotic number of chromosomes to the gametic number; this mechanism is called meiosis (Fig. 2.4). Meiosis occurs in tissues that have not undergone endopolyploidy, such as germ-line cells in animals or sporogenous tissue in plants. Again, as with mitosis, its outlines are the same in all organisms, although in animals it results in gametes and in most plants it results in spores. A cell about to undergo meiosis may be called a meiocyte. The results of meiosis are nearly always four daughter cells with half the number of chromosomes of the meiocyte. In the formation of eggs in animals and in the production of megaspores in plants, three of these may be much smaller and eventually disappear.

Meiosis achieves these results by two cell divisions but only one division of the chromosomes. The following description refers to the

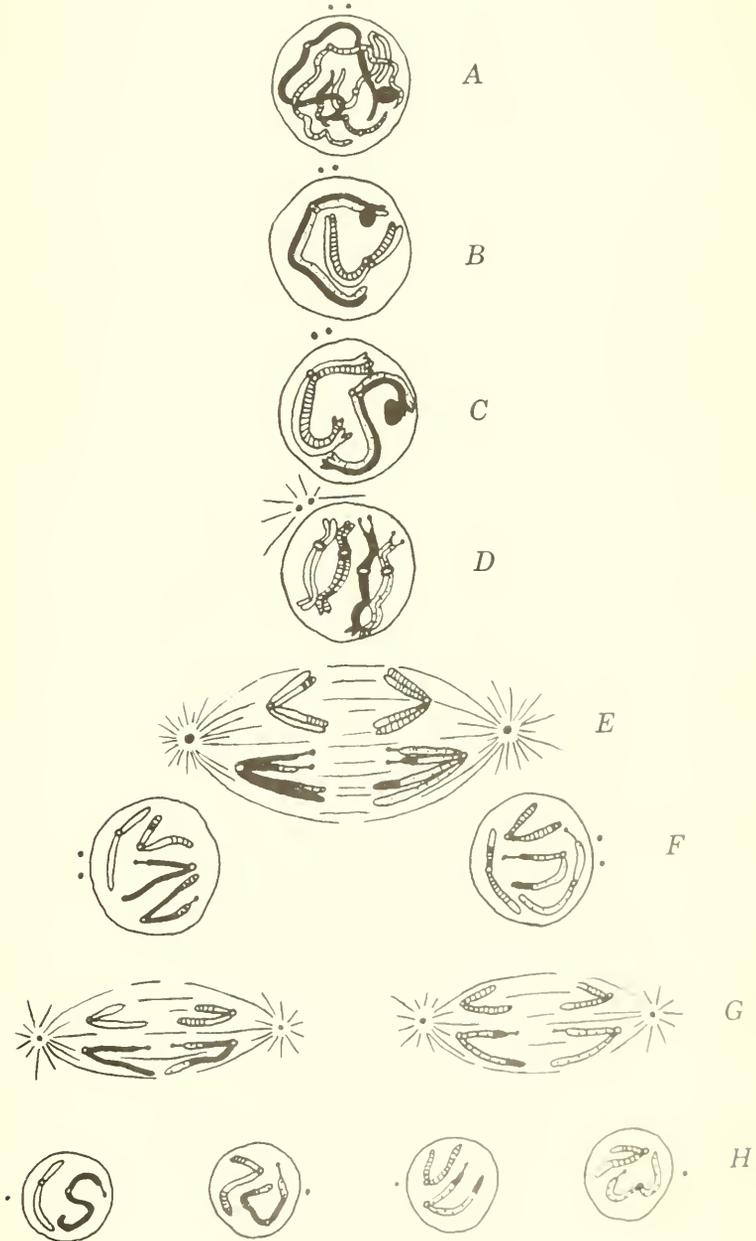
generally observed behavior of the chromosomes as seen with a light microscope. (Variations or exceptions have been noted in some organisms or with special techniques.) When a cell becomes a meiocyte, it usually enlarges somewhat, and its nucleus stains more faintly than before. When the chromosomes become visible in prophase, they often can be seen to be single strands instead of being double-stranded, as in mitosis. Their subsequent behavior is so complicated that the first meiotic prophase is prolonged in time and has been divided into a series of substages, the names of which need not concern us here. The first occurrence is synapsis of the chromosomes (present, of course, in pairs) with their homologues, precisely point for point along their length. After pairs or bivalents have been formed, the chromosomes then appear double-stranded. (It will be remembered that, in mitosis, prophase begins with the chromosomes double-stranded.) Each bivalent thus comprises four chromatids, two of the chromosome that arrived in the maternal gamete and two paternal chromatids. Any chromosome that does not have a homologue, a sex chromosome for example, remains as a univalent but undergoes doubling at about the same time as the others.

Apparently at about the time the chromosomes double, the slender chromatids break and rejoin in the bivalents. Intimately associated, coiled, and twisted, they often reunite in nonsister combinations; that is, instead of sister chromatids rejoining, maternal and paternal chromatids may be connected following a break. This is the phenomenon of cytological crossing-over. In some organisms crossing-over does not occur in one sex, e.g., male *Drosophila* and *Callimantis*. When the chromosomes have become double, they behave as if they now repel one another. Bivalents become widely spaced in the nucleus, and members of bivalents are held together only where crossing-over has occurred. (If crossing-over has not occurred, the chromosomes in a bivalent frequently separate at this stage.) As a result of the repulsion (this term is used only descriptively) of the chromosome arms, the bivalent assumes forms that depend upon the number and position of crossovers; the latter now become visible as chiasmata or cross-shaped configurations.

At this stage of meiosis a chiasma indicates a crossover. Subsequently, as the chromosomes coil and shorten and become more stainable, the chiasmata (but not the points of crossing-over) are pushed to the ends of the chromosomes. This process, known as terminalization (Fig. 2.5), also produces characteristic configurations of bivalents, adjoining loops lying at right angles.

At the end of the first meiotic prophase, the nucleus contains the gametic number of bivalents (plus any univalents that are present). At the first metaphase a spindle is formed, presumably precisely as

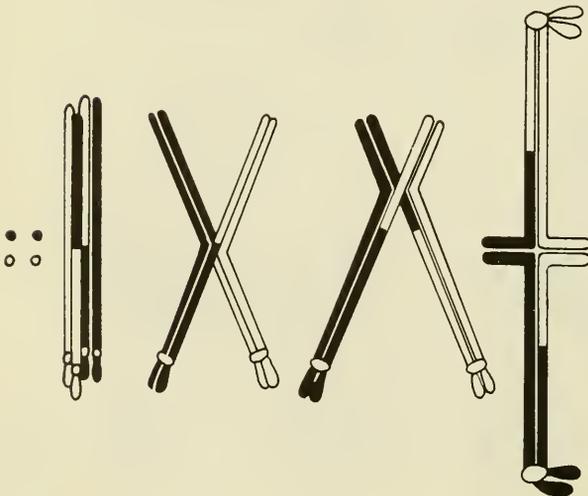
Fig. 2.4 | Meiosis. *A*, single-strand stage; *B*, pairing to form bivalents; *C*, four-strand stage; *D*, opening of bivalents to show chiasmata; *E*, first anaphase, disjunction of bivalents without centromere division; *F*, daughter nuclei with crossover chromatids; *G*, second anaphase, centromeres divide; *H*, four haploid daughter cells. (Adapted from De Robertis, Nowinski, and Saez, 1954, *General Cytology*, 2d ed., W. B. Saunders Company.)



in mitosis, and the bivalents become arranged on its equator. During first anaphase, instead of the centromeres dividing as in mitosis, the two centromeres of a bivalent move to opposite poles. Thus the chromosomes do not divide (for a chromosome is defined by its centromere) but *disjoin*, and disjunction results in two daughter nuclei that undergo the usual telophase transformation (or the latter may be much abbreviated). The centromeres of univalents similarly do not divide, a univalent going to one pole or the other. The distribution of maternal and paternal chromosomes is completely at random.

During the second division of meiosis, the behavior of the chromosomes is like that in mitosis, the difference being that *crossing-over has taken place so that the chromatids attached to a centromere are not identical*. This second division, in which the centromeres divide, results in the formation of the four daughters of the meiocyte. Each has the gametic chromosome number, but the chances of one daughter being genetically like any other are extremely small. Maternal and paternal chromosomes have been segregated at random, chromatids have been segregated at random, and finally, as the result of crossing-over, the genetic material in the parental genomes has been partially exchanged.

Fig. 2.5 | Terminalization of chiasmata. From left to right, chiasmata move to ends of chromosomes. (Note that the point of crossing-over does not change.) Far left, cross section of bivalent. Far right, rotation of chromosomes has occurred. (Adapted from *De Robertis, Nowinski, and Sacz, 1954, General Cytology, 2d ed., W. B. Saunders Company.*)



This then is the tremendous significance of meiosis and crossing-over. It provides a continual reshuffling of the genetic material in reproduction. New gene combinations are continually being produced, and essentially random union of gametes makes it unlikely that any two individuals will have the same genetic make-up. This cytological mechanism of the organism is part of its genetic system, the system that determines the amount of recombination a population will produce and that will be available for the operation of selection. The organisms most familiar to us are diploid, sexual, out-crossing organisms such as cats and dogs, oaks and pines. In later chapters (8, 9) other genetic systems will be discussed as examples of the ways in which the amount of recombination produced by this familiar genetic system may be modified (usually decreased, perhaps to zero).

SUMMARY

The cell is a metabolic unit composed of large and small molecules associated in specific ways, commonly as membrane systems, to form subunits or organelles of specialized function. The nucleus of the cell initiates and controls protein synthesis through the functioning of its chromosomes. When somatic cells divide, the cytoplasmic organelles are apportioned between the daughters in roughly equal quantity. By means of mitosis, the chromosomes are divided equationally between the daughters. Meiosis reduces the number of chromosomes in cells that will produce gametes. In the first division of this two-stage process, homologous chromosomes first synapse and then disjoin without division of their centromere. Cytological crossing-over takes place during the first division, and, when the centromeres divide in the second division, four daughter cells with recombined chromosomes and chromosome segments result. Meiosis provides the recombination that results in the variation upon which selection acts.

REFERENCES

- Swanson, C. P. 1957. *Cytology and Cytogenetics*. Prentice-Hall, Englewood Cliffs, N.J. A rather detailed and excellent discussion of cytology and its bearing on genetics and evolution. The author's introductory *The Cell* (1960, Prentice-Hall, Englewood Cliffs, N.J.) provides an elementary description.
- Wilson, G. B., and J. H. Morrison. 1961. *Cytology*. Reinhold, New York. An excellent modern cytology text which relates structure and cell physiology. The illustrations are generally first-rate.

3

genetics

It seems reasonable to assume that the selective forces involved in the evolution of the genetic mechanism of early organisms must have been concerned with stabilization of what was at first an almost infinitely variable system. The mechanisms for replicating genetic material generally ensure that it will be exactly duplicated and that, in the offspring, proteins similar to those of the parents will develop. In more complex multicellular organisms, self-regulatory developmental mechanisms are combined with the nuclear and extranuclear genetic material; together they provide a system that usually results in what is thought of as a normal, functioning, wild-type organism. As stated before, the basic phenomenon of genetics is that "like begets like."

VARIATION AND MENDELIAN GENETICS

Nevertheless, errors in replication occur; they result in the variability that permits selection. In general, analysis of the nature and transmission of variability, from generation to generation, is the only means of studying the mechanism of inheritance. If the patterns of variation in organisms are examined, it will be seen that some organisms appear to be more variable than others. Furthermore, the type of variation pattern differs with respect to organisms and the traits studied. In some instances, variation occurs in discrete steps and may be termed discontinuous. In other cases, variation appears to be continuous, individual organisms not falling into easily characterized discrete classes. Galton attempted to study continuous variation when he made his classic investigations of the inheritance of intelligence and other traits in human beings. Other workers, even before and including Linnaeus, had studied continuous variation by making crosses between varying plants and animals. The science of genetics was not really born, however, until the inheritance of characteristics that varied discontinuously was studied. Organisms having these characteristics could be classified as one or another of a very few distinct types. By observing the distribution in these classes of offspring of an experimental cross of parents with different characteristics, Mendel was able to describe the basic rules of behavior of nuclear hereditary units.

The importance of Mendel's studies was not generally appreciated; indeed, Mendel was urged to suppress his results by other scientists who felt that he was considerably off the beaten path of scientific research. In 1900 Mendel's papers were discovered by three

biologists who recognized their significance. Almost overnight, genetics became an important and rapidly developing field of biology. However, there were many scientists who felt that Mendel's work had little application to evolution in populations in nature or to the prevailing type of continuous variation found in wild and domesticated populations of both plants and animals. It was only after many years of work that the evolutionary significance of Mendel's laws was established.

THE UNITS OF HEREDITY

The units of heredity postulated by Mendel and subsequently termed genes were identified as specific regions of the chromosome; they are the segment between two closest points of crossing-over. More recent work, especially in the biochemical genetics of microorganisms, has led to other definitions of the gene. For example, it is generally accepted that specific genes control the formation of specific enzymes. By growing microorganisms on media of known composition, it is possible to show that gene mutation results in the loss of ability to carry out some cellular reaction. For example, a mutant bacterium may lose the ability to synthesize a particular substance, such as tryptophan. The number of mutant alleles of genes has been found usually to be quite large. It is necessary to think of the gene, as revealed by these studies, as a region of the chromosome that is mutationally complex. Benzer has referred to the possible mutational sites within a gene as mutons. Evidence suggests that a single muton may consist of only one or a very few nucleotides.

At this level of study, experiments have shown that recombination may occur *within* the limits of a single gene, i.e., within a functional unit. The smallest unit that is interchangeable is called a recon. Recombination studies show that the recon also is about the size of a nucleotide and that the mutons in the functional unit are arranged in linear fashion. Since it appears to make no difference phenotypically how the genes are arranged in an organism heterozygous for two factors, i.e., whether the genes are arranged $\frac{+}{a} \frac{+}{b}$ or $\frac{a+}{+b}$, it is interesting to ask the same question about parts of genes. Will enzyme synthesis take place just as well when the mutants within one gene are distributed between the two chromosomes (the so-called trans state) as when the mutants are on one chromosome (the cis state)? The answer is not clear, but occasionally parts of the gene may be divided between the homologous chromosomes, although the smallest group of mutants that must be in the cis posi-

tion is rather large. These examples of complementation between mutants are somewhat equivocal, however. The cis-trans test may be used to specify the functional gene units, which have been called cistrons.

In the study of populations, the unit of heredity must be given a strictly operational meaning within the context of the study, as, in fact, it must be in all biology. In evolutionary studies this unit cannot be the same as that in biochemical genetics. This must be kept clearly in mind when discussions of genes in an evolutionary context are compared with those based upon studies of microorganisms in the laboratory. In studying inheritance in populations in nature, the unit of heredity in most cases becomes a statistical one, for the factors controlling the expression of continuously varying traits are numerous and complexly interrelated. At present, only the methods of the statistician can sort out the interactions of the heredity units (which are assumed to be similar to those affecting discontinuous variation), the developmental systems through which they are expressed, and the effects of the environment on both these systems. The environment of an organism at any particular time or place is unique and not repeated or repeatable. This means that in experimental studies it is important to make replicate experiments in space and time—an unfortunately expensive and time-consuming process. In the following pages the basic facts of the inheritance of discontinuous and continuous variation will be summarized, together with a discussion of those aspects of gene behavior that are particularly important to evolutionary studies.

MENDEL'S LAWS

The basic rules of heredity deduced by Mendel are familiar to anyone who has had an elementary course in biology. In crossing peas, Mendel found that, when differing parents were mated, the first generation offspring (F_1) resembled one or the other parent. The trait expressed in the F_1 he referred to as dominant to that which did not appear (the recessive). Crossing the essentially uniform F_1 plants to produce a variable F_2 generation in which individuals with the recessive trait appeared, showed that the factors responsible for the appearance of the traits were not lost but merely hidden. By a study of the types of progeny in the F_1 and F_2 , Mendel deduced that each offspring contains two homologous factors, one received from each parent, affecting the expression of the traits studied. An F_1 offspring from a cross between differing parents must contain two different but homologous factors, one for the dominant trait and

one for the recessive. (In other words, the F_1 is heterozygous.) In the formation of the F_2 , these factors are segregated, and the offspring are produced in the approximate ratio of three with the dominant trait to one with the recessive. The individual showing the recessive condition is homozygous for the factors. Further crossing (including backcrosses to the parental types) shows that, of the three with the dominant trait, one will have like factors, and the other two, different factors, as in the F_1 individuals.

When parents differing in, and homozygous for, several characters were crossed, Mendel found that the factors for the different traits he was studying behaved independently. In the F_1 both dominant traits were observed, and in the F_2 each trait segregated by a 3:1 ratio. If the homozygous parents differ in two traits, for example, the proportion of types in the F_2 is the square of a 3:1 ratio or 9:3:3:1. By backcrossing offspring to the parental types, verification of the number of factors and their independence may be obtained.

It is clear that the behavior of these factors parallels the behavior of the chromosomes now known to bear them. The factors affecting the traits in peas studied by Mendel were on nonhomologous different chromosomes. Later studies showed that factors on the same chromosome were linked (tending to occur together more frequently than would be expected if assortment were independent). When numerous traits are studied, their factors are found to fall into as many linkage groups as the haploid number of chromosomes. Within a linkage group the amount of recombination varies from a very low percentage for genes close together to 50 percent for genes far apart (which genetically is indistinguishable from independence—occurrence on different chromosomes).

RECOMBINATION

The cause of genetic recombination of linked genes is cytological crossing-over in meiosis (diagrammed in the previous chapter). In studies of inheritance at a gross level, the factor presumably affecting a particular characteristic is the minimum distance between two points of crossing-over. (This is the operational definition of a gene in this instance.) Crossing-over occurs in all organisms in which meiosis and sexual recombination have been found. The basic mechanism appears to be the same wherever it occurs, and some workers have postulated that meiosis cannot properly take place in the absence of crossing-over (or a specialized substitute).

The precise mechanism of cytological crossing-over is not known. Presumably when the chromosomes are synapsed and twisted to-

gether in the first meiotic prophase, the chromatids break and the broken ends subsequently join. If nonsister chromatids are joined, then crossing-over has occurred. Crossing-over does not occur with equal frequency along the length of the chromosome. It is rare or absent near the centromere and at the very ends of the chromosomes. Near large blocks of heterochromatic material, crossing-over also is reduced. In some organisms, crossing-over is effectively restricted to certain parts of the chromosomes; in others, it seems to occur rather evenly throughout the length of the chromosome arm. Perhaps the difference lies, in part at least, in the amount and distribution of heterochromatin. Occasionally crossing-over is suppressed entirely, as in male *Drosophila* and female silkworms (*Bombyx mori*). The occurrence of a crossover also interferes with the formation of a crossover immediately adjacent. Interference may be measured by studying linkage, and it can be shown to vary along the chromosome and between different chromosomes. Probably interference is also a structural phenomenon.

If two factors are located some distance apart on the chromosome, it is possible that more than one crossover will occur between them. If double crossing-over takes place, the effects on recombination depend upon which chromatids are involved (Fig. 3.1). If the same two chromatids of the four associated in the bivalent are involved in both crossovers, the occurrence will not be detected unless a third factor located between the original two is also observed. Should the other two chromatids experience the second crossing-over, each chromatid will have one crossover. This crossing-over may be referred to as two-strand and four-strand exchange, respectively. Three-strand exchange results in the formation of a noncrossover chromatid and three chromatids with a single crossover. In general with multiple crossing-over between two factors, the resulting chromosomes with an even number of crossovers and those with no crossovers will appear as parental types. Chromosomes with an odd number of crossovers between the factors in question will be recombinant types. Since the number of chromosomes with recombinations equals the number with no or an even number of crossovers, recombination cannot exceed 50 percent.

Crossing-over is influenced by environmental factors, such as temperature, and is also under genetic control. This genetic-control mechanism is rather complex and not well understood. Apparently genes determine the length of time available for synapsis (which affects crossing-over) and the localization of crossovers; there are genes that have the effect of preventing synapsis altogether. Genetic disturbances of other components of meiosis would be expected also

to affect crossing-over. In evolutionary terms, it would appear that these factors directly influencing crossing-over per se have not been important in the control of recombination. When the amount of recombination is reduced in certain organisms, presumably by the operation of natural selection, other mechanisms usually are involved, such as inversion, translocation, or elimination of meiosis altogether (in apomictic organisms; see Chap. 9).

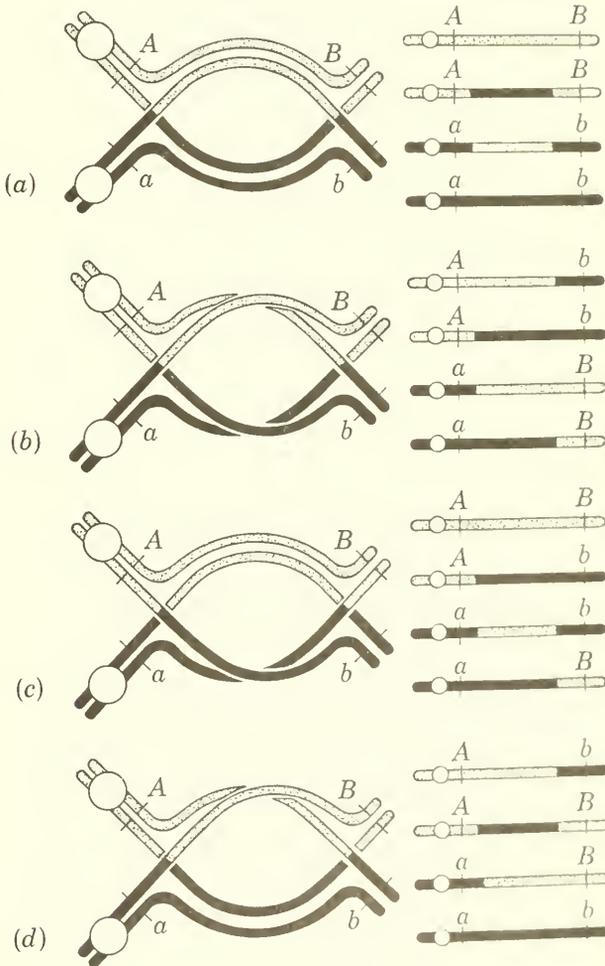
THE EXPRESSION OF GENES

The action of genes in an individual organism has proved to be quite variable. Genes in a population are rarely found in only two alternative states or alleles. Rather, a system of multiple alleles appears to be the common system governing most characteristics, e.g., blood groups in animals, incompatibility systems in plants, coat color in mammals, flower color in plants, etc. Interaction among the genes in the genotype or of the developmental pathways resulting in the phenotype produces complex genetic ratios. For example, where pigment systems leading to the formation of a particular color are involved, several genes may control different steps in the elaboration of the pigment. If any one is missing, color is lacking. Such genes are called complementary genes.

On the other hand, there are many situations where the expression of the gene at one locus masks the expression of another gene. This is known as epistasis; the epistatic gene masks or prevents the expression of a hypostatic gene. In chickens, for example, the Leghorn white color is epistatic to many genes affecting color and pattern. If it is present, no color but white will be expressed. It is obvious that complementary effects and epistasis, as well as other sorts of modified expression, are related developmentally. A similar phenomenon occurs where there appears to be one gene or a group of genes, each with relatively small effect, that operate to alter the action of a gene with major effect. These "minor" genes are known as modifying factors.

It often becomes necessary to specify the type of expression of genes because, for many factors, this is variable. For certain factors, all or almost all individuals with the same genotype develop a characteristic phenotype that distinguishes them from individuals with other genotypes in a certain range of environments. The genes in such cases are said to have high *penetrance*, since most individuals carrying the gene possess the trait. Other genes do not always produce a detectable phenotypic effect in the individuals that carry them in a given environment. These are genes of low

Fig. 3.1 | Different results in double crossing-over. A, two-strand exchange; B, four-strand exchange; C, D, three-strand exchange. (Adapted from De Robertis, Nowinski, and Saez, 1954, *General Cytology*, 2d ed., W. B. Saunders Company; and White, 1954, *Animal Cytology and Evolution*, 2d ed., Cambridge University Press.)



penetrance. It is possible also that the phenotypic expression of a gene may be variable even though it is completely penetrant. If it is relatively uniform in an essentially "normal" environment, the gene has constant *expressivity*, but if there is interindividual variation in the trait, expressivity is variable.

Studies of the manifold or pleiotropic action of genes, as well as of systems of genes controlling the expression of particular characteristics, have suggested that probably no character of an organism is controlled by only one gene, and, conversely, every gene in the genotype of an organism affects a great many (if not all) characters in the complex process of producing the phenotype. But it seems likely that the amino acid sequence of a specific polypeptide is determined by one and only one gene.

MUTATION

It is often possible in controlled crosses to identify specific genes affecting particular characters that show discontinuous variation. The most obvious characteristic of such major genes is that they change or mutate—indeed, that is the only way in which their existence may be detected. Mutations occur spontaneously at varying rates; they also may be induced by treatment of the organisms with ionizing radiation, ultraviolet light, or various chemicals. These treatments appear to affect the DNA more or less specifically. The discussion of spontaneous mutation rate is difficult because there are several ways in which the rate may be expressed. As far as is known, the mutational event is random; it is not possible to specify what gene will be affected or to assign the cause of a given mutation to a specific mutagenic agent. It would be desirable to know the chance of occurrence of a mutation per cell per division, which expresses change with respect to time. This is very difficult to determine in other than microorganisms. Even with bacteria, what is measured is phenotypic change which may involve more than one gene or mutable unit. Rates of from 10^{-6} to 10^{-9} have been measured in microorganisms.

In multicellular organisms, rates must generally be measured differently (except where tissue culture is possible) since the criterion available is the number of gametes producing mutant individuals per generation of the organism. Thus individuals, not gametes, are counted. In the gonads a mutation occurring in a gamete-producing cell may have many or few mutant daughters, depending upon when in gametogenesis the mutation took place. The mutation rate per generation varies with the gene studied but averages about 10^{-5} .

When rates per cell division are measured by tissue-culture studies of bone marrow cells, they average about 10^{-6} .

Mutation rate appears to be under genetic control and is therefore subject to change in the course of evolution. Genes whose major effect seems to be affecting the mutation rate of other genes are known. One would expect that in most organisms selection would have resulted in the genotype that maintains an optimum level of mutations in the population. This is difficult to study, and few data are available. The problem is closely connected with that concerning the effects of heterozygosity in developmental buffering or homeostasis and in genetic homeostasis and is discussed in later chapters.

EVOLUTION OF DOMINANCE

There are several other interesting aspects of mutation about which little is known. Most mutant alleles occurring in the organisms that have been studied in detail are recessive to the wild-type gene. This raises the problem of how dominance-recessiveness arose. It is clear that most mutations that take place will be deleterious to the organism, since they alter a functional system. If they have a major effect, almost certainly the complexly interrelated developmental pathways will be grossly upset and the organism will die. Even if the gene has only a relatively minor effect, however, the integration of the genotype is such that the mutant organism will be less fit than its parents, provided that there is no environmental change. (The chances of improving the operation of a radio receiver by making a small random change in its circuits are slim indeed.) Recessive mutations, when they occur in a diploid organism, are stored in the organism's reservoir of variability. When they are (rarely) combined in the homozygous state, they will be eliminated unless the environment (in the broadest sense) has changed sufficiently to give them positive selective value.

How then does recessiveness arise? There are several hypotheses among which it is difficult to discriminate at present, although all probably have elements of truth. Fisher has suggested that mutations will not necessarily be completely recessive on their first occurrence. They will thus, in general, be disadvantageous unless other modifying genes at different loci reduce the deleterious effects of their expression. Since the homozygous condition for the mutation will rarely occur, selection will operate on the more common heterozygotes to build up systems of modifiers that will result in the heterozygote resembling the homozygous dominant.

Wright and Haldane have discussed the problem of the origin of

dominance in terms of the relation between the gene-produced enzyme and its substrate. In their view, recessive genes are those which are less active than the wild type in the production of a particular enzyme. Selection presumably will have built in a safety factor so that there is an excess of enzyme over substrate, and a mutation reducing the amount of enzyme will have little effect in the heterozygote. Biochemical genetics is supplying answers to the questions concerning the quantitative aspects of gene function in enzyme synthesis.

Wright and Haldane have also suggested that the selective value for the modifying factors might be so low that dominance would arise too slowly for it to have a large chance of appearance when other factors are taken into consideration. In some organisms there is evidence that the selective coefficients for modifying genes may be considerably higher than those postulated by Wright and Fisher. In either event, selection has played an important role in the evolution of the behavior of genes. Hybridization experiments in organisms as diverse as cotton plants and butterflies have clearly shown that the functioning of a gene may change when it is moved from one genetic background to another. Thus selection altering the background (e.g., "modifiers") can affect the expression of a given gene.

There is considerable evidence that this is exactly what has happened during the development of industrial melanism in the moth *Biston betularia* (see Chap. 7). Early samples of heterozygotes for the melanic allele were quite distinct from the homozygous melanics. By the middle of the twentieth century, the heterozygotes were almost identical to these homozygotes. Clearly, dominance has evolved in this case.

CHROMOSOMAL MECHANISMS

The existence of means of artificially inducing mutations in easily grown organisms with relatively short life cycles (such as *Drosophila*, *Zea*, and *Neurospora*) has led to careful studies of linkage and the linkage groups or chromosomes. If it is assumed that the amount of crossing-over between two factors is proportional to the distance between them, then the spacing and arrangement of the genes along the chromosome can be determined. A genetic-linkage chromosome map, based upon recombination data, can be made. In such work it must be kept in mind that there may be interference between adjacent crossovers; that, with factors that are far apart, multiple crossing-over may occur between them; and that only parts of the chromosome with easily studied major phenotypic effect can be mapped.

There are other means of producing chromosomal maps, however, and these give a check on the method. For example, it is possible to map chromosomes by studying the effects of induced deletions of small portions of the chromosome and of chromosomal changes such as inversions and translocations, as well as other techniques. These have confirmed the linear order of the genes mapped by crossover studies, but these maps vary from genetic maps, often strikingly, in spacing and other details. Regions of the chromosome that are heterochromatic and that seem to lack genes with major effect are not easily studied by the recombination analysis; in the main these are responsible for the differences. Progress has been made in localizing specific genetic effects at visible regions of the chromosomes in *Drosophila* (with its giant polytene salivary-gland chromosomes) and in *Zea* (where the chromosomes have characteristic chromomeres visible under the microscope).

Sex Chromosomes

A specialized sort of linkage occurs in animals and plants with differentiation of sexes. In these organisms where there are special sex chromosomes, as opposed to the other chromosomes (known as autosomes), one sex usually has two homologous sex chromosomes. The other sex has only one chromosome homologous with these and either lacks the second or has another only partially homologous chromosome. In *Drosophila* and man the female is the homogametic sex with two X chromosomes (every gamete contains an X), while the male is heterogametic with an X chromosome and its partial homologue Y (there are two kinds of gametes). It is clear that the transmission of genes that are located on the sex chromosomes will be different from those on the autosomes. Furthermore, the characteristics affected by these genes will show genetic linkage with sex. Sex chromosomes in these organisms differ from the autosomes in that they are specialized into two different regions. A portion of the two different sex chromosomes in the heterogametic sex will synapse and crossing-over may occur. In contrast to these *pairing segments*, there are the *differential segments* of the X and Y that do not pair. The differential segment of the Y usually contains few if any genes with detectable effect, and it is heterochromatic and smaller than the differential segment of the X. When it does carry genes, they are passed from father to son and females never show the traits involved. The heterochromatic portion of the Y is necessary for fertility; therefore it cannot be completely without effect.

In some groups the female is the heterogametic sex, while the male

is homogametic. In many species the Y chromosome is lacking and the male is then designated as XO. More complicated sex-chromosome mechanisms have evolved; these are discussed in Chap. 9. For example, there are many sex chromosomes in some organisms. It should be emphasized that the precise mechanism of sex determination varies from group to group, even though the chromosome condition may appear the same. The evolution of sexuality as an aspect of the storage of variability and its release through genetic recombination is discussed in Chap. 8.

Alterations of the Chromosomes

In addition to the mutations discussed above (called gene or point mutations), changes in the structure of the chromosomes take place spontaneously and may be induced by the same agents that cause gene mutation. Although these chromosomal alterations are sometimes termed mutations, it is perhaps less confusing to restrict the term mutation to gene changes. Chromosomal alterations also are frequently referred to as *aberrations* or *abnormalities*. This is because they are compared with an arbitrarily selected standard chromosomal phenotype (usually the wild type); they should not be taken to represent some unusual or deleterious phenomenon that is inevitably disadvantageous to the organism. As with gene mutations, chromosomal alterations usually have low or negative selective value when they appear but may become stabilized in the population or replace the standard type if their selective value increases as a result of environmental change (if the nucleus and the genes are included as part of the environment).

Practically any accident that can be imagined as happening to the chromosomes, during the course of cellular life and division, has been found in laboratory organisms and organisms from the field. Often such modification of behavior can be shown to have become established as a regular feature of particular organisms. A simple classification of chromosomal alterations would include deletions (loss of a segment), duplications (repeat of a segment in a contiguous or remote portion of the karyotype), inversions (reversal of a segment), and translocations (transfer of a portion of a chromosome to a nonhomologous chromosome, usually reciprocally). Changes of chromosome number, often thought of as "chromosomal mutation," are discussed in Chap. 9.

Deletions and Duplications. The role in evolution of loss or addition of chromosome material is very poorly understood. When homozygous, deletions usually are lethal. They are a useful tool for map-

ping chromosomes but of unknown significance in populations. Duplications are of importance because they represent a possible cytogenetic mechanism for an increase in the total amount of genetic material. How the total amount of genetic material has changed in the course of the evolution of life is not known. Nor is it possible at present to decide whether it is necessary that the amount of genetic material increase concomitantly with the increase in complexity that has taken place.

Inversions and Translocations. Inversions and reciprocal translocations are more conspicuous and better-understood chromosomal alterations, and their effects are well known. Organisms in which these changes have become a regular feature of the genetic system are discussed in Chap. 9. Here only the cytogenetic aspects of such changes are considered. Unless pairing behavior is studied, an inverted region of a chromosome ordinarily cannot be detected visually except in organisms with polytene chromosomes or conspicuous chromomeres. During the first meiotic prophase, when homologous chromosomes pair, heterozygosity for an inversion is revealed by the fact that one chromosome must twist in order for synapsis to be accomplished (Fig. 3.2). This characteristic inversion loop is also seen in the salivary-gland chromosomes of *Drosophila* and other Diptera where the polytene chromosomes are somatically paired. If the inversion is a short one, crossing-over may not take place within the inversion loop. If the inversion is sufficiently long and has the proper relation to the centromere, crossing-over will occur and the result will be the formation of a dicentric chromosome and an acentric fragment. The acentric fragment will not behave properly on the spindle at anaphase, and the dicentric fragment will be broken. Gametes that are formed will include, in addition to balanced ones, those in which whole chromosome regions are lacking, and these will be nonfunctional.

Looking at the genetic results, it will appear as though crossing-over had been suppressed. However, only the products of crossing-over have been lost. The number of crossovers within the inversion loop and their distribution among the chromatids of the bivalent determine what effects there will be. Because the genes within an inversion loop are effectively linked in a heterozygote under certain conditions, inversions are discussed in more detail in relation to recombination in Chap. 9. Organisms that are homozygous for a chromosomal inversion can be recognized as such only by mating them with a different type and then observing the pairing behavior of the chromosomes in the hybrid (except in organisms with polytene chromosomes, where they can be detected by careful examina-

tion of the banding patterns). Since synapsis will be unaffected in the homozygote, recombination will not be reduced, but the linear arrangement and linkage relations of the genes will, of course, be changed.

Reciprocal translocations involve nonhomologous chromosomes. Here a portion of one chromosome is transferred to another, and vice versa, so that linkage groups are changed. The size of the segments exchanged may be the same or different, large or small. Sometimes one chromosome will exchange a heterochromatic region (with little specific genetic activity) for a euchromatic region (with typical genetic behavior). Heterozygosity for large reciprocal translocations is visible in meiosis, as well as in organisms with somatically paired polytene chromosomes. Synapsis will result in the association of four chromosomes, two standard and two with translocated regions. At metaphase the appearance of this quadrivalent will depend, among other things, upon the distribution of chiasmata. Usually the chromosomes separate to form a ring. Chromosome ends are held together by terminalized chiasmata. Disjunction may occur so that adjacent centromeres go to the same pole. Examination of Fig. 3.3 will show that there are two different possibilities for this sort of disjunction but that either will lead to the production of unbalanced gametes (i.e., those with duplications and deficiencies). Only if alternate centromeres go to the same pole can balanced gametes result. The fusion of such gametes, randomly, will produce standard homozygotes, translocation heterozygotes, and translocation homozygotes in the ratio of 1:2:1. Organisms that are homozygous for a reciprocal translocation exhibit no meiotic peculiarities since synapsis is undisturbed. The linkage groups are changed, however; this can be detected by genetic analysis.

It is possible for more than one inversion to occur in a nucleus or in a chromosome. Inversions in a chromosome may be in one arm only or may include the centromere. If there are several, they may be independent or overlapping, or one or more may be included within another. Detailed studies of these conditions have been made in *Drosophila* and are discussed in Chap. 9. With more than one translocation, the result depends upon which chromosomes are involved. If a different pair exchanges segments after the first translocation, the result will be the formation of two quadrivalents at metaphase of meiosis. If one of the chromosomes experiencing the first translocation exchanges a segment with a third, a ring of three chromosomes is found. Finally, in some organisms, all the chromosomes exchange arms and all are attached in a ring at meiosis. Examples of this are considered in Chap. 9.

Fig. 3.2 | Result of crossing-over in the loop of a bivalent heterozygous for a paracentric inversion.

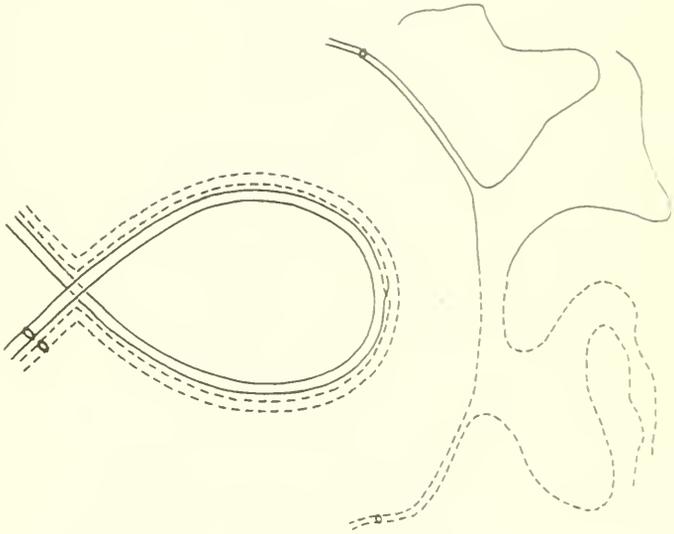
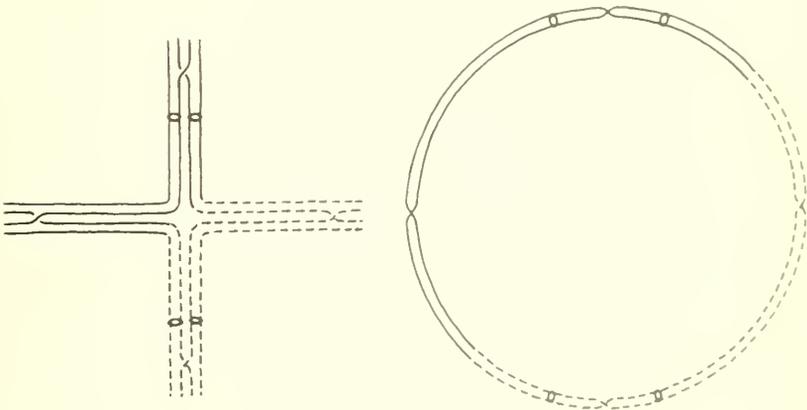


Fig. 3.3 | Result of distal crossing-over and disjunction in an organism heterozygous for a reciprocal translocation. Chromosomes or chromosome segments that are homologous are indicated by same type of line.



CONTINUOUS VARIATION

When one comes to study the genetics of continuously varying characteristics, the problems become much more difficult. Usually it is not possible to identify specific genes controlling specific traits. As has been mentioned above, there is thought to be a continuous spectrum of characters ranging from those which vary qualitatively to those which vary quantitatively. Presumably there is no basic difference between genes with easily detected major effect (often called oligogenes or switch genes) and those with only minor effect individually but which operate as part of a system of an indefinite number of factors (often called polygenes, although this term has been used in a more restricted sense). Operationally, it may be said that the difference between the two types of characters depends more on the relative importance of the genetic material and the environment in determining the phenotype than upon the size of individual gene effects. However, there are polygenic characters in which the role of the environment is relatively unimportant, such as number of abdominal bristles in *Drosophila*.

In studying variation in a quantitative character, as large a sample as possible of differing individuals is measured. All the individuals are unique but their measurements may be grouped into size classes. When these measurements are plotted as a frequency distribution, the nature of the variation may be studied. For instance, the arithmetic mean or average may be calculated for all the individuals in the sample. The amount of variation in the sample may be estimated by the standard deviation S or its square, the variance S^2 .

It is usually difficult to separate genetic and environmental components of variation and to study the genetic portion independently. Various laboratory techniques and rather complex mathematical formulations have been developed to study and separate these components. For example, one way to estimate the size of these two components involves the reduction of the genetic component until it is negligible. The variance in the character measured is observed in a population in a "normal" environment. Then the variance of the same character is measured in individuals of a highly inbred line raised in the same environment. Since these individuals may be considered to be essentially identical genetically, the variance observed may be attributed entirely to the effects of environment. The difference between the two variances is then an estimate of the genetic variance, since total variance (phenotypic variance S_p^2) is, in this

case, equal to genetic variance S_G^2 plus environmental variance S_E^2 . Thus $S_P^2 - S_E^2 = S_G^2$. This procedure for estimating the variance components rests on the assumption that the environmental variance is independent of genotype, an assumption that is often incorrect.

Even if the genetic variance can be determined, further complexities exist. It cannot be assumed for all characters that the effects of genes are additive in a simple cumulative fashion. The genetic variance itself must be broken down into components. There is the additive component representing the differences between the homozygotes and heterozygote(s) for each locus. Also to be taken into account are a component resulting from interactions of alleles, i.e., a dominance component, and a component resulting from interactions of nonalleles, an epistatic component. In many situations the additive genetic component is the only one that may be estimated conveniently. Then the phenotypic variance is partitioned into additive genetic and remainder variances. The latter is a catchall term for the nonadditive components of the genetic variance plus the environmental variance and gene-environment interactions. The proportion of the phenotypic variance attributable to additive genetic effects is known as the heritability ($h^2 = S_G^2/S_P^2$). Sometimes heritability is defined in a narrower sense as S_A^2/S_P^2 , where S_A^2 is the additive genetic variance. Heritability is a good estimator of the degree of resemblance between offspring and parent and as such is of great value to the plant and animal breeder.

The evolutionist must deal with these complexities since the great majority of traits found to be variable in organisms vary quantitatively and are under the control of multiple factors. Where crosses can be made between races, species, or even genera, the F_1 offspring generally prove to be more or less intermediate and the F_2 show the continuous variation characteristic of polygenic inheritance. (This is an overgeneralization of a complex situation; those wishing further information should consult Falconer, especially the sections on *inbreeding depression* and *heterosis* in chap. 14.)

Control of a characteristic by many genes provides a stability of phenotypic expression that may not occur when only single genes are involved. For instance, a single mutational event is unlikely to disturb seriously the expression of a character dependent upon, say, the additive effects of 35 loci. However, a single mutational event $i \rightarrow I$ in the color-inhibitor gene of an onion will result in a white onion rather than a red or yellow one. In view of the possible drastic effects of changes in "major" genes, it is not surprising that most characteristics of organisms are controlled multigenically. Selection would have favored the development of such systems since they tend

to reduce the possible deleterious effects of minor events such as a single base-pair substitution.

Polygenic systems that express relatively little variability may store tremendous potential variability simply because they have the ability to respond to selection by producing genotypes which, in the absence of selection, would never be produced. Let us suppose that a character is controlled by 40 loci, at each of which there are + and - alleles, and that the effects of the genes are additive (e.g., the most extreme phenotypes have all loci homozygous ++ or homozygous --). If the gene frequency at each locus were +.50 and -.50, then, in the absence of selection, the probability of a single diploid individual having the extreme + phenotype (being homozygous ++ at each locus) would be $(\frac{1}{2})^{80}$, a number infinitesimally smaller than one divided by the number of electrons in the universe—for all practical purposes, zero. However, this potential could be realized in perhaps 8 or 10 generations by selection favoring individuals with a maximum of + alleles. Multiple-factor systems of inheritance provide, then, an important mechanism for maintaining balance between fitness for the immediate environmental situation and flexibility for response to long-range change in the environment.

SUMMARY

In the majority of organisms, genetic material, DNA, is associated with long protein strands forming chromosomes. The chromosomes are linearly differentiated into functional units called genes, existing in numerous allelic states, which control the formation of specific enzymes. Mutation of genes to different allelic states occurs spontaneously with a frequency of from 10^{-5} to 10^{-9} per generation. Meiosis and crossing-over result in recombinational units, usually equivalent to the functional genes. Except for chromosome linkage, genes segregate and recombine independently in the zygotes. Intra-allelic interaction or dominance and interallelic interaction or epistasis occur. Some characters are affected by genes with conspicuous major effect, although modifying factors also may be found. Most characters are controlled by a very large number of nonhomologous genes, each with relatively small effect. Study of the resulting quantitative variation is complicated by the difficulty of separating the various fractions of the genetic component of variation from each other and from the environmental component. The basic source of variation is gene mutation. In populations of sexual higher organisms, recombination is more important as a source of immediate variability in the short-term analysis.

REFERENCES

- Falconer, D. S. 1960. *Introduction to Quantitative Genetics*. Ronald, New York. A clearly written modern text dealing with both quantitative and population genetics.
- Sager, R., and F. J. Ryan. 1961. *Cell Heredity*. Wiley, New York. Excellent for biochemical genetics but making no attempt to integrate this subject with the rest of biology.
- Sinnott, E. W., L. C. Dunn, and T. Dobzhansky. 1958. *Principles of Genetics*. McGraw-Hill, New York. A fine general text. For developments in biochemical genetics since this book was published, the preceding source and issues of *The Scientific American* may be consulted.

4

development

The genetic mechanisms described in Chap. 3 presumably evolved because they preserved successful combinations of genetic material. Some protoorganisms may merely have continued growth until accidents led to their disintegration. Many may have died because changing surface-volume relationships disrupted their inefficient internal organization. Some may have fragmented into smaller entities, with chance alone determining whether the offspring fragments would have the organization to continue growth. Any mechanisms arising by chance that would tend to ensure that subsequent fragmentation products retained the capacity for growth (and further successful fragmentation) would automatically be perpetuated. Thus evolved the mechanisms that led to a stabilization of the marked variation which must have occurred in early division and development. The origin of these mechanisms is, in a sense, the basic problem in the origin of living systems, as has been discussed in Chap. 1. It has been facetiously suggested that human beings are merely one means that DNA has evolved for making more DNA; it may also be said that DNA is merely one device used by human beings to keep from having nonhuman offspring. Genetic material does not replicate without other components of living systems. The course of evolution has involved increasingly complex systems, including the genetic one.

GROWTH AND HOMEOSTASIS

Presumably the earliest organisms were unicellular (or noncellular). In such organisms only one or two cell divisions (and possibly one fusion of cells) produce separate functioning entities. Here the distinction between heredity and development or differentiation that we are accustomed to draw for multicellular organisms is often difficult to make. Each cellular component is a hereditary unit that is replicated with greater or lesser accuracy during cell multiplication.

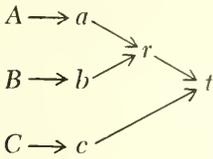
With the development of multicellularity and increased complexity, other problems arise. There is eventually a separation of germ-line cells and somatic cells. Nuclear and nonnuclear replicable components of cells that were present in unicellular organisms now appear to diverge somewhat in function. Greater stabilization and control are characteristic of the nuclear material, which we think of as *the* genetic information (genotype). The nonnuclear material plays a major role in development and differentiation, changing

its properties through time and interacting with the nuclear material and the environment (including other cells). A unicellular organism is, in a way, immortal. The "end" of a cell usually is the result of accidental destruction (including the result of predation) or the division of one cell into two. Death comes eventually to the somatic cells of multicellular creatures and may be considered a part of the genetic system.

Increase of size, or growth, is inherent in the idea of continuing reproduction. The term development refers to the changes that take place during the life of an organism. Simple changes in surface-volume relationships, which may have constituted development in a protoorganism, seem a far cry from the life cycle of a monarch butterfly (egg-larva-pupa-adult), but the difference is one of degree, not of kind. Organisms change size in growth, and what is a working design at one size may be completely nonfunctional at another. Given the physical limitations of the size of mammalian cells (imposed by such factors, among many others, as the size of protein molecules and rates of diffusion), it is easy to see that a perfect miniature human the size of an ovum, or a sperm cell 6 feet long, would be impossible. A genetic mechanism thus does not ensure the production of duplicates of the parental multicellular organism but rather the production of entities that, within certain limits of variation, will *develop* into replicates of the parental type.

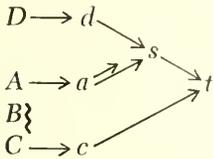
This regulation may be termed developmental homeostasis and is closely tied to the concept of "wild type." Most kinds of organisms seem to vary greatly only in rather superficial characteristics. The *Drosophila* wild type has been extensively described genetically. The human wild type does not have each eye of a different color or six digits on each hand. Redwood trees may vary in height and branch number, but they have characteristic green leaves of distinctive arrangement and rough red bark. One is more readily struck with variation in large organisms than in small organisms, but this does not necessarily mean that small organisms are less variable. In all organisms, it seems to be true that critical developmental systems are relatively immune to genetic alteration. It is advantageous for an organism to avoid reproductive waste by producing optimum phenotypes from a number of minor variant genotypes. In many organisms the processes of development of a specific form have become canalized, leading to a uniform phenotypic expression of individuals in a given population in spite of the genetic variability among them. With this mechanism, genetic variability (of long-range importance) can be present with a minimum of reduction of fitness.

How is this buffering accomplished? Using the model of Lerner, let us assume that gene *A* produces substance *a*, which is modified by the action of *b* (a product of gene *B*) into *r*, and that *r* interacts with *c* (produced by gene *C*) to give substance *t*.



(After Lerner, *Genetic Homeostasis*, Wiley, New York, 1954.)

Now if mutation removes *B* or if the environment lacks the substrate from which *b* can be manufactured, then *a* will accumulate. A system in which high levels of *a* interact with *d* (product of gene *D*) to make *s*, which in turn can be transformed by *c* into *t*, is a buffered system.



(After Lerner, *Genetic Homeostasis*, Wiley, New York, 1954.)

This is a true feedback system, since the exact course leading to normal character expression is determined by the “information” that the organism has with respect to the level of *a*. This does not mean that all buffering is genic, however.

It is common practice to draw a sharp line between genotype and phenotype. As a pedagogic device, this is useful for emphasizing the relative permanence and continuity of the genetic information, and, although an oversimplification, it has led to considerable progress in the science of genetics. However, it has also led to the impression that the genotype is somehow the basic entity and that the phenotype is merely a crude reflection of the genotype (the image of which has been distorted by the environment). One might well wonder why selection has not done away with the phenotype altogether, permitting the genotype to evolve unsullied. The answer is, of course, that what can be separated in textbooks or in theory cannot be separated in living organisms. If the genetic material were dissected from a fruit fly, one would obtain a long meaningless string of nucleotides, itself an aspect of the “phenotype.” It is clear that at this level of study the distinction between genotype and phenotype is meaningless. The genetic information becomes mean-

ingful biologically only when it is translated through contact with the environment. Indeed, the value of the information is judged only by the translation, not the original. Natural selection operates on the phenotype, not directly on the genotype, which merely determines the responses of the developing organism to the environment.

Only in recent years have evolutionists given proper attention to the processes of development that result in the production of an adult functioning organism from a fertilized egg or zygote. These processes are interrelated to form a system which Waddington has termed the epigenotype. This may be visualized as a branching system of developmental pathways, each of which leads to one of the components of the adult form. Because the biochemical reactions determining each path are so interlocked with one another (as discussed above, there is a strong tendency for the normal end result to be produced even when there is considerable disturbance at early stages. Thus the paths are canalized or buffered as a result of feedback or cybernetic mechanisms interconnecting the paths.

This epigenetic system must have been the result of natural selection acting upon the genes that affect more or less directly the expression of particular characteristics of organisms. However, selection also must have involved the many genes that have as their only obvious phenotypic effect the modification of the expression of other genes. Waddington has pointed out that, in a population of organisms in a given environment, each individual will have its own genotype, and therefore its own epigenotype, which will eventually result in the adult phenotype. Selection to preserve fitness in this particular environment may act to eliminate genotypes that produce deviant phenotypes. It may also act to eliminate individuals that are imperfectly buffered against environmental effects. There would thus be selection for a well-canalized epigenetic system.

Should the environment change, some well-buffered individuals would be likely to respond by producing fit phenotypes without the necessity for immediate genotypic change. After a period of time in the new environment, however, genotypic change is inevitable, and it is to be expected that selection would lead to the stabilization of the new developmental paths. When the organisms are returned to their original environment, it would be found that, as a result of this change in the genotype, they no longer produce their original phenotype. Thus what was originally a phenotypic (actually epigenetic) response to environmental change becomes incorporated into the genotype, as a result of selection for a well-buffered developmental

system in the new environment. What appeared to be an “acquired characteristic” becomes hereditary through the effects of natural selection. This process, known as *genetic assimilation*, is discussed in Chap. 7.

LIFE CYCLES

Cyclic growth is characteristic of all organisms. Yeast cells go through sequences of fusion and fission, including both a haplophase and a diplophase (Chap. 3). In most higher plants, development occurs both in the haplophase and in the diplophase, although the haplophase (male and female gametophytes) is usually much less conspicuous and of shorter duration than the diplophase (the sporophyte). In most animals there is virtually no development in the haplophase, which usually is restricted to the gametes. (Male hymenopterans, which are haploid, constitute a conspicuous exception; see Chap. 9.)

The simple growth-fragmentation-growth cycle hypothesized as the most primitive form of development has been altered by selection in diverse ways. As an example of a complex developmental system, consider the protozoans that cause malaria. The sporozoites of *Plasmodium*, which in a mosquito environment migrate to the salivary glands, will, when injected into the blood stream of *Homo sapiens*, invade specific cell types. Here they may reproduce asexually producing merozoites which infect other cells or invade the erythrocytes. Those in the erythrocytes may reproduce asexually, producing merozoites which will infect other erythrocytes, or they may develop into gametocytes and eventually produce gametes which will fuse in the gut of another mosquito. The motile zygote thus formed migrates to the gut wall, and develops into a sporocyst. Sporozoites are formed in the sporocyst by cell division.

The same genotype responsible for the efficient feeding machine that we call a caterpillar also contains the information needed for the manufacture of the highly dissimilar reproducing-dispersing machine called a butterfly. The zygote that develops into a giant sequoia also contains the information necessary for the manufacture of its tiny pollen grain (few-celled male gametophyte). The single cell of the human zygote, through division, gives rise eventually to such diverse descendants as erythrocytes, muscle cells, and nerve cells. These deviations from the simplest cycle of development have been in response to selection operating on the entire life cycle of the organism from zygote formation till death.

The details of how selection operates and has operated to produce these systems will become clear only when the mechanics of the systems themselves are elucidated. Therefore it will be necessary to consider briefly developmental systems.

DIFFERENTIATION AND MORPHOGENESIS

Mitosis has been described as a means of ensuring the equal allocation of genetic information to the daughter cells in the course of cell division. That mitosis can accomplish this is easily demonstrated in a number of ways, as previously discussed. For example, if the zygotic nucleus of the dragonfly *Platycnemis* is permitted to divide seven times (to the 128-cell stage) and then all but one daughter cell are killed with a narrow beam of ultraviolet light, a complete embryo still will develop. Obviously all the necessary genetic information has been passed on from the original nucleus to its descendants. In view of the complex mechanism that seems to exist for the purpose of ensuring this successful transfer of necessary genetic information (and considering the demonstrable success of this system), it is pertinent to ask how cells and tissues become differentiated and arranged into a functional organism. Why is a nerve cell so different from an erythrocyte when both are descended from the same zygote?

One answer might be that the two cells were exposed to different environments during development. Even in very early cleavage stages, when few cells are present, the differences in cellular environment may be striking. Differentiation of animal cells may be influenced by such things as their positions relative to the animal and vegetal poles, the outside or inside of the blastula, and proximity to the blastopore in the gastrula. Position may affect the amounts of vital nutrients reaching the cell, the amount of oxygen available, the rate of accumulation of excess metabolites, etc. Once differentiation has begun, the effects multiply exponentially. Various combinations of differentiated elements add to the heterogeneity of the cellular environment, and complex interactions could provide the basis for the development of the entire organism. (The complexity of the developmental system, of course, varies greatly from organism to organism.) It can thus be said that development of the organism is controlled entirely by interactions within the cluster of dividing and growing cells. Each cell possesses the same information but uses it differently because it is operating in a different physiological environment.

This picture of development is supported by a vast array of data from experimental embryology. Interactions of cells may be seen in cultures of microorganisms in which density of the culture may affect rate of growth (or determine whether growth is possible at all). The literature on induction (by contact or at a distance) and organizers testifies to the potency of effects of cellular environment and to the complexity of the systems that have evolved. None of these data, however, demonstrates that the genetic information takes merely a passive role in development. That mitosis does not parcel out portions of genetic information to the proper parts of the developing organism seems certain. Experiments such as those mentioned above on *Platynemis* have demonstrated that in most organisms, at least, the earliest cleavage cells are totipotent, retaining the information necessary for the development of the entire organism. In addition, cells taken from various parts of the body and examined microscopically do not seem to be deficient in their chromosome content, as would be expected if gross partitioning took place. In those insects that have polytene chromosomes with distinct banding in more than one body tissue, it has been reported that the banding does not change from tissue to tissue.

The study of these giant chromosomes has provided other critical data for the interpretation of development. During the course of ontogeny certain bands become enlarged tremendously and are known as *puffs*. This puffing process is reversible. At the same stage in other tissues, different bands are in the puff condition. Clearly there is differential behavior of the chromosomal material, but the mechanisms controlling this behavior are unknown. It is assumed that the presence of puffs is an expression of gene action. The number of puffs that may develop on a chromosome is much lower than the number of bands; therefore the activity of other parts of the genetic code must be "invisible."

If the genetic material participates more actively in differentiation than outlined above, it must do so in a very subtle manner. Interesting recent experiments of Briggs and King have shown that the nuclei in the cells of some embryonic tadpoles are in some way altered in the course of development. When the nucleus of a frog egg was removed and replaced with one from a frog blastula, normal development ensued. When it was replaced with a nucleus removed from a gastrula or neurula, deformed embryos resulted in which the only normal tissues were those derived from the germ layer from which the donated nucleus was taken. While this does not necessarily indicate that the genetic information has been altered in the course of development, it certainly does not militate against that hypothesis.

Of course, other nuclear constituents may have changed, altering the translation of the code rather than the original information.

Perhaps the greatest challenge facing embryologists today is the exact elucidation of the mechanisms controlling differentiation. The question is of more than casual interest to the evolutionist. If portions of the genotype can somehow be turned on and off (as is suggested by the "puffing" process), the operation of selection might be quite different from that in a situation in which the entire genotype always is operant. If a portion of the information that controls, say, the color pattern of a caterpillar is somehow inactivated when the adult tissues are differentiating, it might be possible for selection to alter the larval color but not affect the adult in any way. Equally, if genes affecting hair were inactivated in endoderm tissue, the form and color of the hair could be changed without any effect on the gut. If, on the contrary, such differential activity does not exist, then all changes in genetic information would, to one degree or another, be reflected throughout the life of the organism and at all stages in the life history. In many cases the effect might be so small as to be lost in the normal developmental "noise." In view of the known physical dispersion in the genome of the genes affecting the same character (e.g., the genes controlling wing characters in *Drosophila melanogaster* are not concentrated on any one chromosome), the high frequency of pleiotropy, and the lack of a known mechanism to act as an off-on switch for major portions of the genotype, it seems most reasonable to assume that the genetic material available in most cells of an organism is essentially identical (except in quantity in endopolyploid tissues).

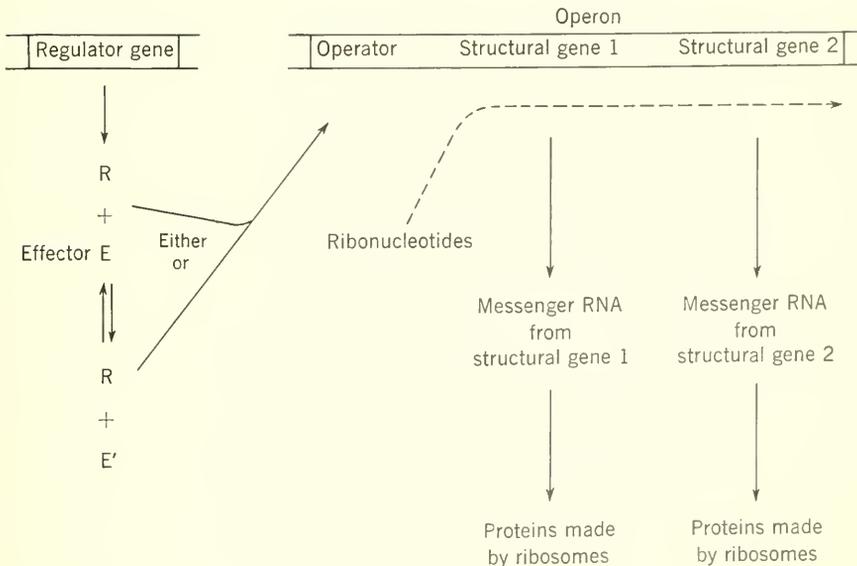
It is known that the cells in different tissues of the same organism (each cell presumably containing identical genetic information) do not have the same complexes of proteins. For protein synthesis, then, there must be specific control mechanisms that regulate the quantities of various gene products.

An interesting model describing such a mechanism has been proposed by Jacob and Monod. This model concerns the transcription of the DNA code as discussed in Chap. 1. It is suggested that genes may be classed as either structural genes or regulator genes. The primary product of structural genes is messenger RNA, the synthesis of which is a sequentially oriented process initiated at certain regions of the DNA strands. These regions of initiation are called operators. An operator may control the transcription of more than one structural gene. The adjacent genes controlled by one operator form a unit of transcription, the operon.

The product of regulator genes is a cytoplasmic repressor substance, perhaps the RNA transcription of the gene. It is postulated that the repressor substance tends to associate reversibly with a particular operator, and the combination of operator and repressor prevents the transcription of an entire operon. Protein synthesis is thus blocked. The repressor is also viewed as reacting reversibly with small molecules, called effectors, in the cytoplasm as well as with the operator. In certain systems, only the unaltered repressor can associate with the operator and block the operon. Presence of the effector will then eliminate the effect of the repressor and *release* the operon from repression. In other systems, only the reactant of the repressor and the effector can combine with the operator. Transcription of the structural gene is thus *prevented* by the presence of the effector. A simplified diagram of this model is given in Fig. 4.1, which should be compared with Fig. 1.5.

The details of the Jacob-Monod model are beyond the scope of this book. It is necessary only to add that microbial genetics pro-

Fig. 4.1 | A model of gene function. *R*, cytoplasmic repressor substance; *E*, effector substance; *R'*, repressor modified by association with effector; *E'*, effector modified by association with repressor. (Adapted from Jacob and Monod, 1961, *Cold Spring Harbor Symp. Quant. Biol.* 26.)



vides considerable evidence for the various postulated processes and systems. It seems clear that some feedback mechanism of this sort must operate at the level of transcription of the DNA code and protein synthesis, just as such mechanisms are believed to be responsible for developmental homeostasis at later stages.

MODIFICATION OF THE DEVELOPMENTAL SYSTEM

Of all the phenomena of morphogenesis, none has received more attention from evolutionists than so-called recapitulation. It was soon observed by embryologists that early developmental stages of vertebrates resembled one another (at least superficially) to a much greater degree than did the adults. This has been interpreted by some workers to mean that, in the course of development, each organism goes through a condensed version of its phylogenetic history—that man, for instance, goes through a one-celled stage (zygote), fish stage (when gill pouches appear), a mammal stage, etc. This generalization was originally called the biogenetic law by Haeckel and is often stated as “ontogeny recapitulates phylogeny.” This crude interpretation of embryological sequences will not stand close examination, however. Its shortcomings have been almost universally pointed out by modern authors, but the idea still has a prominent place in biological mythology.

The resemblance of early vertebrate embryos is readily explained without resort to mysterious forces compelling each individual to reclimb its phylogenetic tree. It first should be emphasized that an early mammalian embryo resembles a fish embryo, not an adult fish. Virtually all organisms begin development as a single cell. The great diversity of life forms is the result of different courses of development determined in large part by the sets of genetic information that cause alterations of the course of development. However, each change does not mean transformation of the developmental system. These tremendously complex integrated systems may be successfully modified only through accumulation of minor changes, with concomitant readjustments of balanced interactions of the various factors. By careful examinations of living and fossil organisms, we can infer these gradual changes of developmental pattern. A good example is the slow change in the vertebrate jaw structure, with the articular and quadrate, which were parts of the jaw in mammal-like reptiles, having been utilized as the ossicles of the hearing apparatus in mammals. All such changes have involved the modification of a preexisting developmental sequence and were possible only when

this sequence could be modified without throwing it lethally out of balance. For example, gill pouches (embryonic precursors of gill slits in fishes) became altered into other structures, such as eustachian tubes and thymus glands, in higher vertebrates. This course of evolution avoided the possible complications which might have resulted from altering the entire set of processes producing the pouches themselves. Such alteration might well have caused great disturbance in the inductive systems responsible for, say, the development of the aortic arches.

The idea of recapitulation involves resemblance of developmental stages to ancestral forms. However, there are some cases in which adult forms appear to be similar to embryonic stages of their putative ancestors. For example, the females of some moths and beetles are larviform; certain salamanders do not metamorphose into adults but reproduce as larvae. Many characteristics of adult human beings (relative hairlessness, large head, etc.) are reminiscent of those of young anthropoid apes. The milk teeth of *Australopithecus*, the earliest known fossil man, resemble the adult teeth of *Homo sapiens*, while the permanent teeth of *Australopithecus* are like those of apes. In these and in a great many other similar cases, evolution seems to have altered the developmental system so that an intermediate ancestral growth stage becomes the terminal form in the descendant. This phenomenon is known as neoteny.

The sequence of stages in the development of an individual organism often is thought of as merely steps toward a final goal: the adult. It is surely more realistic biologically to think of ontogeny as the continually changing response of a given body of genetic material to a given environment. The various processes of the epigenotype regulate in varying degree the expression of the initiating genotype. Evolutionary change may involve any of the arbitrarily delimited stages of development.

SUMMARY

A line of descent does not consist of a straight-line sequence of individuals but of a series of cyclic phases. Each complete cycle is a developmental sequence, traditionally thought of as extending from the beginning of one diplophase (zygote) to the beginning of the next. Changes in the genetic information cause a variation in developmental sequence, and the accumulation of these genetically initiated changes constitutes evolution. It is important to remember that the entire life cycle evolves and that all stages of any given cycle are essential to survival and thus equally important from the

standpoint of evolution. Many students of evolution, viewing the process from the end of a diplophase, have tended to ignore this fact of life.

REFERENCES

- Cellular Regulatory Mechanisms*. 1961. Cold Spring Harbor Symposia on Quantitative Biology, vol. 26. See especially the articles by Jacob and Monod.
- Darlington, C. D. 1958. *The Evolution of Genetic Systems*. 2d ed. Basic Books, Inc., New York. The relationships between heredity and development are boldly explored in this stimulating book.
- Waddington, C. H. 1957. *The Strategy of the Genes*. G. Allen, London. The steps (epigenotype) between genotype and phenotype are discussed in one of the few synthetic works in the field.

2

populations: properties

*Biologists working at the population level of organization have been oriented in large degree by the characteristics of the organisms studied. For instance, cytological features of genetic systems are more readily studied in *Drosophila* and *Oenothera* than in *Papilio* or *Sequoia*. Unusual combinations of circumstances have presented opportunities for studying the operation of natural selection in certain organisms, organisms about which there may be little or no cytogenetic information. Much of our knowledge is gleaned from work on organisms of economic importance, such as crops, domestic animals, and pests. Thus circumstances have made it impractical to produce a unified description of all aspects of evolution within populations.*

The theory of population genetics has been created largely to treat diploid, outcrossing organisms. It is therefore convenient to present this body of theory and related examples from nature before discussing the complexities of systems controlling recombination in various kinds of organisms. It is hoped that eventually a theory may be constructed which will consider the interactions of the genetic system of an organism and the evolutionary forces acting upon the organism. In the meantime, the warning of Norbert Wiener must be kept in mind: It is very difficult to study the interactions of two systems with very different rates of time course. This is true when we attempt to understand history on the basis of day-to-day human behavior or when we try to understand phylogenetic history on the basis of individual gene changes in contemporary organisms.

5

populations

In a sense, every phenomenon is unique. No two objects can occupy the same space and time. Sets of energy relations, if recurring with exact precision, at least differ in time. However, the perceptual universe is one of ordered uniqueness. The human mind is an apparatus that functions by imposing relationships upon unique events. A collection of objects having characteristics in common are grouped into a class (e.g., table, race, butterfly), and this group concept is useful for communication. Indeed, the existence of virtually all organisms depends upon their ability to generalize in some sense from collections of unique events. A completely unique event, one for which there could be perceived no relationship with any other event, would be totally without *meaning*.

All human understanding is based upon populations of things and events and the patterns of interrelationship thought to exist among them. In order to understand the workings of cells, a biochemist studies the populations of chemical constituents and processes within the cell. For insight into the organization of organisms, physiologists and embryologists study populations of cells and tissues and the interactions among them. At the highest level of biological organization, the population biologist investigates populations of organisms and the relationships within and among them. In this book the term population will be restricted to aggregations of individual organisms, the sense in which it customarily is used by evolutionary biologists. Population biology deals, then, with the properties of aggregations of organisms, particularly those emergent properties not possessed by the individual constituents of the populations. Populations rarely can be studied in their entirety but must be sampled at one or more points in time. Unfortunately, it is not possible to sample the same population twice.

INDIVIDUALS AND COLONIES

The first problem arises with the definition of an individual organism. At first sight this appears to be easy, since familiar plants and animals exist as discrete units. However, the situation is complicated by the existence of forms such as lichens. These plants consist of a fungus now known to be parasitic upon algal cells included in its thallus. Different lichens have different morphological and biochemical characteristics, but these fail to appear unless the correct combination of alga and fungus occurs. The alga and fungus reproduce separately, but the lichen reproduces as well, with propagules

consisting of both alga and fungus. Often the alga can be grown without the fungus, but the latter does not survive without its algal host.

Complex colonial organisms also present difficulties. The colonies of social insects present analogies with organisms, but usually such colonies are referred to as *quasi* organisms. The Portuguese man-of-war, a colonial hydrozoon, can be analyzed into its constituent polyps, which exhibit a striking division of labor. Among the algae and protozoa there are less specialized aggregations of individuals, in which what appear to be units may exist separately or as part of the colony. Even such forms as yeast (*Saccharomyces*) may show different behavior, depending upon environmental conditions. In liquid culture, yeast cells (plants?) are small ovoid cells that reproduce most frequently by budding. Short chains of cells may occur. When grown on a solid medium, however, yeast forms a giant "colony." This structure is a flattened object, several centimeters in diameter, with characteristic color and surface texture as well as biochemistry. Cells from the outermost layer, from the center, and from the portion adjacent to the medium are very different in form and presumably in function. Nevertheless, cells from any region may be used to start a new colony or liquid culture.

In the higher organisms there also may be difficulties in defining individuals. Many plants reproduce vegetatively (see Chap. 9), and if the "offspring" remain attached to the parent, the whole is considered an individual. Should they become separated, each plant usually is thought of as an individual even though it is genetically identical with its "parent." The self-sterile triploid day lily *Hemerocallis fulva* is one *genetic* individual throughout its range in much of the eastern half of the United States. Populations of hydra derived from a single budding individual likewise genetically constitute an individual, but ecologically and functionally they consist of many individuals.

Complexes of individuals belonging to what are called different species may also occur. Many scale insects form amazing compound colonies in symbiotic association with a fungus (*Septobasidium*). Forest trees commonly become grafted when their roots touch in the course of growth. It has been found that, if a root-grafted tree is cut down, the stump may survive for many years. Although without photosynthetic tissue of its own, it may produce new bark from the cambium so that the stump is completely covered. Individual organisms are genetically different in these situations, but they are united closely into an ecologically meaningful unit. In the same way, a clone of viviparous onions (see Chap. 9) that are genetically iden-

tical constitutes an ecologically meaningful assemblage as it forms part of the environment of other organisms.

An individual is a set of operations (or machine) programmed in advance to do particular things. In organisms, of course, the program is established by the coded genetic information. A group of genetically identical individuals is one individual reproductively. Ecologically they represent a population of individuals with different epigenotypes. If we had, historically, begun to think about biology in ecological terms rather than taxonomic terms, we would probably now deal with biological “facts” very differently.

It is obvious that the concept of “individual,” like other concepts in biology, can be given only operational meaning. To make the definition clear, one must specify whether he is concerned with taxonomy, genetics, or ecology. In what follows, a genetic definition of individual will be employed. Most of the evolutionary work on populations has been done with organisms among which the discrete individuals are the result of sexual reproduction and thus are, usually, genetically diverse. In sexually reproducing organisms the most inclusive populations are generally considered to consist of those individuals sufficiently alike that, given the opportunity, successful reproduction will occur. The criteria for just what sort of assemblage may be labeled a population are hard to establish, and the degree of conformity with these criteria in natural aggregations is usually only guessed.

In this chapter, examples will, in general, replace definitions. A butterfly and a bison obviously do not belong to the same population; a pair of robins raising a brood in the garden obviously do. Near the center of the continuum, problems arise: Could the European brown bear and the American grizzly be part of the same population? Are the eastern and western sycamores part of the same population? They have been geographically separated since the Miocene, but their hybrid is a vigorous and much-used street tree. Since our interest is primarily in the process of evolution, rather than in making arbitrary decisions, no answers will be sought to these questions.

SPATIAL DISTRIBUTION

One property possessed by populations, but not (in the same sense) by their constituent organisms, is distribution. At any instant in time, checkerspot butterflies (*Euphydryas editha*) are distributed along an outcrop of serpentine rock on Stanford University’s Jasper Ridge Biological Experimental Area. The distribution of adults in

two successive years is shown in Fig. 5.1. The distribution in the second year is somewhat different from that in the first. Such colonies of *Euphydryas editha* occur throughout the San Francisco Bay area; indeed, they are found along the West Coast from Baja California to British Columbia. It is difficult to specify the limits of the most inclusive population in which the Jasper Ridge individuals could be placed. Most biologists would place in this most inclusive grouping individuals from colonies as far away as Montana.

Similarly, clusters of individuals in various-sized aggregates are found in plants. *Clematis fremontii* var. *riehlii*, which occurs on limestone glades in the midwestern United States, is a perennial plant that has been studied in some detail by Erickson. Individuals are grouped into aggregates of several hundred plants, many such aggregates occupying a single glade. The outcroppings of limestone are clustered and aggregated geographically with respect to the mountain systems and rivers. In the Midwest, the plant has a much wider distribution that represents the most inclusive population (Fig. 5.2).

In its loosest usage, distribution generally means the smallest geographic area that will enclose all the area normally occupied by the organisms under discussion. On a small world map of the distribution of *Homo sapiens*, the entire United States would be shaded to indicate its occupation by man. (Oceanic areas and most of the Greenland ice cap would be left blank.) In contrast, if we were mapping the occurrence of man on a large-scale map of Colorado, many high mountain peaks and some other areas would be left blank. The problems of such a mapping are obvious. Organisms are mobile at some stage of their life history, and their distributions are constantly changing. Furthermore, no known organisms are uniformly distributed over large areas. Thus the more resolution one strives for in describing a distribution, the more difficult the task becomes.

ECOLOGICAL DISTRIBUTION

The nonuniformity of geographic distributions can usually be explained by the relationships of the organisms with their living and nonliving environments. Gross examples of ecological factors controlling distribution are easily understood; the factors controlling the fine points of the distribution of a given organism virtually are never fully understood. In the San Francisco Bay region *Euphydryas editha* larvae feed on *Plantago erecta*, a small native plantain especially abundant on serpentine outcrops. In this area the butterfly occurs only where both *P. erecta* and serpentine are found, but the

Fig. 5.1 | Distribution of individuals of the butterfly *Euphydryas editha* on Jasper Ridge in two successive years. The colony occurs in an island of grassland surrounded by chaparral. Each dot indicates the place of first capture of an individual. Letters refer to areas into which the colony has been arbitrarily divided for study. (From Ehrlich, 1961, *Science* 134 and unpublished.)

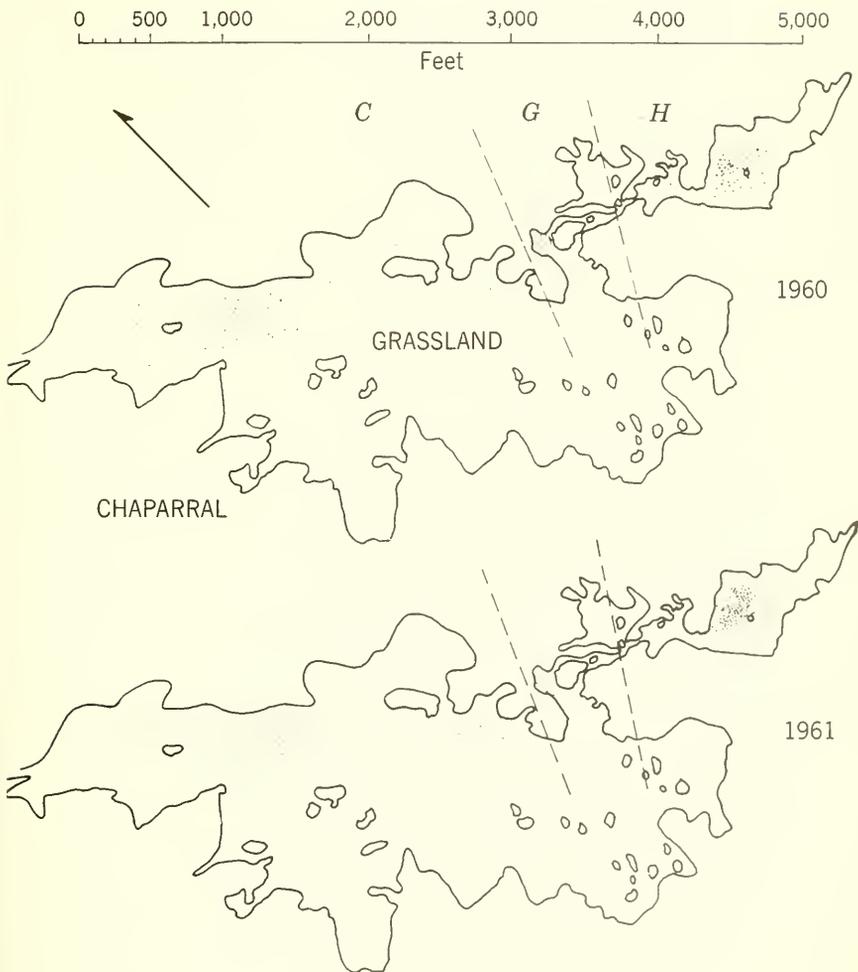
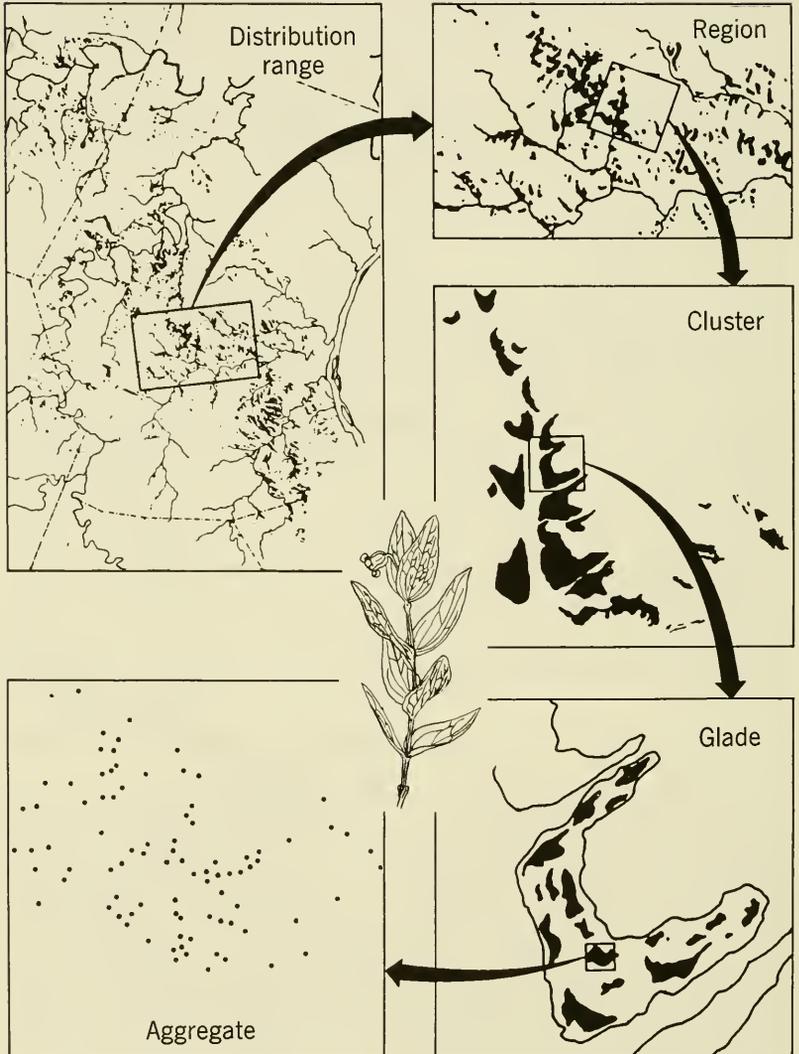


Fig. 5.2 | Hierarchy of aggregates of *Clematis fremontii* var. *riehlii*.
(After Erickson, 1945, *Ann. Missouri Bot. Gard.* 32.)



presence of both plant and rock does not guarantee that the butterfly also will be there. On Jasper Ridge, areas of serpentine with abundant *Plantago* remain unoccupied although they are immediately adjacent to the colony. Not only must *all* environmental conditions be suitable for a habitat to be occupied, but chance must supply access to the suitable area. Thus some suitable areas for *E. editha* may not support colonies simply because no fertilized females have ever reached them. Man has provided many organisms with access to previously uninhabited but suitable regions, as starlings, English sparrows, cabbage butterflies, honeybees, dandelions, and mustard constantly remind us.

STRUCTURE

The *structure* of a population is considered here to be the totality of all the factors that govern the pattern in which gametes from various individuals unite with each other. The structure can vary from situations in which combinations might seem to be essentially random (e.g., certain marine animals that release gametes into the sea, some wind-pollinated plants) to those in which the probability of certain combinations is much higher than others. The latter case is certainly the rule, if for no other reason than that close neighbors usually have higher probabilities of mating than more distant ones.

Such factors as length of generation and size of individuals also are important. If the variable to be measured is the number of new gene combinations produced in a given area per unit of time, then small organisms will differ from large ones. In any place there are fewer large organisms than small ones and thus less recombination. Organisms with a short life cycle produce more gene combinations than those with long generation time, and their mutation rates also differ.

Especially in higher animals, there have evolved many behavioral systems that profoundly affect the structure of a population. Many animals are effectively sedentary in spite of great dispersal potential. Birds often return from long migrations to exactly the same breeding location as was occupied in previous years. Twitty has shown that California newts have incredible perseverance and navigating ability, returning precisely to a particular segment of a stream to breed. Indeed, displaced individuals have returned to their home pool over several miles of mountainous country. Specificity within a stream is clearly shown in Fig. 5.3. Butterflies often use their powers of flight merely to patrol a restricted area. In the Jasper Ridge colony of *Euphydryas editha*, 625 out of 647 recaptures of marked adults

(98.6 percent) were made in the area of previous capture. Similar behavioral restriction of physical-dispersal ability seems to be the rule rather than the exception in nonmigratory butterflies.

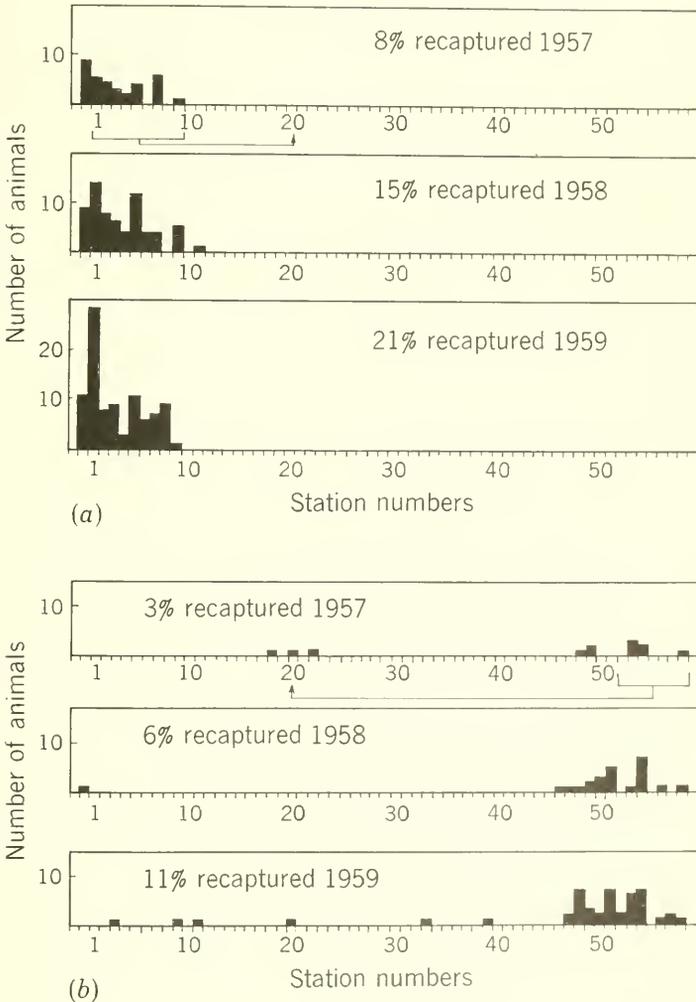
Few animals seem to be truly nomadic. Most (including most human beings) stay close to their birthplaces, occupying a *home range* which was "good enough for their parents." Many animals defend all or part of their home ranges from intruders of their kind—the well-known phenomenon of *territoriality*. This behavior, common in birds, mammals, reptiles, fishes, and some invertebrates, results in a nonrandom distribution of individuals in the population; they are dispersed more evenly than one would expect in a distribution governed solely by chance. Among other things, this often keeps the population size at a level where the supporting resources of the environment (food, nesting space, etc.) are not strained or entirely consumed. Individuals, often young adults, that do not successfully occupy and defend a territory must find greener pastures or starve; thus a dispersing component is added to the population.

Statistically, the opposite of territoriality is aggregating behavior which results in more "clumping" than if individuals were randomly distributed. Animals showing this behavior may have little or no known social organization, as in the case of prehibernation aggregations of ladybird beetles or snakes. At the opposite extreme we have the highly social insects, among which there are morphologically differentiated castes and the reproductives in a colony may consist of a single pair of individuals. At this extreme, selection operates largely through differential reproduction of colonies, not individuals. In many vertebrates a social hierarchy (peck-order) is established in which some individuals dominate others, obtaining perquisites ranging from first choice in mate to first place in line going through the barnyard gate. Dominant males may control large harems and, in contrast with their less aggressive brethren, make a large contribution to the pool of genetic information of succeeding generations. Often, social groups (colonies of social insects and bands of howler monkeys, for example) exhibit territoriality.

NUMBERS OF INDIVIDUALS

One of the most obvious attributes of any population is the number of items, events, or individuals that it contains at a given time. The number of individuals in biological populations is of great interest, but unhappily it usually is difficult or impossible to ascertain with accuracy the size of any natural population. The most inclusive populations may include billions of individuals (e.g., man, house

Fig. 5.3 | Homing behavior of newts. (a) Recaptures of individuals displaced in 1956 to a point about one-half mile downstream from place of original capture. (b) Recaptures of individuals displaced in 1956 to a point about one mile upstream from place of original capture. Area of original capture and point of release shown by arrows. Station numbers refer to arbitrary subdivisions of stream course. All individuals leave the stream after each breeding season. (From Twitty, 1959, *Science* 130.)



flies, some microorganisms, various algae) or less than 100 individuals (whooping cranes or certain rare endemic plants such as *Pedicularis dudleyi* and *Tetracoccus ilicifolius*). In the strictest sense, whenever the number of individuals in a population changes, the distribution of the population changes; often a change in distribution also means a change in numbers. Study of Fig. 5.1, on which the position of first capture of *E. editha* adults for two consecutive years is plotted, will give some idea of the problems of dealing separately with distribution and abundance. In area *C* there was little increase in numbers between 1960 and 1961 but some change in the distribution pattern. In area *G* the numbers decreased, and there was a concomitant shrinkage in the area occupied. In area *H* the numbers increased greatly, and the population occupied an area that was virtually devoid of individuals in the previous year. It is important to note that the figures, like virtually all representations of distribution, are a stylized, static representation of a dynamic situation. The numbers and distribution of individuals in biological populations are constantly changing, the speed of the changes varying greatly from organism to organism.

Population dynamics, the study of changes in population size, is a very complex subject which cannot be pursued here. It is of considerable interest to the evolutionist, for, as will be seen, changes in population size affect the evolution of a population in diverse ways. This can be understood intuitively, since each individual in a population is part of the environment of every other individual. Therefore any change in population size is automatically a change in the environment of the population, and populations evolve in response to environmental changes.

The factors that control population sizes are diverse and in many cases poorly understood. There is little doubt, however, that usually feedback mechanisms operate to regulate the size of populations; that is, the size of the population influences its growth rate. Basic references from the abundant literature on this subject are cited at the end of this chapter.

ENVIRONMENT

An individual organism, when such can be recognized, is in a sense the morphological resultant of the physiological processes of which it is composed. Each of these processes is interrelated with the other functions of the organism, and the complex of processes cannot be separated from the environment, except artificially. The functioning of an individual is determined by the relationship of its constitu-

ent processes to factors of the environment. Each process has a range of tolerance for the environmental factors that must fall within the intensity span of the factors. Organisms do not function unless the ranges of tolerance of all these processes fall within the intensity spans of all the environmental factors. These ranges of tolerance of any organism are, of course, determined by the genotype assembled in the zygote and by the developing epigenotype (see Chap. 4). It is important to note that, until reproduction occurs, there are at most physicochemical, not biological, functions among individuals. Organisms may be considered part of the physical environment of other organisms until they cooperate to reproduce.

There is no satisfactory way, at present, of dealing with the complex interactions of organism and environment. Usually some very rough classification of environmental factors is employed. For example, Andrewartha and Birch have divided the environment of a given organism into four components: weather, available nutrition, other organisms, and a place to live. These components may be further subdivided as required. All are continually changing in some degree. Just as the range of tolerance of a particular process changes during the course of development (resistance to desiccation, heat or cold sensitivity), so the intensities of environmental factors change cyclically, as well as in complex and little-understood patterns. The soil around an oak tree's roots may become leached of mineral elements, which are restored by leaf fall and disintegration. The food plant of a butterfly dies out in a drought year. The required environmental factors for the establishment of seedlings or for the pollination of flowers may be present for a brief period at only one time of the year, and the behavior of the plant must be closely correlated with the occurrence of these factors.

Interactions of amazing intricacy may be seen in natural populations. For example, "other organisms" in the environment may be classified also as nutrition (host, prey, food plants of herbivores) or as a place to live (host, trees, etc.). A young muskrat may find all suitable burrow sites (a place to live) occupied by older stronger individuals (other organisms) and be forced to migrate. During its migration it may freeze (weather), starve before it finds suitable forage (nutrition), or be killed by a coyote (other organism).

As part of the environment of an organism, other organisms may change the microclimate (as in the shade, leaf-fall zone, and root range of a tree). They may serve as vectors of genetic material in infection or reproduction, as well as of propagules. The flowers, fruits, and seeds of the angiosperms show a great diversity of devices effecting successful pollination and dissemination by specific animal

vectors. Everyone knows of the instances of pollinating insects carrying the pollen grains (male gamete-producing plants) from flower to flower on their legs or bodies. Less familiar are those orchids in which the flower resembles the abdomen of a female fly or wasp so closely that males of the mimicked species attempt to copulate with the flower. The pollen is carried, in tiny bags or pollinia, from one flower to another on the end of the abdomen of the male insects.

Similar situations are not unknown among animals. An interesting instance is that of the adult human botfly (*Dermatobia hominis*), which catches mosquitoes and attaches eggs to their bodies before releasing them. The eggs hatch when the mosquito lands on the warm skin of a man, and the larvae burrow in and start to develop. This fly parasitizes a number of mammals other than man.

Besides the interactions among plants and animals commonly observed in the temperate zone, there are less well-known examples of extreme intricacy in the tropical rain forest. On the branches of the giant trees, plants of various kinds accumulate water and soil among their leaves. In this specialized niche the larvae of mosquitoes and of frogs hatch, grow, and metamorphose. The mosquito fauna is stratified in part because of the distribution of the epiphytic plants in which they grow. In the same forests lives the three-toed sloth, the hairs of which are colored greenish by symbiotic algae. The sloth moth *Bradypodicola hahneli* spends its entire life on the sloth, its larvae presumably feeding upon the algae. Explaining the evolutionary history of associations such as these, and others perhaps even more bizarre, is a challenge to the evolutionist interested in the structure of the ecosystem.

Changes in climatic patterns strongly affect the kinds of organisms that can exist in an area. Arctic fossils of tropical plants and amphibia testify to warmer times in the past, and long-empty desert cities to changes in rainfall pattern or soil fertility. Years of commercial grazing, with no return of essential elements to the soil from decaying plants and animals, have changed the nutritional characteristics of many areas of the Great Plains of the United States, with a resultant change in the flora and fauna. English-sparrow populations in our cities have become much smaller since the disappearance of the horse and its seed-laden droppings. Grasslands have diminished in some areas as roads and other sorts of fire control increase.

Man's activities in transplanting organisms have provided many striking instances of change in the influence of "other organisms." The imported cabbage butterfly, *Pieris rapae*, has increased in North America at the expense of our native cabbage butterfly, *P. protodice*, presumably by out-eating it. Storks-bill, mustard, and wild oats

(*Erodium*, *Brassica*, and *Avena*) have extirpated native plants in some areas of California. Shipborne rats have virtually destroyed the fauna of small vertebrates on numerous islands.

Changes in the availability of places to live also constantly occur. Silting and slowing down of streams make them untenable for larval and pupal black flies and other organisms depending on swift-running, oxygen-rich water. Planting of trees across the Great Plains has permitted range extensions by tree-nesting woodland birds. The slow accumulation of humus and disintegration of rocks into soil make homes for oribatid mites, centipedes, fungi, and other lovers of dank, dark places. Often the organisms living in areas subject to frequent catastrophic change have specialized genetic systems affecting their genetic behavior (see Chap. 9).

All these examples are of relatively spectacular variation in the environment. Important also are the smaller, more frequent changes: the day-to-day temperature variation that affects the plankton population of a shallow pond or the yearly precipitation changes that determine the condition of a butterfly's food plant. None of these changes can be viewed as an isolated event. Increased moisture may improve the condition of the larval food plant of a butterfly, and a large adult population may result. Among other things, this may mean more food for nestling song birds and, in the long run, more food for hawks. Large numbers of butterflies may mean more caterpillars next year, a year when little moisture means a poor crop of food plant. Thus few adults survive, almost no food plants survive, and topsoil is lost through erosion. Large numbers of song birds from the previous season may find no suitable substitute food, with resultant starvation, emigration, and unsuccessful reproduction. The hawks go hungry.

This somewhat overdrawn example illustrates only a few of the many permutations of effects which might be hypothesized as resulting from a simple change in precipitation. Actually such gross effects are relatively infrequent, for most ecological systems are made up of a great many elements and have a historical dimension. Complexity leads to less one-to-one dependence. Drought which reduces butterfly populations may lead to an increased supply of grasshoppers, and the song birds readily shift their diet. Long-term associations have presumably experienced most of the usual variations in climate, and their members presumably can respond to it. Thus the butterfly food plant will probably survive a drought (perhaps, if it is an annual, as ungerminated seeds) and be ready to return to abundance when moisture reappears. If erosion has not proceeded too far, it may be stopped. Doubtless, however, many organisms would be permanently affected.

COMMUNITIES

Even if a single interbreeding population were found in an environmentally diverse area, it would be expected that, in time, genetic processes would lead to diversification (Chap. 6). The processes involved in the formation of complex communities of organisms are virtually unknown. It is clear that a denuded area will become repopulated. During the early stages of repopulation, the aggregations of plants and animals are short-lived. Several different aggregations can be distinguished over a period of time before a relatively stable community develops. These stages make up what is referred to ecologically as succession, and the terminal stage often is called a climax community.

Ecologists do not agree on the best methods of studying succession or terminal communities. Modern workers feel that communities are part of a continuum and that they can be distinguished as units only artificially. Indeed, since there are no biological functions operating between reproductively isolated populations, one would not expect communities to be discrete units. Each interbreeding population behaves according to its own cytogenetic processes, producing individuals whose genotypes determine ranges of tolerance that enable them to function. Each entity has had an evolutionary history dependent on, among other things, its own genetic processes. Because of these differences one would not expect any two populations to follow the same historical pattern for even a short period of time. The community, however defined, results from the overlapping ranges of tolerance of the individual organisms for the various factors of the environment at a particular place.

If studied for relatively short periods, the terminal communities in a successional series usually appear to be stable or in a steady-state equilibrium. Within such communities, cycling of energy and matter is constant and regulated by feedback mechanisms. Much energy is stored in organic materials (plants, animals, humus, etc.). Such a community is disturbed by outside influences only with difficulty. It is thought that organisms from other environments find it difficult to migrate into the community. Energy relations appear to be clearly established, and primary producers (green plants), primary consumers (herbivores), secondary consumers (carnivores), and decomposers (microorganisms) can be distinguished. Natural selection has resulted in an ecological unit of great complexity. Organisms have evolved with respect to their position in this complex (or in successional stages) as the environment of the earth has changed through time.

It is obvious that the different populations of organisms found in a given place are not a random sample of organic diversity. Caribou are found with *Cladonia* (reindeer moss), and wolves with caribou. If a butterfly collector seeks the larvae of *Battus philenor* in the Arizona desert he must find the decumbent pipe vine, *Aristolochia watsonii*. He soon learns that this often grows in the shade of other desert plants, especially along the edges of depressions. From the searching behavior of adult female butterflies, it seems obvious that they use similar associations in their search for an oviposition site. Oaks and hickories are often found together, and oak-hickory forests are a good place to hunt the Virginia deer. Wheat, dogs, house flies, body lice, and *Treponema pallidum*, as well as many other organisms, are often found in association with man.

Most of the ecological analyses that have been made are descriptive. The results, on the whole, have been disappointing, especially for the evolutionist. A recently developed ecological school is attempting to formulate mathematical descriptions of the structure observed in communities. It is perhaps still too early to decide whether these efforts will be successful, but the results thus far are encouraging. At any rate, it seems certain that no special mechanisms are necessary to account for "community evolution." Extremely complex interactions of those processes described in this book seem to explain all community phenomena that have been observed. Some of the complexities of dealing with aggregates of populations are considered in the final chapter.

SUMMARY

Although for some organisms the concept of individual is difficult to define, in most organisms aggregations of individuals referred to as populations arise. These, or aggregations of these, may form interbreeding populations; the latter are variously combined to form taxonomic groupings. The functioning of individuals is physiological and is determined by the genotype and epigenotype that set the ranges of tolerance of the organism to intensity spans of complexly varying environmental factors. The organic functions of the population are genetic and determine the genetic constitution of the zygotes. Communities are aggregations of diverse populations which form part of each other's environment, and they become structured with respect to energy relations. There are no biological functions between populations in a community. Communities owe their existence only to the mutuality of the tolerance ranges of the constituent organisms at a particular period of time.

REFERENCES

- Andrewartha, H. G., and L. C. Birch. 1954. *The Distribution and Abundance of Animals*. Univ. of Chicago Press, Chicago. A comprehensive modern treatment of certain aspects of animal ecology (mostly "autecology").
- Ehrlich, P. R., and R. W. Holm. 1962. Patterns and populations. *Science* 137: 652-657. Problems of dealing with the properties of populations are discussed and recent literature cited.
- Slobodkin, L. B. 1962. *Growth and Regulation of Animal Populations*. Holt, Rinehart and Winston, New York. An excellent short exposition of the ideas of "the new ecology." Mathematical treatments of population growth, cycles, predator-prey interactions, communities, and the like.
- Stebbins, G. L. 1950. *Variation and Evolution in Plants*. Columbia Univ. Press, New York. See especially the first chapter.
- Wynne-Edwards, V. C. 1962. *Animal Dispersion in Relation to Social Behavior*. Hafner, New York. This book presents a mass of evidence to support the author's contention that the size of animal populations usually is kept far below the starvation level by what is described as "conventional competition" (competition for such things as territories or high places in the peck-order).

6

the theory of population genetics

In the first part of this book, the origin of life, the coding and transfer of genetic information, the development of organisms, and some features of populations have been discussed. We shall now begin to deal with the very core of evolutionary theory—changes not in individuals but of populations. This chapter will be concerned with the theoretical aspects of the genetics of *mendelian populations*. A knowledge of the basic ideas of population genetics is absolutely essential to an understanding of how the mass of inherited information possessed by a population changes from generation to generation. Familiarity with the simple mathematical ideas presented here will permit the reader to comprehend the more complex situations discussed in ensuing chapters. Although nonmathematical descriptions accompany the various algebraic examples, a firm grasp of the material will be facilitated by working through the simple algebra.

The examples in this chapter are gross oversimplifications. The integrative aspects of the genotype, multiple alleles, simultaneous operation of different evolutionary forces, and other complicating phenomena are largely ignored. For the moment, it is assumed that a single locus can be torn from its substrate and subjected to conditions of our choice; complex interactions are left for later consideration.

MENDELIAN POPULATIONS

Only sexual organisms comprise mendelian populations, which can be defined loosely as aggregates of interbreeding individuals. A more precise definition is neither possible nor desirable, for the word “interbreeding” may refer to any situation from panmixis to almost complete isolation. One might consider the potato beetles on a single potato plant as a mendelian population, or the definition might be broadened to include those in a single potato field, those in a group of adjacent potato fields, or indeed those in a county or larger area. It is therefore important to indicate the scope of a population under discussion and to state what is known of its structure.

Panmixis

A population is *panmictic* if the individuals within it mate at random. Each individual is equally likely to mate with every individual of the opposite sex within the population as defined. The expected frequency of any given kind of mating is the product of the frequency

of the type of the male participant and the frequency of the type of his female partner. For example, consider a hypothetical animal which has both black and white forms and exists in a panmictic population consisting of 100 males (90 black, 10 white) and 100 females (70 black, 30 white). The expected frequencies of the various matings are given in Table 6.1.

Statistical study of the frequencies of the various matings might show that observed deviations from these expected frequencies are satisfactorily explained by sampling error (i.e., chance), leading to the conclusion that, *at least with respect to color*, the population was panmictic. To look at panmixis another way, it can be said to occur when the genotypes of the individuals in each mating pair are a random sample of the genotypes present in the population. Complete panmixis seems rare or nonexistent in nature, if for no other reason than that relatives often tend to live close together and thus mate with one another. When this happens, the mating pairs are *not* a random selection from the population, and a component of inbreeding is added to the population-genetic picture.

Gene Pool and Gene Frequency

The total genetic information possessed by a population may be referred to as the *gene pool* of the population. If the gene pool could be described completely, one would know not only what kinds of information were present but also the frequencies of the different kinds. This chapter is concerned mostly with the distribution within the gene pool of the information at a single locus.

One of the basic ideas of population genetics is that of gene frequency. If it is assumed that there are only two alleles at the locus (A, a) under consideration, there are then N diploid individuals of which D are homozygous for one allele (AA) with respect to the

Table 6.1

Mating	Product	Expected Frequency
Male Female		
Black × black	$.90 \times .70$.63
Black × white	$.90 \times .30$.27
White × black	$.10 \times .70$.07
White × white	$.10 \times .30$.03
		<u>1.00</u>

locus studied, H are heterozygous (Aa), and R are homozygous for the other allele (aa). Then $D + H + R = N$, and there are three types of individuals carrying two types of genes. The N individuals have $2N$ genes at this locus. Since each AA individual has two A genes and each Aa individual has one A gene, the total number of A genes in the population is $2D + H$. The proportion p of A genes in the population is

$$p = \frac{2D + H}{2N} = \frac{D + \frac{1}{2}H}{N}$$

The quantity p , the proportion of A genes in the population, is known as the *gene frequency* of A . By convention, the gene frequency of the other allele (a) is q . Since these are the only two alleles at the locus, $p + q = 1$, and $q = 1 - p$.

Hardy-Weinberg Law

If there is random mating in a population and if the gametes produced by the mates combine at random, there is complete random union of all the gametes produced in the population. As each gamete contains only one of the alleles, the frequency of the two different kinds of gametes (A and a) and the gene frequency are the same. Combining the gametes at random to produce zygotes gives us

$$\begin{aligned} & [p (A \text{ sperms}) + q (a \text{ sperms})] \times [p (A \text{ ova}) + q (a \text{ ova})] \\ &= (p + q)^2 = p^2 (AA \text{ individuals}) + 2pq (Aa \text{ individuals}) + q^2 \\ & \quad (aa \text{ individuals}) \end{aligned}$$

Populations with this distribution of *genotype* frequencies are in an equilibrium condition.

This equilibrium is described by the Hardy-Weinberg law, which may be stated briefly as follows:

If alternate forms of an autosomal gene are present in a large panmictic population, then in the absence of mutation, selection, or differential migration the original proportions (gene frequencies) of these alleles ($p_1, p_2, p_3, \dots, p_n$) will be retained from generation to generation, and after one generation the proportion of genotypes will also reach an equilibrium. The genotype equilibrium frequencies are given by the terms of the expansion $(p_1 + p_2 + p_3 + \dots + p_n)^2$.

Further discussion of population genetics will center around this law, which is one of the fundamental concepts of biology. An algebraic demonstration of the maintenance of Hardy-Weinberg equilibrium is given in Table 6.2.

Table 6.2 | Matings and Offspring in a Population in Hardy-Weinberg Equilibrium

Type of Mating °	Frequency of Mating	Proportions of Offspring		
		AA	Aa	aa
AA × AA ($p^2 \times p^2$)	p^4	p^4		
AA × Aa ($p^2 \times 2pq$)	$2p^3q$	p^3q	p^3q	
Aa × AA ($2pq \times p^2$)	$2p^3q$	p^3q	p^3q	
Aa × Aa ($2pq \times 2pq$)	$4p^2q^2$	p^2q^2	$2p^2q^2$	p^2q^2
AA × aa ($p^2 \times q^2$)	p^2q^2		p^2q^2	
aa × AA ($p^2 \times q^2$)	p^2q^2		p^2q^2	
Aa × aa ($2pq \times q^2$)	$2pq^3$		pq^3	pq^3
aa × Aa ($2pq \times q^2$)	$2pq^3$		pq^3	pq^3
aa × aa ($q^2 \times q^2$)	q^4			q^4
Totals	1.00 †	p^2 ‡	$2pq$ §	q^2 ¶

° The frequency of types of both males and females is given by the terms of the expression $p^2 + 2pq + q^2$; therefore, with random mating the frequencies of the different matings are $(p^2 + 2pq + q^2)(p^2 + 2pq + q^2) = p^4 + 4p^3q + 6p^2q^2 + 4pq^3 + q^4$.

† The sum of this column is $p^4 + 4p^3q + 6p^2q^2 + 4pq^3 + q^4 = (p^2 + 2pq + q^2)^2 = [(p + a)^2]^2 = [(1)^2]^2 = 1.00$.

‡ The sum of this column is $p^4 + 2p^3q + p^2q^2 = p^2(p^2 + 2pq + q^2) = p^2(\bar{1}) = p^2$.

§ The sum of this column is $2p^3q + 4p^2q^2 + 2pq^3 = 2pq(p^2 + 2pq + q^2) = 2pq(1) = 2pq$.

¶ The sum of this column is $p^2q^2 + 2pq^3 + q^4 = q^2(p^2 + 2pq + q^2) = q^2(1) = q^2$.

If an arbitrary initial population has a gene frequency $p = 0.2$ ($q = 0.8$) and genotype frequencies $AA = .10$, $Aa = .20$, and $aa = .70$, the population reaches equilibrium in one generation and then remains there (Table 6.3).

Table 6.3

Generation	Genotype Frequency			Gene Frequency	
	AA	Aa	aa		
1	.10	.20	.70	$p = 0.2$	$q = 0.8$
2	.04	.32	.64	$p = 0.2$	$q = 0.8$
3	.04	.32	.64	$p = 0.2$	$q = 0.8$
4	.04	.32	.64	$p = 0.2$	$q = 0.8$
...
N	p^2	$2pq$	q^2	p	q

Note that there is no change whatsoever in the *gene frequency*, which can be determined after the first generation by taking the square root of the frequency of the proper homozygote. Under the conditions described, there is a genetic inertia in mendelian populations. Unless mutation, selection, differential migration, certain changes in the mating pattern, or a drop in population size disturbs the equilibrium, there is no change in the genetic structure of the population. To a very large degree, overcoming this inertia (especially changing of the *gene frequency*) is what is described as "evolution."

The ideas associated with the Hardy-Weinberg law are basic to any consideration of evolutionary processes, and it is essential that the reader become thoroughly familiar with them. For a discussion of extensions of the Hardy-Weinberg law and properties of equilibrium populations, the reader is referred to the excellent book on population genetics by Li (1955).

Although populations in equilibrium are rare (or nonexistent) in nature, the law is of great value in describing a situation in which there is *no* evolution, as it provides a base line for measuring evolutionary change. Now some ways in which populations deviate from Hardy-Weinberg equilibrium are considered.

POPULATION SIZE

In all populations there are some random fluctuations in gene frequency. Because of sampling error, no set of gametes drawn from a parental population will have exactly the same gene frequency as the parental population. In addition, because of chance occurrences in the union of gametes, the population of zygotes formed will not have precisely the same gene frequency as the population of gametes. Finally, even if the deaths among maturing individuals are completely random, sampling error will intervene to produce a filial breeding population in which the gene and genotype frequencies once again deviate from the gene and genotype frequencies of the original population of zygotes. In large populations these sampling errors tend to balance each other, since they are different in different areas and at different stages in the reproductive process. Changes in gene frequency because of sampling error are therefore usually negligible. However, in small populations these random fluctuations take on considerable importance.

Thus the size of a population may have a considerable effect on its genetic structure. Biological populations are always finite in size. The gross population size is simply the number of individuals in a population at a given time. Of greater significance is the breeding

size N , defined as the number of parents responsible for the genetic composition of the next generation. That the breeding size of a population may be considerably smaller than the overall size of a population should be obvious from the situation of man, where individuals under 10 years of age and over 60 years of age are generally excluded from the breeding population.

Effective Breeding Size

Most important evolutionarily is what is known as the *effective breeding size* N_e . This is equivalent to the breeding size N only in an "ideal" population of continuing large size in which there are equal numbers of the two sexes, mating is at random, and the gametes are drawn at random from the parents. This ideal population is an abstraction; for practical purposes the effective breeding size is *always* smaller than the breeding size. In some cases, however, the difference may be quite small. Uneven sex ratios, inbreeding, cyclic reduction of breeding size, and nonrandom sampling of the gametes all depress the effective breeding size. As an example, consider a population of N breeding individuals, mating at random, not fluctuating in size, and having the gametes drawn at random from the parents. Table 6.4 shows the effects of different sex ratios on the effective breeding size, where $N_e = 4N_{\sigma}N_{\varphi} / (N_{\sigma} + N_{\varphi})$, and $N_{\sigma} + N_{\varphi} = 400$. The derivation for this formula is given in Li.

Similarly, if the effective size for four successive generations is 10, 100, 10,000, and 100, the *average* effective size (which is the harmonic mean, the reciprocal of the mean of the reciprocals, of the sizes at each generation) over those generations is approximately 33. Note that this is much closer to the minimum number in the series than to the maximum. Effective breeding size indicates the size of the "ideal" population whose genetic behavior would be the same as that of the population under consideration. This permits valid comparisons of population size. To equate two populations with 400 breeding individuals, one with 200 males and 200 females, and the other with 5 males and 395 females, would be to ignore the genetic consequences of the sex-ratio inequality of the latter population. (For example, all other factors being equal, it would lose its variability much more rapidly than the former because the males, in essence, would become a bottleneck in the transfer of genetic variability from generation to generation.) One sometimes can point out the individuals that are members of a breeding population, but one cannot segregate a group and label it the "effective population." Unless otherwise specified, population size will refer in what follows to the effective population size and will be designated simply by N .

Table 6.4 | Breeding Size—400

Males	Females	N_e
200	200	400.00
100	300	300.00
50	350	175.00
25	375	93.75
5	395	19.75
1	399	3.99

Genetic Drift

Consider a barrel containing 10,000 black marbles and 10,000 white marbles representing the gametes of a population with a gene frequency of $p = q = .50$ at some locus. A random sample of 2,000 marbles from this barrel represents the 1,000 diploid individuals that will make up the breeding population of the next generation. Perhaps the first sample consists of 979 white marbles and 1,021 black marbles ($p = .49$). The “gene pool” barrel is then reconstituted with 9,790 white marbles and 10,210 black marbles, and the sampling of 2,000 marbles is repeated. This time assume that a sample of 1,033 white and 967 black marbles represents the gene frequency ($p = .52$) of the breeding population of the next generation. Once again the barrel is reconstituted, with 10,350 white and 9,670 black marbles. A continuation of this process would, under most circumstances, produce a very slight fluctuation of gene frequency around the original figure of $p = .50$. Note that this model is constructed so that the population size remains constant.

Now consider another barrel containing 500 white marbles and 500 black marbles to represent the gametic gene pool of a smaller population with gene frequency of $p = .50$. Suppose 10 marbles representing 5 individuals are withdrawn at random and that 6 are black and 4 are white ($p = .60$). The original gametic population is reconstituted with 600 black and 400 white marbles and the procedure repeated. Now 8 black and 2 white marbles are drawn (gene frequency $p = .80$) and the barrel reconstituted with 800 black and 200 white. On the third sampling one might get 7 black and 3 white (gene frequency $p = .70$), and thus reconstitute the barrel with 700 black and 300 white. It is easy to see that, in carrying through this procedure, much more violent fluctuations in gene frequency have been caused than arose with the larger population. This random

fluctuation of gene frequency due to chance occurrences is known as *genetic drift*. The term drift is quite descriptive, as the frequency of p seems to drift around without approaching any particular value, unlike the directional movements caused by the so-called systematic pressures of mutation, selection, and differential migration.

Figure 6.1 shows the probability distribution of p in 50 and 5,000 offspring from a parental population in which the gene frequency was $p = .50$. In this and succeeding examples it will be assumed that all the conditions for maintaining a Hardy-Weinberg equilibrium are present, except in the factor under study. In other words, the factors will be manipulated one at a time to show how they may alter the equilibrium.

The possible values of p in the two different groups of offspring are given in the two histograms of Fig. 6.1. The ordinate represents the approximate probability of p falling in each interval. As expected, the chances for large fluctuations due to sampling error are much greater for the smaller group of offspring.

Figure 6.1 also shows the fates of large numbers of loci, all of which were at gene frequency of .50 in their parental population. With $N = 50$, one would expect only 3 loci in 100,000 to fluctuate to a value greater than .70, whereas with $N = 5,000$ only 3 loci in 100,000 would fluctuate to a value greater than .52. On the other hand, one may wish to consider the distribution of the gene frequency of a given locus in a large number of populations, all with an initial gene frequency of .50. According to Fig. 6.1, with $N = 5,000$, we would expect 99.994 percent of the populations to have a gene frequency between .48 and .52 for the specified locus, whereas with $N = 50$ the same percentage would have a range from .30 to .70.

Decay of Variability

The possible consequences of drift in a small population are shown diagrammatically in Fig. 6.2. The gene frequency is analogous to a pinball; moving down the slope (through time), it ricochets from value to value, *as long as it stays on the table*. However, in the absence of mutation and migration, the values of 0 (loss) and 1.0 (fixation) are *dead ends*; once the ball drops into one of these slots it stays there. That is, gene A is either fixed (all individuals AA) or lost (all individuals aa). Thus the gene frequency of A can move from any intermediate value to the end points 0 and 1 but not vice versa; the gene frequency will ultimately be 0 or 1 if the population is left undisturbed long enough. Since, when the gene frequency reaches 0 or 1, heterozygotes no longer can be formed at the locus,

the more genes that are lost or fixed, the fewer heterozygotes there are in the population. The process of reduction of heterozygosity through loss and fixation at various loci is known as the *decay of variability*.

Fig. 6.1 | Probability distribution of p in 50 and 5,000 offspring from a parental population in which the gene frequency was $p = .50$. For details see text.

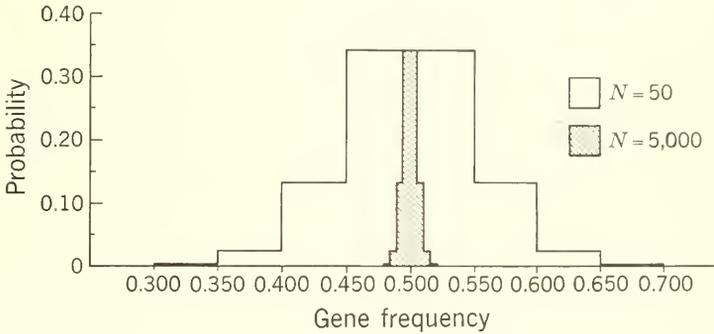
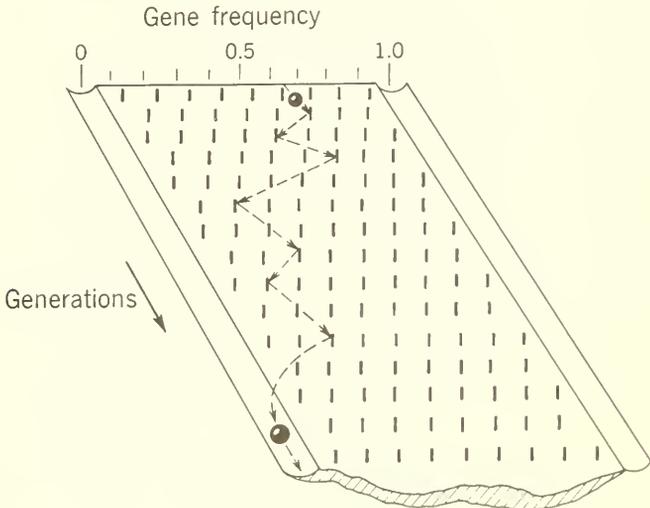


Fig. 6.2 | Model illustrating genetic drift. See text for explanation.



The rate of this decay is intimately tied to the population size. Genes are lost at a rate of $1/4N$ per generation and fixed at a rate of $1/4N$ per generation. Thus this decay of variability takes place at the rate of $1/2N$ genes per generation. Consider some extreme examples. If p has a value of .125 in a breeding population of only 4 individuals, 1 individual has the only gene representing p , and only one-eighth of the gametes have that gene. If that single individual fails to reproduce, the gene is lost. If the individual does reproduce, the chance of loss of the gene is $1/2$ when it leaves only 1 offspring, $1/4$ when it leaves 2 offspring, $1/8$ when it leaves 3 offspring, etc. However, in a population of 4,000 breeding individuals, an absolute minimum of 500 individuals carry the gene in question if the gene frequency is .125. All these individuals would then be homozygous for the gene in question, and all must fail to reproduce to cause loss of the gene. Drift (sampling error) is a *mathematical fact*. However, the significance of drift as opposed to selection has been widely debated. It seems certain that drift is of very little importance in large populations (say N greater than 500), but in small populations drift may be an active evolutionary factor.

Loss of Mutations

An additional aspect of loss of variability through sampling error concerns the probability of loss of a mutant gene. Imagine a mendelian population in which N is constant (a pair of adults produce, on an average, two offspring) and in which a certain locus is at fixation (all individuals homozygous AA). If, in a single individual, A mutates $A \rightarrow a$ producing a single heterozygote Aa , this heterozygote must, if it breeds, backcross with an AA individual (no others being available). The offspring of this backcross will consist, on an average, of 50 percent AA and 50 percent Aa . Owing to chance, this mating may produce 0, 1, 2, 3, \dots , r offspring, the probability of each family size following a Poisson distribution with a mean of 2 (the average number of offspring). If no offspring are produced, the gene is lost; if 1 offspring is produced, the probability of loss is .50; if 2 offspring are produced, the probability of loss is .25; and if r offspring are produced, the probability of loss equals 2^{-r} . Using the coefficients from the Poisson distribution, one can calculate the limit of the aggregate probability of loss to be equal to .3679. Fisher has calculated the probabilities of extinction for a mutation appearing in a single individual under the condition that the mutation is of no selective value and also under the condition that the mutant has a

1 percent selective advantage over its wild-type allele. These probabilities are reproduced in Table 6.5, which shows that a new mutation has virtually no chance of survival in a population unless selection counteracts the decay of variability.

MUTATION

Mutations are changes in genetic information and as such have been discussed in Chap. 3. Mutation will now be considered as one of the systematic pressures tending to cause deviation from the Hardy-Weinberg equilibrium. If A is the "type gene" and a is the mutated gene, $u =$ mutation rate, $A \rightarrow a$, and $v =$ back mutation rate, $A \leftarrow a$. Such a system has an equilibrium point, as shown in the following calculations:

$$\Delta q = up \text{ (gain)} - vq \text{ (loss)}$$

$$\Delta q = 0 \text{ at equilibrium point } (\hat{p}, \hat{q})$$

$$\begin{aligned} \text{Therefore } \Delta q = 0 &= u(1 - \hat{q}) - v\hat{q} \\ 0 &= u - u\hat{q} - v\hat{q} \\ -u &= \hat{q}(-u - v) \\ \hat{q} &= \frac{u}{u + v} \\ \hat{p} = 1 - \hat{q} &= 1 - \frac{u}{u + v} = \frac{u + v - u}{u + v} = \frac{v}{u + v} \end{aligned}$$

where $p =$ gene frequency of A

$q =$ gene frequency of a

$$p + q = 1; q = 1 - p$$

$\Delta q =$ change in q

$\hat{q} =$ equilibrium value (referred to as "q hat")

A graphic representation of this equilibrium is shown in Fig. 6.3. Note that Δq is the net change per generation in the frequency of a and that Δq is positive when $q < \hat{q}$, and Δq is negative when $q > \hat{q}$. The change at 1 (all a) is one-half as great as at 0 (all A) since $A \rightarrow a = u = .00004$ and $a \rightarrow A = v = .00002$. Thus we can see that, in a population meeting all the requirements of Hardy-Weinberg equilibrium except the absence of mutation, the equilibrium value for the frequency of a gene is determined by the mutation rate and back mutation rate at the locus in question.

**Table 6.5 | Probability of Extinction of a Mutation
Appearing in a Single Individual**

Generation	Probability of Extinction	
	No advantage	1% Advantage
1	0.3679	0.3642
3	0.6259	0.6197
7	0.7905	0.7825
15	0.8873	0.8783
31	0.9411	0.9313
63	0.9698	0.9591
127	0.9847	0.9729
Limit	1.0000	0.9803

From *The Genetical Theory of Natural Selection*, Second Rev. Ed., by Ronald A. Fisher, 1958. Published by Dover Publications, Inc., New York, N.Y., and reprinted through permission of the publisher.

SELECTION

Selection is the nonrandom (differential) reproduction of genotypes. One might regard the streams of life of a population as made up of continually varying, dividing, fusing, and disappearing particles flowing from the past to the present through a series of immensely complex screening sieves. Selection can be said to have occurred when the stream at a lower point differs from the stream at a higher point to such a degree that it is highly improbable that the observed difference is due to sampling error (drift) or mutation. In looking for selection, one must be sure that the stream neither branches (emigration) nor receives a tributary (immigration) in the stretch observed.

If a population is genetically heterogeneous, the probability of success of some genotypes will be higher (with possible rare exceptions) than the probability of success of others. Thus certain kinds of genetic information will become more and more common in the gene pool of the population and other kinds will become less and less common. The gene frequencies p and q will change with time rather than remaining constant, as would be expected under the conditions of Hardy-Weinberg equilibrium.

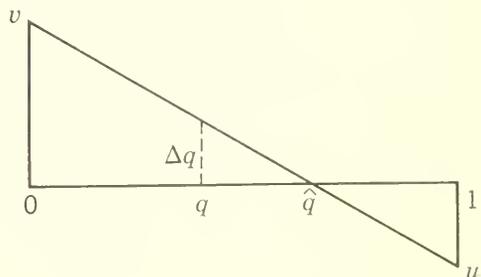
It is popular to speak of selection as a great “creative force” in evolution, the “cause” of observed trends. In fact, it is a phenomenon observable only a posteriori—a description of occurrences. When a

nonrandom set of genotypes leaves more offspring than others, selection has occurred. In the broadest view, selection reduces the diversity of living organisms; organisms containing certain types or combinations of genetic information are inviable or do not persist. This process “creates” what we recognize as a certain order in nature, in the same way that the order we see in a team with seven heavy, muscular linemen is “created” by the game of football. It is only in this restrictive sense of combating a trend toward increasing entropy that selection is “creative.”

Critics of the theory of natural selection have claimed that selection can in no way be creative since it functions merely to eliminate certain types. They would point out that, in the common analogy of natural selection with a sieve, if large and small rocks are screened, the end result is a pile of the smaller rocks from the original pile. Nothing new has been created. What is forgotten is that the analogy is too simple, for it ignores the potential mutational and recombinational variability of biological entities. It is as if two small rocks could mate and their offspring included rocks smaller than either parent. If a sufficiently fine sieve were used, screening would create a heap of rocks smaller than any in the original pile.

There are two types of selection: natural selection, in which the environment determines which genotypes are the most “fit,” and artificial selection, in which man determines which genotypes are the most “fit.” It is important to note that, while natural selection must always operate on the genotype *through the phenotype*, it is sometimes possible for artificial selection to act directly on the genotype. For example, let us suppose that a moth has a melanic form produced by a dominant gene M . If the dominance is complete, only two distinguishable phenotypes will be presented to the environment, melanic and nonmelanic ($M-$ and mm). As far as natural selection is concerned, the homozygous dominant (MM) and hetero-

Fig. 6.3 | Equilibrium with mutation and reverse mutation. See text for explanation. (From Wright, 1940, *The New Systematics*, Oxford University Press.)



zygous (Mm) genotypes are indistinguishable. In the laboratory the situation would be quite different; appropriate test crossing would permit the selection of either genotype.

Fitness or Adaptive Value

In any given environment, the product of the relative survival value and relative reproductive capability of a given genotype constitutes its fitness or adaptive value. Fitness has many components, examples of which are the relative fertility, duration of reproductive period, ability to find a mate (in animals), efficiency of pollination mechanism (in plants), and general hardiness of individuals of the genotype in question. By convention, the continuum of adaptive values runs from 0, as for a zygote homozygous for a lethal gene, to 1, for the genotype that donates the largest number of gametes to individuals of the next generation. This maximum number depends, of course, on the organism under consideration. Thus, in this book, the term fitness indicates the success of a genotype in transmitting genetic information to the next generation, this success being measured relative to all other genotypes along a scale running from 0 (no information transmitted) to 1 (the most information transmitted). Some authors include within the concept of fitness such things as long-range fitness, the ability of a population to meet hypothesized future changes in the environment. There can be no doubt that, as noted under genetic systems and later in this chapter, certain types of populations are better able to adjust to environmental changes than others. However, because of the difficulties of working with this aspect of fitness, it seems best to utilize the concept in a restricted time sense, as above. Further discussion of these and related problems will be found in the last chapter.

It should be noted that these definitions of selection are a long way from the popular "bloody tooth and claw" picture usually painted by the uninformed. The creative aspect of the process consists almost entirely of the environment, *through selection*, affecting the genetic structure of populations so that they produce the fittest phenotypes.

Types of Selection

There are three basic types of selection operating within populations: *directional*, *stabilizing*, and *disruptive*. Directional selection has occurred when there is a shift in the position of the population mean for the character considered. Stabilizing selection is lowered

fitness of extreme individuals and the concomitant reduction of the variance of the character, resulting in a more uniform population. Disruptive selection has occurred when two or more different types have been favored but intermediate types were at a disadvantage. It usually increases the variance and, under some conditions, may lead to fragmentation of the population. Examples of all three types will be found in the next chapter.

Extensive work has been done to describe various types of selection mathematically. Most of this work lies outside the scope of this book, and the interested reader is again referred to Li. However, a few examples of this quantitative treatment follow, both to illustrate the methodology and to relieve the reader of the necessity of accepting on faith the results of certain selective processes.

Homozygous Recessives Completely Unsuccessful

Taking an array of genotypes (for example, *AA*, *Aa*, *aa*), one may, by assigning to each one an adaptive value *W*, measure the differences in their capacity to contribute to the filial gene pool. As stated above, the most successful genotype is given the value 1, while less fit combinations have lower values. Thus we might find the following situation:

Genotype	<i>AA</i>	<i>Aa</i>	<i>aa</i>
Adaptive value <i>W</i>	1	1	1- <i>s</i>

In this case the homozygous recessives would be adaptively inferior to either the heterozygote or homozygous dominant. The degree of disadvantage is measured by *s*, the selection coefficient, 1 - *s* being the fitness or adaptive value. In this situation the coefficient could vary from 0 (no disadvantage, making the comparison pointless) to 1 (homozygous recessives lethal).

The consequences of complete removal of the recessives from the population (homozygous recessives lethal, *s* = 1) are shown in Table 6.6.

The relationship between the gene frequencies of any two consecutive generations is

$$q_{n+1} = \frac{q_n}{1 + q_n}$$

where the subscripts indicate the generation numbers. Thus

$$q_0 = q_0$$

$$q_{0+1} = q_1 = \frac{q_0}{1 + q_0}$$

$$q_{1+1} = q_2 = \frac{q_0/(1 + q_0)}{1 + q_0/(1 + q_0)} = \frac{q_0/(1 + q_0)}{(1 + q_0)/(1 + q_0) + q_0/(1 + q_0)}$$

$$= \frac{q_0/(1 + q_0)}{(1 + 2q_0)/(1 + q_0)} = \frac{q_0}{1 + 2q_0}$$

$$q_{2+1} = q_3 = \frac{q_0}{1 + 3q_0}$$

These successive q 's (gene-frequency values) fall into a harmonic series, i.e., one whose terms are the reciprocals of those in an arithmetic series. When the initial gene frequency is known, the gene frequency for any succeeding generation may be found by substituting in the equation $q_n = q_0/(1 + nq_0)$. The change in gene frequency per generation is again symbolized by Δq and is given by the following equation:

$$\Delta q = \frac{q}{1 + q} - q = \frac{-q^2}{1 + q}$$

Note that the *rate of change* of gene frequency is itself a *function of the gene frequency*. When the gene frequency is high, the gene is removed from the population rapidly. A few representative values are given in Table 6.7.

Table 6.6 | Complete Elimination of Recessives

Genera- tion	Before or After Selection	Genotype Frequencies			Gene Frequency of a
		AA	Aa	aa	
0	Before	p^2	$2pq$	q^2	q
	After °	$\frac{p^2}{p^2 + 2pq}$	$\frac{2pq}{p^2 + 2pq}$	0	$\frac{q}{1 + q}$
1	Before †	$\frac{1}{(1 + q)^2}$	$\frac{2q}{(1 + q)^2}$	$\frac{q^2}{(1 + q)^2}$	$\frac{q}{1 + q}$
	After ‡	$\frac{1}{1 + 2q}$	$\frac{2q}{1 + 2q}$	0	$\frac{q}{1 + 2q}$
...

° $p^2 + 2pq$ represents the total after the aa (q^2) genotypes are removed. To find the frequencies of the two remaining genotypes they must be expressed as proportions of the total. These two frequencies are obtained simply as follows:

$$\frac{p^2}{p^2 + 2pq} = \frac{p(p)}{p(p + 2q)} = \frac{1 - q}{1 - q + 2q} = \frac{1 - q}{1 + q}$$

The reason for this change in rate of removal is that the proportion of recessive genes in the *heterozygotes* increases rapidly as the gene frequency decreases. Where q = gene frequency of a , the percentage of a genes in the heterozygotes is as follows:

q	Genotype Frequencies			Percent in heterozygotes
	AA	Aa	aa	
.9	.01	.18	.81	10
.1	.81	.18	.01	90
.01	.9801	.0198	.0001	99

The recessive genes in the heterozygotes are “hidden” from selection, since only the homozygous recessives are lethal. The lower the gene frequency, the smaller the proportion of recessive genes exposed in homozygotes becomes, and the progress toward removal of the gene from the population slows down accordingly. This result is of particular interest to students in eugenics. If a particular undesirable gene (a) had a gene frequency $q = .01$ in the human population, so that q^2 (aa) individuals made up .0001 of the individuals (one defect per 10,000 “normals”), it would take 100 generations (roughly 2,500 years) of a program of sterilization of defective

and similarly $\frac{2pq}{p^2 + 2pq} = \frac{2q}{1 + q}$

$$\frac{1 - q}{1 + q} + \frac{2q}{1 + q} = 1 \quad q = \text{gene frequency of } a = \frac{1}{2} \times \frac{2q}{1 + q} = \frac{q}{1 + q}$$

$$p = 1 - q = 1 - \frac{q}{1 + q} = \frac{1}{1 + q}$$

† The genotype frequencies before selection are obtained by using the *new* p and q values and expanding the following:

$$\left(\frac{1}{1 + q} + \frac{q}{1 + q} \right)^2$$

For example, the zygotic frequency of

$$AA = (\text{new } p)^2 = \left(\frac{1}{1 + q} \right)^2 = \frac{1}{(1 + q)^2}$$

‡ Frequencies after selection are calculated as in the first footnote, e.g.,

$$\frac{1/(1 + q)^2}{1/(1 + q)^2 + 2q/(1 + q)^2} = \frac{1}{1 + 2q}$$

Table 6.7

Gene Frequency	Decrease per Generation
.9	.426
.5	.167
.1	.009
.05	.0024
.01	.000099

individuals to halve the gene frequency and reduce the number of defective individuals to 1 in 40,000. The problem of carrying out such a program without mistakes for such a protracted period makes it highly unlikely that such meager results would justify the effort involved. On the other hand, selection against dominants is relatively highly effective. If a dominant gene became lethal, for instance, it would be removed from a population in one generation.

Homozygous Recessives Relatively Unsuccessful

The situation where the dominants are favored over the recessives but the homozygous recessive individuals make some contribution to the gene pool of the succeeding generation is probably more common than that of complete homozygous recessive lethality.

If fitness values of 1 are assigned to the two dominant genotypes, and $1 - s$ to the homozygous recessives, after one generation of selection there would be p^2 AA individuals, $2pq$ Aa individuals, and $q^2 - sq^2$ aa individuals out of a total of $p^2 + 2pq + q^2 - sq^2 = 1 - sq^2$ individuals. Using the same procedure as in the previous example, the change in gene frequency per generation is

$$\Delta q = \frac{pq + q^2(1 - s)}{1 - sq^2} - q = \frac{-sq^2(1 - q)}{1 - sq^2}$$

Thus the change in gene frequency under these conditions is small when q is very large or very small and is relatively large when the value of q is intermediate. When q is large, progress is slow because of the relatively large reproductive contribution of the recessive homozygotes (in contrast with the dominants). As q becomes small, the sheltering effect of the heterozygotes slows progress, as it does when the homozygous recessives are lethal. A few sample values are given in Table 6.8, where the selection coefficient operating against the homozygous recessives is $s = .5$.

Table 6.8

q	Δq
.99	-.00961
.90	-.06807
.50	-.07143
.30	-.03298
.05	-.00119
.01	-.00005

Homozygotes Inferior to Heterozygotes

As a final detailed example of selection models, consider the case in which both homozygous genotypes are inferior (i.e., the locus shows overdominance with respect to fitness) to the heterozygotes so that

Genotype	AA	Aa	aa
Adaptive value	$1 - s_A$	1	$1 - s_a$

The proportions after one generation of selection will then be $p^2(1 - s_A)$ AA, $2pq$ Aa, and $q^2(1 - s_a)$ aa out of a total of $1 - s_A p^2 - s_a q^2$. The latter quantity, obtained by summing the values for the three genotypes and simplifying, is thus

$$\begin{aligned} & p^2(1 - s_A) + 2pq + q^2(1 - s_a) \\ &= p^2 + 2pq + q^2 - s_A p^2 - s_a q^2 = 1 - s_A p^2 - s_a q^2 \end{aligned}$$

Since the initial gene frequency is $q_0 = pq + q^2$, q_1 (the frequency of a genes after one generation of selection) is

$$\frac{pq + q^2(1 - s_a)}{1 - s_A p^2 - s_a q^2} = \frac{pq + q^2 - s_a q^2}{1 - s_A p^2 - s_a q^2} = \frac{q - s_a q^2}{1 - s_A p^2 - s_a q^2}$$

Then the change in q per generation is

$$\begin{aligned} \Delta q &= \frac{q - s_a q^2}{1 - s_A p^2 - s_a q^2} - q = \frac{q - s_a q^2 - q + s_A p^2 q + s_a q^2(1 - p)}{1 - s_A p^2 - s_a q^2} \\ &= \frac{-s_a q^2 + s_A p^2 q + s_a q^2 - s_a p q^2}{1 - s_A p^2 - s_a q^2} = \frac{pq(s_A p - s_a q)}{1 - s_A p^2 - s_a q^2} \end{aligned}$$

Therefore, if $s_A p > s_a q$, then Δq is positive and the frequency of a is increasing, and if $s_A p < s_a q$, then Δq is negative and the frequency of a is decreasing. When $s_A p = s_a q$, $\Delta q = 0$, and the frequency of a is at equilibrium. In this situation, then, the equilibrium value of q (\hat{q} – “ q hat”) is determined solely by the magnitude of the selection coefficients:

$$s_A \hat{p} = s_a \hat{q} \quad s_A(1 - \hat{q}) - s_a \hat{q} = s_A - s_A \hat{q} - s_a \hat{q} = 0$$

$$s_A = s_A \hat{q} + s_a \hat{q} = \hat{q}(s_A + s_a) \quad \hat{q} = \frac{s_A}{s_A + s_a}$$

Similarly,

$$\hat{p} = \frac{s_a}{s_A + s_a}$$

If the adaptive values of the three genotypes remain constant, the equilibrium value will also remain constant. If some incident, such as the arrival of a group of migrant individuals, shifts the gene frequency away from the equilibrium value, the selective forces will restore the equilibrium. Therefore, we refer to this as a “stable” equilibrium.

Balanced Polymorphism and the Retention of Variability

The selective system in which the heterozygotes are superior to either homozygote results in the retention of both alleles in the population rather than a trend toward fixation of one or the other. A situation in which two or more forms of an organism persist in the same population, with the rarest form in a frequency *too high to be accounted for by mutation alone*, is known as *polymorphism*. When heterozygotes are favored over homozygotes, the establishment of a gene-frequency equilibrium creates a *balanced polymorphism*. This type of polymorphism is important in evolution in part because it permits a certain amount of variability to be retained in the population. This means that the population may be able to react very rapidly to an environmental change and thus avoid extinction. For example, suppose that a certain locust living in a semiarid environment shows the following array of adaptive values at a locus: BB , .50; Bb , 1.00; bb , .40. The heterozygotes are physiologically superior to either homozygous type, and the BB nymphs are slightly more resistant to desiccation than the bb nymphs. In such a population the gene frequency would reach a stable equilibrium at

$$\hat{B} = \frac{s_b}{s_b + s_B} = \frac{.60}{.60 + .50} = .545$$

(Note that the *bb* adaptive value is .40 but the selection coefficient is .60, since $1 - s$ equals the adaptive value.) The maintenance of the equilibrium at $\hat{B} = .545$, $\hat{b} = .455$ by this selective system is shown in Table 6.9.

Suppose that a climatic change suddenly increases the rainfall in the area occupied by our hypothetical locusts, encouraging the growth of a mold which is fatal to *BB* and *Bb* eggs but to which the *bb* eggs are relatively immune. The adaptive values *W* are now *BB* = .00; *Bb* = .00; *bb* = 1.00. The survival of the population now depends entirely on the presence of *bb* eggs. If a prerin (polymorphic) adult population of 100 pairs and an average egg production of 100 eggs per female are assumed, there would be 10,000 eggs exposed to the mold. Of these, 2,070 (.207 × 10,000) would be of the resistant kind, presumably giving the population a reasonable chance of survival.

On the other hand, if the prerin population had been monomorphic (all individuals *BB*, perhaps because of strong selection against *Bb* and *bb* individuals), the outcome would almost certainly be different. If a mutation rate $B \rightarrow b$ of 10^{-5} is assumed, only one egg in 10 billion would be of the surviving genotype. (The chance of both members of a pair of alleles being mutant in a single individual is the product of the chances of either one being mutant: $10^{-5} \times 10^{-5} = 10^{-10} = 1/10,000,000,000$.) The advantage of balanced polymorphism to the population is obvious.

Table 6.9 | Balanced Polymorphism

Generation	Before or After Selection	Genotype Frequencies				Gene Frequencies	
		<i>BB</i>	<i>Bb</i>	<i>bb</i>	Σ	<i>B</i>	<i>b</i>
0	Before °	.297	.496	.207	1.000	.545	.455
	After †	.148	.496	.083	.727	.545 ‡	.455
1	Before	.297	.496	.207	1.000	.545	.455
	After	.148	.496	.083	.727	.545	.455

Succeeding generations continue this pattern as long as assumptions hold.
 ° Random mating is assumed in the calculation of this row, giving the following genotype frequencies: $B^2 = .545^2 = .297$; $2Bb = 2(.545)(.455) = .496$; $b^2 = .455^2 = .207$.

† The selection pressure is included by multiplying each genotype frequency by its adaptive value: .297 (.50) = .148; .496 (1.00) = .496; .207 (.40) = .083.

‡ *B* gene frequency is given by $(D + \frac{1}{2} H)/N$. Half of .496 = .248, thus $(.148 + .248)/.727 = .545$. Gene frequency of *b* is $1 - .545 = .455$.

Simplified and overdrawn as it is, this example demonstrates how balanced polymorphism *may* be advantageous to a population because it prevents loss of variability due to fixation at the locus. Another mechanism that tends to slow the loss of variability at a locus is dominance, which permits the “sheltering” of otherwise undesirable mutants in heterozygotes. However, viewed in another way, it might be said that both these phenomena tend to keep “undesirable” genes in a population. To understand this point of view, the question of “genetic load” must be examined.

Genetic Load

If one genotype in a population at a given time is superior to all others, it may be assumed that a population consisting only of individuals with that genotype would have the highest possible fitness. Thus, if the most fit genotype is assigned an adaptive value $W = 1.00$, the population fitness \bar{W} will also equal 1.00, since $\bar{W} = \sum W_i g_i$ (where W_i is the adaptive value of the i th genotype and g_i is the frequency of the i th genotype, i being any number from 1 to n and n the number of different genotypes). Under this model, any population consisting of a mixture of genotypes will be “less fit” than the ideal monomorphic population. The amount by which a population differs from this ideal is its *genetic load* L , which may be viewed roughly¹ as the complement of \bar{W} or $L = 1 - \bar{W}$.

Given this model, two extreme possibilities may be considered. In one case the “ideal” genotype is homozygous at all, or nearly all, of its loci. At the other extreme all loci may be overdominant with respect to fitness, and the “ideal” genotype in this case is a multiple heterozygote. Considerable controversy has surrounded the question of which of these two extreme possibilities is more realistic. Evidence from response by populations to inbreeding is at the moment inconclusive. There is considerable evidence for the importance of overdominance with relation to fitness in animals, and it has been suggested that for many organisms extreme deviant phenotypes may be the result of multiple homozygote genotypes segregating in populations where multiple heterozygotes are the “normal” genotypes. Many plants, however, have genetic systems that seem to ensure

¹ Actually it is defined as $L = -\ln \bar{W}$. Thus $\bar{W} = e^{-L}$, so that L is the average number of potential deaths per individual and \bar{W} is the probability of genetic survival, that is, the probability of an individual not suffering death because of the properties of its genome. (Of course, an individual with the equivalent of five lethal genes in its genome dies only once, although it contributes five “deaths” to the average.) The reader familiar with statistics will recognize the expression $\bar{W} = e^{-L}$ as the first term of a Poisson distribution.

almost complete homozygosity, for which they appear to suffer not at all.

As discussed in the preceding section, balanced polymorphism permits a population to store variability for future evolution. Interpopulation selection thus may have favored populations with balanced polymorphic systems at many loci, in which case the concomitant increase in genetic load could be viewed as the penalty paid for increased evolutionary flexibility. It should be noted, however, that load is calculated at a given point in time and that the question of future potential for evolution is therefore not germane to the question of which kind of genotype is "ideal" as it is phrased here.

A basic problem lies in two of the assumptions upon which the load controversy in large part rests. The first is that an "ideal" population would be monomorphic (that is, made up of only one kind of genotype). This would not be true if there were different niches in the area occupied by the population and if different genotypes within the population had high adaptive values in one or more niches and lower values in others. It would also not hold if there were some sort of ecological synergism in which the presence of different genotypes added to the adaptive value of each genotype.

A second basic assumption is that \bar{W} is a measure of a biologically important quantity and that one population can reasonably be considered "better adapted" than another. It can be cogently argued that any population that is maintaining itself is just as well adapted as any other and that any standard for comparing "adaptedness" is arbitrary. For instance, there is one population of *Drosophila tropicalis* in which all surviving individuals are heterozygous for an inversion, both homozygous types being lethal. In spite of this huge segregational load, it is difficult to see any reason for considering this population "poorly adapted."

Finally, it must be pointed out that the character of the human genetic load is of some practical consequence. We need to know what portion of the load is segregational (due to unfit homozygotes segregating at balanced polymorphic loci) and what portion is mutational (due to harmful mutations at loci already homozygous for "good" alleles). This information would help us to evaluate the long-term effects of mutations caused by ionizing radiation. Although the problem is quite complex, it seems that if the load is largely mutational the additional mutations will add proportionately more to the load than if it is largely segregational. (An oversimplified explanation of this is that at loci showing overdominance for fitness the new mutations would make a positive contribution when they

occurred in heterozygotes, while at loci not showing such overdominance they would be “all bad.”)

Heterozygotes Inferior to Homozygotes

When selection is *against* the heterozygotes, an unstable equilibrium point exists at $p = q = .50$. Any deviation from this value leads to extinction of the allele that is made less frequent by the deviation. As shown by the values given in the discussion of selection against recessive homozygotes (p. 107), the rarer an allele is, the larger is the proportion of that allele in the heterozygotes. Therefore when selection is against the heterozygotes, the less frequent allele is at a disadvantage which *increases* as it becomes rarer. This means that there is no tendency to return to the equilibrium point, once a deviation has occurred; rather, the situation proceeds to fixation of one allele or the other.

MIGRATION AND POPULATION STRUCTURE

When a population is not completely isolated from other populations, its gene frequencies are subject to alteration through the incorporation of migrants which, as a group, have gene frequencies deviating from that of the recipient population. At any locus the change in gene frequency per generation is given by the expression

$$\Delta q = -m(q - q_m) = -mq + mq_m$$

where m is the number of migrant individuals divided by the population size of the recipient population, q is the gene frequency in the recipient population, and q_m is the gene frequency in the migrant group. Manipulating the right-hand side of this equation by adding and subtracting the quantity mq_mq , we get

$$\begin{aligned} -mq + mq_mq + mq_m - mq_mq &= -mq(1 - q_m) + mq_m(1 - q) \\ &= -mq(p_m) + mp(q_m) \end{aligned}$$

This final equation is in the same form as the expression for Δq in the discussion of the action of mutation and back mutation (p. 101); indeed, the situations are analogous.

Figure 6.4 shows how the distribution of gene frequencies changes with changes in m or N , where the gene frequency of the migrants is .50. Diagrams such as Fig. 6.4 are known as stationary frequency

distributions. Each curve in the figure represents a probability density function of the form

$$y = Cq^{4Nm}q_m^{-1}(1 - q)^{4Nm(1 - q_m)^{-1}}$$

where C is a constant making the function integrate to 1, and the other notation is as above. Such a function may represent the manner in which the probability is distributed over the possible events. The area under each curve is unity, and the area between the curve and each section of the abscissa (q axis) is the probability that the gene frequency will lie along that stretch of the q axis. Thus in Fig. 6.4 one can see at a glance that, under the given conditions, there is a much smaller probability that q will lie between .4 and .6 when $m = 1/4N$ than when $m = 4/N$. Stationary frequency distributions are a very convenient way of illustrating the effects of various evolutionary forces on different kinds of populations and are widely used for this purpose. Readers interested in further information on probability density functions and other subjects relating to the mathematical treatment of probabilities are referred to any introductory text on probability theory.

Stationary frequency distributions may be used to represent the distribution of the gene frequency under consideration in a large number of populations under the same evolutionary conditions, the

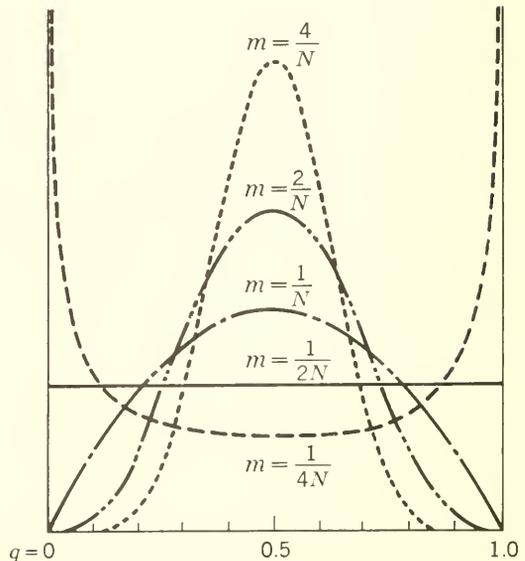


Fig. 6.4 | Distribution of frequencies of a gene among subdivisions of a population, where the gene frequency of the migrants is $p = q = .50$. For further explanation of this type of diagram see text. (From Wright, 1931, *Genetics* 16.)

distribution of the gene frequencies at a large number of loci subjected to the same pressures within a single population, or as the probability distribution for the chances of a given gene frequency occurring in any one generation. Thus the $Nm = 4$ curve ($m = 4/N$) in Fig. 6.4 may be interpreted in the following ways. It can be said that *under the same given conditions* the gene frequencies of a large number of populations (or loci within one population) would tend to cluster rather tightly around the value of .50, or that among all loci within a population subjected to the same conditions the probability of any given locus having a gene frequency between .35 and .65 is high. Finally, the curve represents the probability of the gene frequency at one locus having a given value in the generation observed. Thus the chance of observing a value of $q = 1$ in any one generation is vanishingly small.

The type and amount of movement of genetic information ("gene flow") found within and among populations are important factors in determining their evolution. Obviously, a situation in which a group of semi-isolated subpopulations randomly exchange genetic information among themselves (the "island model") is quite different from a situation in which the gene flow is unidirectional along a linear array of subpopulations (the "river model"). In turn, both of these differ from a situation in which a group of organisms is continuously distributed over a large area. In the latter case, although semi-discrete clusters of individuals may not exist, the probability of mating by two widely separated individuals may be very low because of their remoteness alone. The effects of such "isolation by distance" have been dealt with mathematically by Wright, who showed that the amount of local differentiation in a population is largely a function of the size of the panmictic units (neighborhoods) of which it is composed. When a population is divided into semi-isolated subpopulations or when some degree of inbreeding is found in the population as a whole, the general result is a reduction in the frequency of heterozygotes. An important aspect of this change in genotype frequencies is illustrated by the effects in such a population of selection against the homozygous recessives. This would be much more effective in a subdivided or inbreeding population because the reduced number of heterozygotes would "shelter" fewer recessive genes.

JOINT PRESSURES

Up to this point, only single evolutionary forces acting on isolated loci have been considered. However, in virtually all cases studied,

two or more pressures act jointly to affect the gene frequency at a given locus. In addition, the gene frequencies at different loci are not independent of each other, and the gene frequency at one locus may have a profound effect on the gene frequency at another. To appreciate this, one need only recall the phenomenon of linkage.

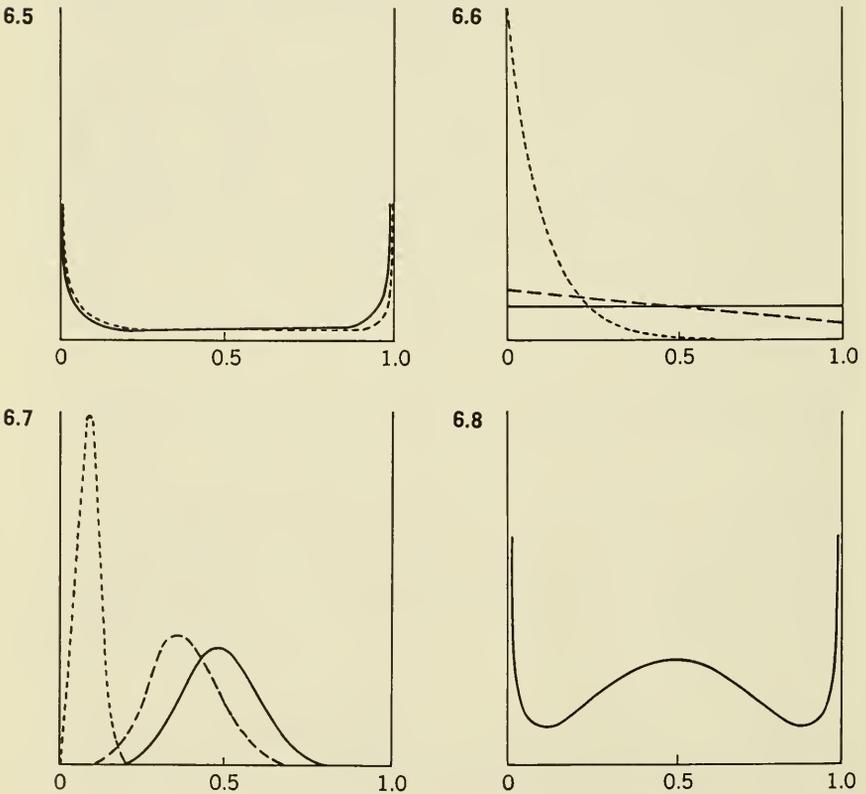
Some progress has been made in describing mathematically the results of various types of interactions in mendelian populations. Whether a completely satisfactory mathematical description of the simultaneous action of all evolutionary forces (varying with the environment) on an integrated genotype will ever be possible is an open question. Progress in the development of computers gives reason for hope, but the extreme complexity of the situation to be analyzed would require a computer of as yet undreamed-of sophistication. For the moment we must be satisfied with combining gross oversimplifications. There is solace in the fact that these simple models seem to approximate some natural situations and have proved quite useful in describing them.

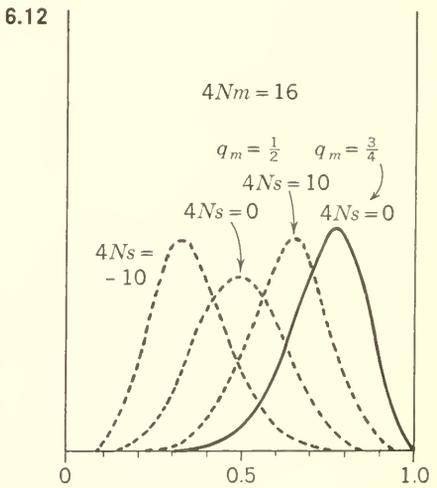
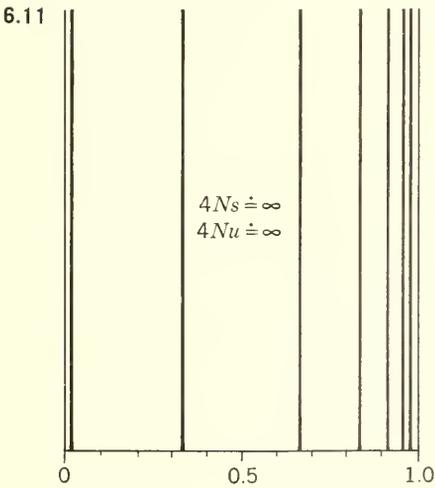
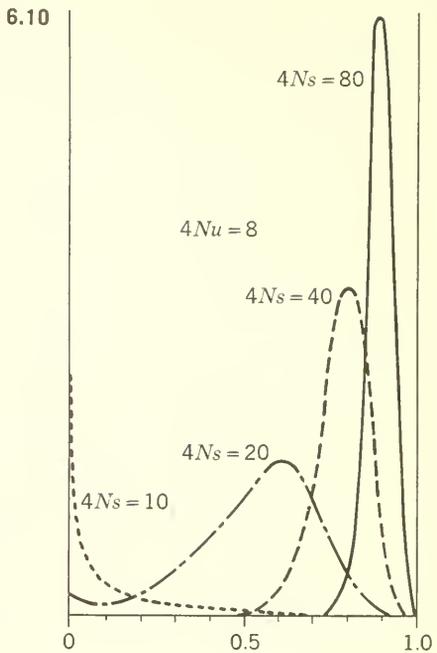
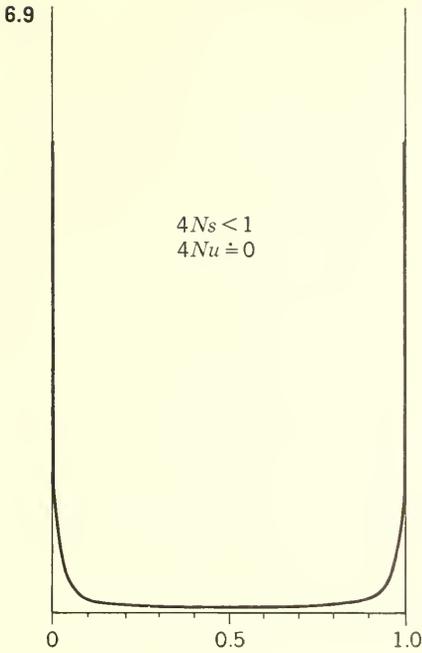
As a short excursion into more complex situations, consider Figs. 6.5 to 6.12. Figures 6.5 to 6.8 illustrate the effects of different selection pressures in populations of different sizes. In Figs. 6.5 to 6.7 mutation and back mutation rates are considered constant and equal ($u = v$). In Fig. 6.5 the population size is $N = 1/40v$; in Fig. 6.6, $N = 10/40v$; in Fig. 6.7, $N = 100/40v$. In all three figures the solid line is the case with the least selection ($s = -v/100$), the broken line the case with selection ten times as severe (not represented in Fig. 6.5 since it is practically indistinguishable from the preceding), and the dotted line the case with selection 100 times as severe. Note that selection in the very small population (Fig. 6.5) merely slightly alters the symmetry of the distribution, the probability of loss or fixation remaining high. As the population size increases (Figs. 6.6 and 6.7) the selection effects become much more pronounced. Figure 6.8 illustrates the distribution when the heterozygotes are favored and there is no difference between the selective values of the two homozygotes. Again $u = v$, $N = 1/40v$, and $s = 100v$. (Note that in these figures and in Figs. 6.9 to 6.12 the selection coefficient is not used as defined earlier but is given both positive and negative values. Thus $s = 100v$ is an index of the advantage of the heterozygotes, whereas above $s = -v/100$ is an index of the disadvantage of the allele under consideration.)

Figures 6.9 to 6.12 show the distribution of gene frequencies in populations of different sizes and different states of subdivision, under various selection and mutation pressures. Figure 6.9 depicts a small population under virtually no selection or mutation pressure.

The majority of alleles are fixed or lost at random. An intermediate-sized population under opposing selection and mutation pressures is shown in Fig. 6.10. There is random variation around modal values established by the opposing pressures. The case of a large population with gene frequencies at equilibrium points determined by the magnitudes of opposing selection and mutation pressures is covered in Fig. 6.11. Finally, Fig. 6.12 gives the gene frequencies in subdivisions of a large population fluctuating around modal values established by opposing forces of migration and selection.

Figs. 6.5 to 6.8 | Distributions of gene frequencies under different selection pressures and in populations of different sizes. For details see text. (*From Wright, 1937, Proc. Nat. Acad. Sci. 23.*)





Figs. 6.9 to 6.12 | Distributions of gene frequencies in populations of different sizes and different states of subdivision under various selection and mutation pressures. See text for details. (From Wright, 1931, *Genetics* 16.)

ADAPTATION AND GENE COMBINATIONS

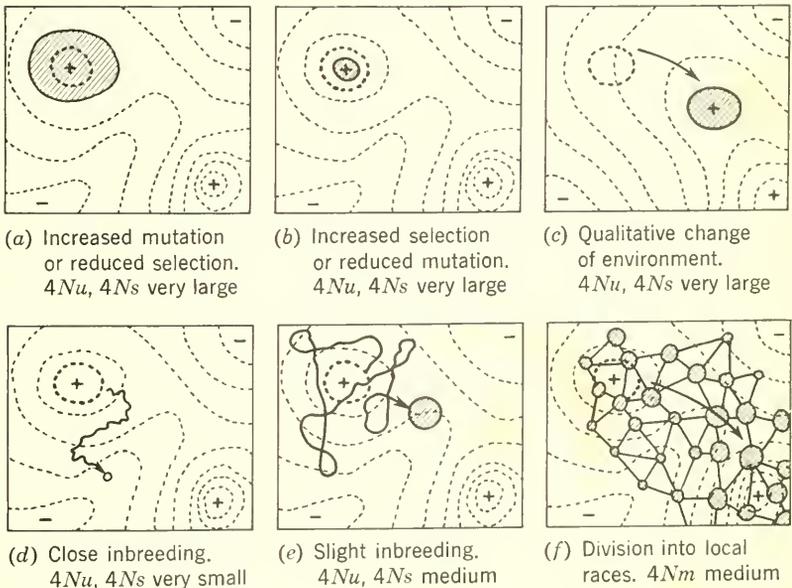
As Sewall Wright pointed out, sexual organisms have available to them a tremendous number of possible gene combinations. A species with only 1,000 loci, each occupied by a series of 10 alleles, could, through recombination, produce $10^{1,000}$ different genotypes (a number inconceivably greater than the number of electrons in the universe). While many of the theoretically possible combinations would be inviable or would yield identical phenotypes, such a species obviously has a very large capacity for genotypic variation. Within this vast field of possible combinations, there must be a large number of highly adaptive combinations and also many less highly adaptive or even lethal combinations. Wright represented this field as a contour map in two dimensions, with adaptive peaks and nonadaptive valleys, and stated that "the problem of evolution . . . is that of a mechanism by which the species may continually find its way from lower to higher peaks in such a field." A population of mosquitoes selected to avoid insecticides by not landing on poisoned surfaces might be considered as occupying an adaptive peak. A higher adaptive peak might be the development of a method of physiological resistance (allowing, perhaps, better access to houses). In order to acquire the more efficient physiological resistance, considerable reorganization of the genotype could be required; this reorganization might result in the loss of the behavioral resistance. The species would then have to cross an adaptive valley (little or no resistance) in order to attain the higher peak.

Figure 6.13*a* to *f* illustrates what might happen to certain kinds of populations occupying the adaptive field under different specified conditions. The field is represented as a topographic map with contour lines indicating different levels of adaptation. The heavy broken line represents the initial position of the population, and the arrow the direction of subsequent change. In Fig. 6.13*a* one sees the effect of increasing mutation rate or reducing selection pressure, a general increase in the variance and lowering of the average adaptive value of the population. If it spreads far enough, a portion of the population may occupy the lower slopes of an adaptive peak that is higher than the initial one; if this occurs, the entire population will move over and occupy the new peak. The effect of increasing the selection pressure or decreasing the mutation pressure is shown in Fig. 6.13*b*. The average level of adaptation increases at the expense

of evolutionary plasticity. The chances of capturing a neighboring higher peak are reduced.

Figure 6.13c illustrates the consequences of the omnipresent changes in the environment (adaptive peaks becoming valleys and vice versa). Here the result depends on the severity of selection and the speed of the environmental change. A species occupying a small field under strong selection pressure may not have the variability to permit it to move to the emergent peaks and may thus be left in a "pit" and become extinct. A population under less stringent selection will merely move as the conditions change. Figure 6.13d shows the effects of great reduction in population size and close inbreeding. Random fixation and loss move the population erratically down from its adaptive peak, and inbreeding (producing homogeneity) reduces the size of the adaptive field occupied by the population. This process (if unchecked) leads ultimately to extinction. In Fig. 6.13e one sees the results of an intermediate relationship between population size and mutation rate. The population tends to wander from

Fig. 6.13 | Field of gene combinations occupied by various kinds of populations under different conditions (explanation in text). (From Wright, 1932, *Proc. VI Congr. Genetics 1.*)



its peak, though remaining in the vicinity. This is a trial-and-error situation which may lead to the capturing of higher and higher peaks, although under the described conditions progress would be extremely slow.

In Fig. 6.13f a large species is subdivided into numerous semi-isolated populations. The part of the field occupied by each subpopulation shifts continually in a largely nonadaptive fashion and at a much faster rate than in the preceding case (since it is dependent on the amount of intermigration rather than mutation rate). With the rapid movement in the general neighborhood of one peak, sooner or later one subpopulation will cross the lower slopes of a higher peak and ascend it. This subpopulation will then expand in numbers; by migration its genes will flow into the other subpopulations, and the whole species will be brought into the field of influence of the new peak. This situation, featuring *intergroup* selection, permits trials of new combinations with a smaller risk to the species than a situation involving only *intragroup* selection. Such a subdivided population, then, provides the best opportunities for low-risk evolutionary change.

SUMMARY

In this chapter an attempt has been made to give a brief introduction to evolutionary processes from the viewpoint of population-genetic theory. One of the fundamental concepts of biology is the Hardy-Weinberg law which states that, in an idealized population and in the absence of evolutionary forces, the gene frequencies of autosomal alleles in the population will not change and, after one generation, the proportion of genotypes will reach an equilibrium. The ways in which mutation, migration, drift, and selection may cause deviations from this equilibrium have been formulated mathematically. The effects of these forces depend not only on the interactions among them but also on the structure of the population and the feedback effects of this structure on the forces themselves. Theoretical descriptions of possible responses of populations to various combinations of factors have been developed. Considering populations as shifting and interacting arrays of gene frequencies has given the evolutionist tools (however crude) for analyzing his observations with some degree of rigor and precision. Population-genetic theory is extremely useful in describing what may happen in natural populations and in interpreting data gathered from such populations.

REFERENCES

- Crow, James F. 1958. Some possibilities for measuring selection intensities in man. In J. N. Spuhler [ed.], *Natural Selection in Man*, Wayne State Univ. Press, Detroit. This paper and those cited in its bibliography deal with the problem of genetic load.
- Li, C. C. 1955. *Population Genetics*. Univ. of Chicago Press, Chicago. Every student should be familiar with this clear, concise, and generally excellent text. The bibliography contains references to most of the theoretical literature, including very important general works by Fisher and Haldane and the classic papers of Hardy and Weinberg.
- Population Genetics: The Nature and Causes of Genetic Variability in Populations*. 1955. Cold Spring Harbor Symposia on Quantitative Biology, vol. 20. The papers in this volume are a good sampling of recent thinking in population genetics. See especially the papers in the section Integration of Genotypes.
- Wright, Sewall. 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proc. Sixth Intern. Congr. Genet.* 1: 356-366. In this important paper Wright develops his idea of "adaptive fields."
- . 1958. *Systems of Mating and Other Papers*. Iowa State College Press, Ames, Iowa. This useful booklet reprints four of Wright's most important papers, including Evolution in mendelian populations (*Genetics* 16: 97-159).

7

changes in populations

Now that some of the theoretical aspects of population genetics have been discussed, it is appropriate to ask if it is necessary to rely on inference for the investigation of evolutionary mechanisms or whether it is possible to study them directly. Especially in recent years, examples of evolution in natural populations have been investigated, and some of these will be considered in the first part of this chapter. The remainder of the chapter is devoted to more general discussion of some aspects of evolutionary changes in populations.

EXAMPLES FROM NATURE

Differential Mortality in Sparrows

There have been numerous efforts to demonstrate the action of natural selection by comparing the characteristics of surviving and nonsurviving individuals. A brief summary of one of the earliest of these studies, Bumpus's work on sparrows, will serve to represent them all. In the winter of 1898, after a severe snow, rain, and sleet storm, H. C. Bumpus brought 136 stunned English sparrows into his laboratory at Brown University. Of these birds, 72 revived and 64 died. Bumpus measured the total length, wingspread, weight, length of beak and head, length of humerus, length of femur, length of tibiotarsus, width of skull, and length of keel of sternum on all the birds. His measurements showed that these various characters of the surviving birds generally were closer to the mean than those of the birds that died.

This mortality of sparrows with extreme measurements is an example of stabilizing selection. Many other studies also have demonstrated the correctness of the widespread notion that selection often results in the elimination of deviant individuals. As has been previously mentioned (Chap. 6), this is only one aspect of natural selection. The examples which follow often involve complex interactions of the so-called basic types of selection. It is to be expected that stabilizing selection in the form of failure of extreme deviants occurs in virtually all natural populations.

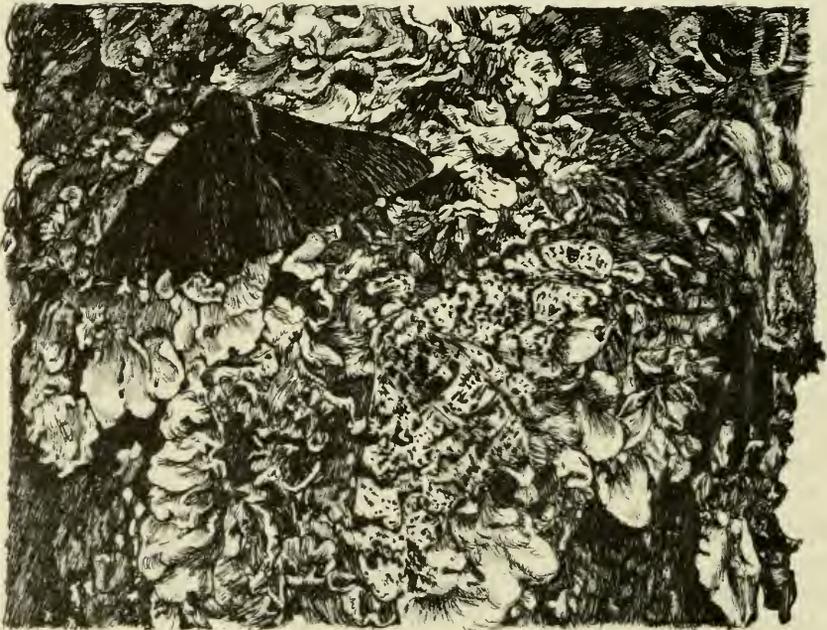
Industrial Melanism

During the past 120 years, dark forms of numerous cryptically colored (camouflaged) species of moths have appeared in certain areas

of northern Europe and North America. In many of these areas the melanic forms have become predominant, replacing or partially replacing protectively colored “typical” forms. These changes have taken place primarily in heavily industrialized areas and have been especially spectacular in England where they have been studied extensively. It has been estimated that in the area of Manchester, in 1848, the dark form of the moth *Biston betularia* made up a maximum of 1 percent of the population and that in the same area, in 1898, it made up more than 99 percent of the population. In most of the known cases the melanism is produced by a single dominant gene.

The following hypothesis has been developed to account for the phenomenon of “industrial melanism.” The spread of melanic forms seems to be intimately connected with the pollution of woods by soot in industrial areas. Apparently in unpolluted areas the dark forms

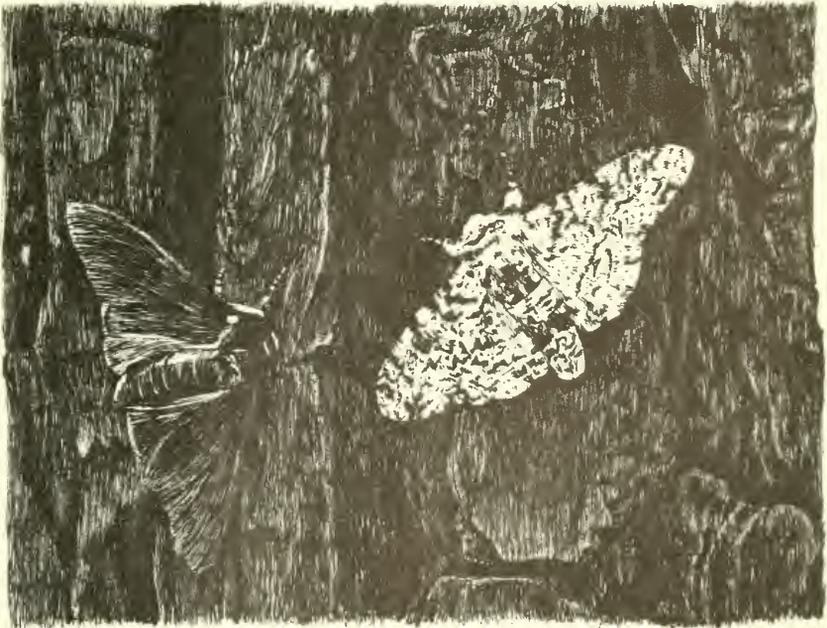
Fig. 7.1 | Two individuals of *Biston betularia*, one typical, one melanic, resting on an unpolluted, lichen-covered tree trunk. (After Kettlewell, 1958, *Proc. X. Int. Cong. Ent.* 2.)



are removed from the populations by visual predators (those which hunt by sight) because they are conspicuous when resting on lichen-covered tree trunks (Fig. 7.1). This disadvantage outweighs a possible selective advantage of the larvae of the melanics which may be *physiologically superior*. In polluted areas the situation is reversed; the typical (light, mottled) forms, which are nearly invisible on sooty trees where pollution has killed the lichens (Fig. 7.2). Thus the melanics are protectively colored in the polluted area; in addition, any physiological advantage they possess is magnified under the stress of eating contaminated food. Selection therefore strongly favors the melanics in industrial areas and the typicals in unpolluted areas. In polluted districts a *directional selection* moved the frequency of melanic individuals toward 100 percent.

What evidence supports this hypothesis? Some of the most com-

Fig. 7.2 | Two individuals of *Biston betularia*, one typical, one melanic, resting on a soot-covered tree trunk. (After Kettlewell, 1958, *Proc. X. Int. Cong. Ent.* 2.)



elling is the strong correlation, in time and space, of industrialization and the appearance of the melanic forms. This is so striking as to make virtually certain some relationship between the two phenomena. The composition of various English populations of *Biston betularia* is shown in Fig. 7.3. The populations in the industrial midlands are highly melanic, as are those in eastern England on the downwind side of the industrial areas where pollution fallout has been most intense.

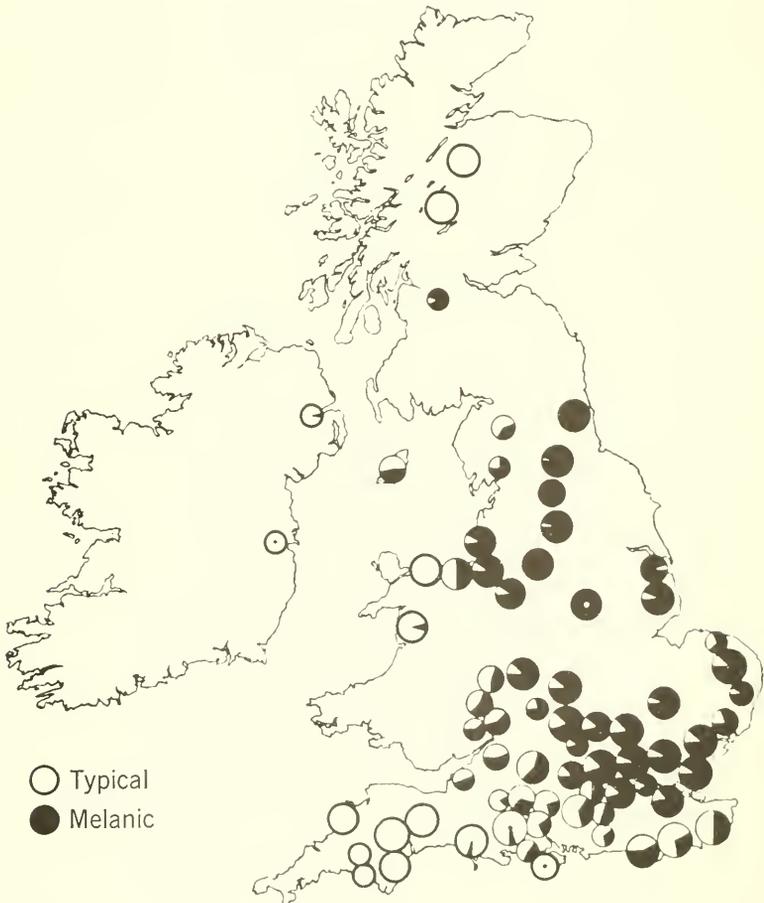
The most elegant demonstration of one factor responsible for industrial melanism is the observations and experiments on differential predation by Kettlewell and Tinbergen. In an unpolluted wood in Dorset, equal numbers of melanic and typical individuals were released; predation was observed and photographed from a blind. Spotted flycatchers (*Muscicapa striata*), nuthatches (*Sitta europaea*), yellow hammers (*Emberiza citrinella*), robins (*Erithacus rubecula*), and thrushes (*Turdus ericetorum*) ate 164 melanic individuals but only 26 typical individuals ($P \ll .01$).¹ In a polluted wood near Birmingham, opposite results were recorded, with redstarts (*Phoenicurus phoenicurus*) eating only 15 melanics in contrast to 43 typical individuals ($P \ll .01$). Very impressive motion pictures were made of these experiments, with repeated sequences of birds searching tree trunks and eating the conspicuous moths without noticing adjacent protectively colored individuals.

A series of release and recapture experiments supported the visual-predation hypothesis. Known numbers of marked individuals of both types were released in an area, and the percentage of each recaptured later at a light was recorded. The percentage of recovered moths contrasting with their background (melanics in unpolluted and typicals in polluted areas) was considerably lower than the percentage of cryptically colored moths recaptured. For instance, near Birmingham (where the population is 85 to 87 percent melanic) 154 melanics and 73 typicals were marked and released. Later 98 marked moths were recaptured, 82 melanics (53 percent of 154 released) and 16 typicals (25 percent of 64 released). If experimental error is ignored and the survival value of the favored melanics is set equal to 1, the survival value ($1 - s$) of the typical

¹ Probability much less than 1 in 100. This means that a statistical test has indicated that a deviation from the expected frequencies of this magnitude would, on the basis of chance alone, be expected much less than 1 percent of the time. The notation ($P < .02$) means probability less than 2 in 100. Many biologists conventionally consider "significant" any result where the probability of chance alone being responsible is less than 5 percent. An elementary discussion of the use of statistical inference in biology may be found in Simpson, Roe, and Lewontin, *Quantitative Zoology*, 2d ed. Harcourt, Brace & Co., New York.

phenotype becomes $.25/.53 = .47$. Hence, s is equal to $.53$, coincidentally the same value as the percent recovery of the melanics. It is highly unlikely that these results were due to chance alone ($P < .01$). Similar experiments in unpolluted areas have given reverse results. The relationship between the release-recapture experiments and the observations of visual predation is this: The release-recapture work shows that selection occurs; the observations show what the selective agents are.

Fig. 7.3 | Distribution of *Biston betularia*, showing proportion of typicals and melanics. (From Kettlewell, 1958, *Hereditry* 12.)



There have been numerous experiments testing the viability of larvae of the melanic form. Ford, working with the moth *Cleora repandata*, produced backcross broods by mating melanic heterozygotes with typical recessive homozygotes. As in all test crosses, a 1:1 ratio of melanics to typicals was expected, and when the broods were well fed there was no significant deviation from this ratio. However, when the caterpillars were starved every day (put under physiological stress), the ratio found was 51 melanic to 31 typical ($P < .02$), a significant departure from the expected 41.5 of each type. Kettlewell exposed six backcross broods to stress and found 108 melanic survivors as opposed to 65 typical individuals ($P = .01$).

There can be little doubt that, under certain conditions of stress, the larvae of the melanic moths are better able to survive, but the most recent work on the subject indicates that the situation is more complex than was previously thought. In some recent experiments, the expected deficiency of nonmelanic individuals was not found. In other experiments the results showed interbrood heterogeneity: While the offspring from some matings showed a significantly higher proportion of melanics, the offspring from others did not. Furthermore, a study of backcross broods of *Biston betularia* raised between 1900 and 1905 showed no surplus of melanics but rather a slight (not statistically significant) deficiency of them. It is possible that, early in the evolution of industrial melanism, melanic larvae were not physiologically superior and that this superiority, where it now exists, is a rather recent development. Perhaps it was only with the easing of the severe selection against melanic adults that melanic individuals increased sufficiently in populations to permit selective reorganization of the melanic genotype to gain the physiological advantage. Just as selection for modifier genes increased the dominance of the genes producing melanism (Chap. 3), so could selection enhance the effects of the melanic genes on viability.

Kettlewell tried experiments to see whether melanic moths tended to settle on dark surfaces and typical moths on light surfaces. He painted the inside of a barrel with alternate black and white surfaces and then released in it an assortment of moths to see which surfaces they chose. Seventy-seven moths selected the noncontrasting background, while forty-one selected the contrasting background. It has been suggested that this choice is possible because the moth can determine the degree of contrast between the scales around its eyes and the background on which it is resting.

In some areas, melanics are becoming predominant where the

countryside appears to be unpolluted. Two reasons may be given for this. First, pollution is often greater than meets the eye. Smog clouds tend to drift a long distance, and, in spite of its overall green appearance, the countryside may actually have a considerable layer of soot and industrial chemicals. A second reason is that man's other activities alter the countryside, and these changes (e.g., decimation of the predators in an area) may be enough to shift the balance to the melanics.

Although recessive melanics are known, the spread of industrial melanism is due to the spread of dominant genes. The possible reasons for this were discussed in Chap. 3 in relation to the origin of dominance.

Industrial melanism is an example of *transient polymorphism*. Remember that polymorphism is the occurrence in the same habitat of two or more distinct forms of a species in such proportions that the rarest of them cannot be maintained by recurrent mutation. Transient polymorphism is the situation in which the two forms coexist while one is in process of replacing the other. Another example of what is probably transient polymorphism involving melanic moths has been studied in an old woods in Scotland. In these woods, which are essentially free from pollution, one species of moth (*Cleora repandata*) had a population in which 10 percent of the individuals were melanic. At rest on lichen-covered trunks (light background) the typical forms were very inconspicuous. On dark trunks the melanics were inconspicuous, but their protective coloration was (to the human eye) not as effective as the camouflage of the light form. In flight, in the dark woods, the light forms were much more conspicuous. (Three were observed to be taken on the wing by birds in a period during which no melanics were observed to be eaten.) If the advantages were the same both at rest and in flight, progress toward fixation would be more rapid than in the situation described. Nevertheless fixation will still occur unless conditions change.

Microevolution in British Lepidoptera

British lepidopterists have pioneered in studies of other types of evolutionary changes in populations of butterflies and moths. Long-term studies of the gene frequency at a single locus in the scarlet tiger moth, *Panaxia dominula*, have been made by Fisher, Ford, and Sheppard. In the only colony (near Oxford) where the gene in question has been detected, its frequency has been estimated every year since 1939, and population-size estimates have been made for all years since 1941. Three phenotypes occur in the colony: *dominula*

(homozygous for the common allele), *medionigra* (heterozygous), and *bimacula* (homozygous for the rare allele). The frequency of the rare gene was .012 prior to 1928, .092 in 1939, and .111 in 1940. After 1940 it dropped rapidly, leveled off around 1947, and since then has fluctuated between .011 and .037. There seems to be little doubt that these changes are due largely to fluctuating selection pressures. Among other things, the gene is known to affect color pattern, mating behavior, fertility of the males, and larval viability. There has been some controversy over the possible role played by drift in this situation; the degree to which random changes interact with selection has not been determined.

Dowdeswell, Fisher, Ford, and others have made a long series of studies of the frequency distribution of spot number on the underside of the hind wings of the satyrine butterfly *Maniola jurtina*. Over most of southern England the spot distributions are remarkably uniform, in spite of the great diversity of environments. However, the spot distribution in females was found to be sharply different between populations in Devon and Cornwall. Furthermore, the change was found to be extremely abrupt; indeed, in 1956 the border between populations with the two kinds of spot distribution was found to be a hedge which was not a barrier to the passage of individual butterflies. There was no sign of a gradient between the two types; if anything, the difference was greatest at the point of contiguity. In 1957 the border between the two forms was found to be 3 miles east of its 1956 location, and the transition was more gradual. The boundary itself was a strip some 150 yards wide which was occupied by an intermediate population. Spot distributions also have been studied extensively on a small archipelago, the Scilly Isles, off the western tip of Cornwall. Numerous differences were found among the islands, but each island tended to have a characteristic population which remained the same from year to year.

Spot distributions certainly are under strong selective control, although it seems clear that the selective value is manifest in other effects of the genes involved rather than in inconspicuous spot changes. It is difficult to formulate any other explanation for the sharp and mobile border between the Devon and Cornwall types than the shift from one highly integrated gene complex to another. The types seem highly successful, as they extend for a considerable distance in either direction from the border (especially eastward) and are relatively undisturbed by the heterogeneity of the habitats they occupy. It does not seem likely that the environmental factors responsible for the change in selection coefficients actually change as abruptly as the spot frequencies; the reason for the sharp border almost certainly lies in the genetics of *Maniola*.

Polymorphic Land Snails

The microevolution of polymorphic land snails of the genus *Cepaea* has been studied in detail, mostly with the very variable species *C. nemoralis*. The shell of this snail may be yellow, brown, or any shade from pale fawn through pink and orange to red. The lip of the shell may be black or dark brown (normally) or pink or white (rarely), and up to five black or dark brown (rarely transparent) longitudinal bands may decorate it. The genetic basis of many of these characters is fairly well understood, and fossil evidence shows that this polymorphism has existed since before the Neolithic.

The snails have been studied extensively in Europe, where the frequencies of different forms vary greatly from colony to colony. The roles played by selection and drift in accounting for the intercolony differences have been the subject of controversy. Lamotte in France originally claimed that genetic drift accounted for the observed diversity. However, Cain and Sheppard demonstrated that, at least in some English colonies of the snails, selective forces were at work. Near Oxford they found that the frequencies of the different kinds of shells were correlated with the microhabitat of the snails (Fig. 7.4). Collections were made in six main types of habitats: downland beech woods, oak woods, mixed deciduous woods, hedgerows, open areas with long coarse herbage, and open areas with very short turf. Analysis of the frequencies of color and pattern types in these samples showed that they were highly correlated with the color and uniformity of the background. For instance, the percentages of effectively unbanded shells in the five localities with the most and the least uniform backgrounds (uniformity decreases to the right in each series) were as follows:

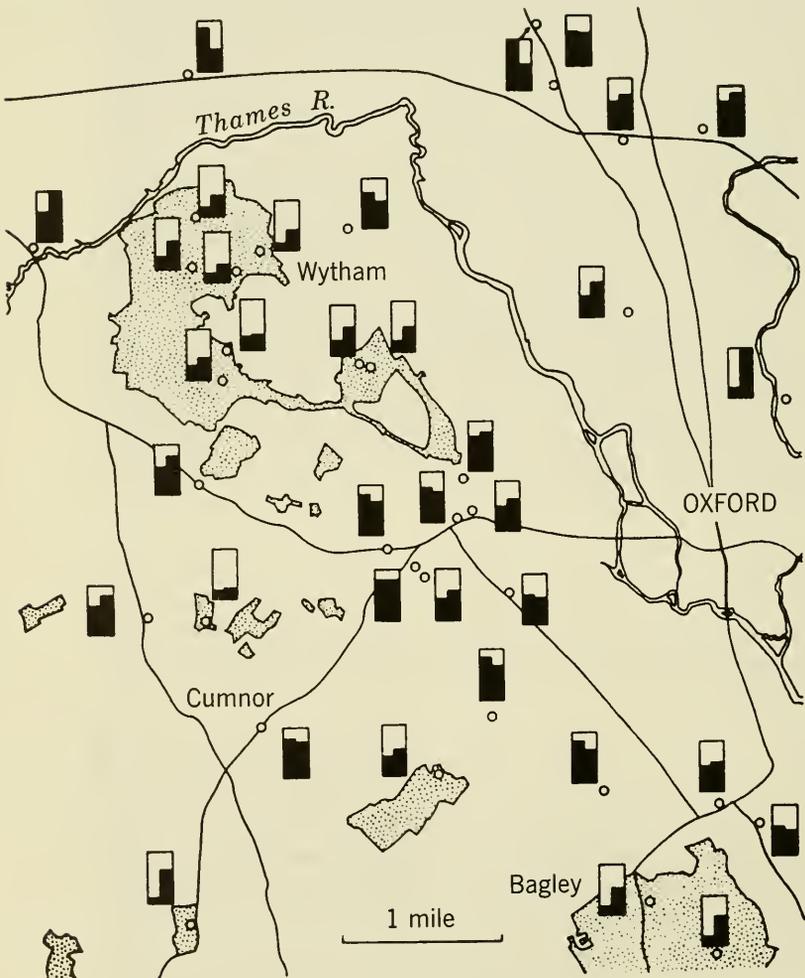
Most uniform	100	100	100	93	79
Least uniform	39	35	34	25	4

The percentages of yellow shells in the five greenest and in the five least green localities (greenness decreases to the right in each series) were:

Greenest	76	64	45	43	41
Least green	17	8	4	0	0

This association between the frequencies of shell types and the character of the habitat suggested that visual predators eating the most conspicuous snails might be a selective agency causing differences among colonies. One such predator is the song thrush, *Turdus ericetorum*. In the summer of 1951 Cain and Sheppard studied a colony of snails in a small hillside bog in Wytham Woods near

Fig. 7.4 | Map of Oxford district showing the correlation of *Cepaea* shell type and environment. In each histogram, the left-hand column represents percent of yellow shells and the right-hand column, percent of effectively banded shells. Woodlands are stippled; all colonies outside of woodlands are in hedgerows or rough herbage. (From Cain and Sheppard, 1954, *Genetics* 39.)



Oxford. Thrushes removed snails from the colony, cracked their shells on stones on a nearby bank, and ate the soft parts. Thus a sample of the predated portion of the population could be obtained by collecting the broken shells from around the thrush anvils, and a sample from the entire population by collecting individuals from the bog. Of 560 individuals taken from the bog, 296 (52.8 percent) were unbanded, while of 863 shells collected around the rocks only 377 (43.7 percent) were unbanded. This significant difference ($P < .02$) indicates that unbanded individuals in this colony were less likely to be eaten than banded individuals.

Similar methods had been used by Sheppard in 1950 to study two other colonies. He found that there was a decrease in the percentage of yellow snails killed as the season progressed and that the rate of decrease appeared to be the same in both localities. There was no evidence that this was due to the thrushes hunting in different areas or to a change in the percentage of yellow shells in the population at large. Apparently the selective value of the yellow phenotype was at least partly a function of the background on which it occurred. Early in the spring, when the woodland floor was predominantly brown, the yellow shells were relatively conspicuous and thus at a selective disadvantage. As the season progressed, the background became greener and this disadvantage lessened. By late April or early May the yellow shells were selectively neutral; by mid-May they were at a selective advantage.

These data indicate a rather strong selective pressure. Because of this, one would expect populations living on uniform backgrounds to be composed only of unbanded individuals, and those living in rough tangled habitats to contain only banded individuals. How then is the polymorphism maintained? Shifts of selective values with the seasons would delay, but not prevent, the removal of the less favored varieties. Interchange of individuals among colonies in different habitats would account for some of the variability, but the range of movement of snails is too small to support this hypothesis for more isolated colonies.

The answer is that there are physiological factors genetically correlated with pattern type. Thus experiments with *Cepaea nemoralis* have shown that unbanded individuals (especially yellow ones) are more heat-resistant than banded individuals. Yellow snails are more resistant to cold than pink snails, and unbanded snails are more cold-resistant than banded snails. These and other similar characteristics indicate that color and banding are subject to strong nonvisual selection because they are associated with important physiological advantages. In some cases, heterozygotes may be expected to be

more viable than either homozygote, so that physiological selection would tend to establish a stable polymorphism. These nonvisual selective forces, interacting with the selection pressures created by visual predation, seem to be responsible, in large part, for the observed pattern of variation in *Cepaea*.

Several other factors may be of importance in some situations. One is predation in which the selection pressure is a function of the relative frequency of the type of individual predated. Certain predators may form search patterns that result in selection against the commonest type in the population, without regard for which type is commonest. This sort of predation pattern could lead to a stable polymorphism. Random processes, once considered to be the prime factor in differentiating *Cepaea* populations, may have relatively minor importance. Undoubtedly drift plays some role in the smaller populations, and it may account for some patterns of variation recorded by Lamotte in France. Recently established colonies may not have achieved equilibrium with their environment, and their composition may be strongly influenced by the genetic information possessed by the snail or snails that established them. This influence of the genetic endowment of the individuals involved in starting a new colony is known as the "founder principle" and is discussed further in Chap. 10.

One of the arguments used to demonstrate that visual selection does not play an important role in determining the characteristics of *Cepaea* colonies is that, in mixed colonies of the two closely related species *C. nemoralis* and *C. hortensis*, the phenotype frequencies of the two snails were uncorrelated. Clarke has satisfactorily explained this by showing that both species respond to visual selection pressure but in different ways. It appears likely that the selective values of various pattern and color genes differ in the different genotypes of the two species. As a hypothetical example, a strongly banded pattern might be at a selective disadvantage in a certain dry habitat. In one species the genes for strong banding may also be involved in producing individuals resistant to desiccation. In the other species there may be no such system. Thus in the same habitat one species may have a population with a large proportion of strongly banded snails (because of heavy selection for resistance to desiccation), whereas the other species may have no banded snails at all (because of the selection against banding). Although the genes controlling the various factors seem to be homologous, they cannot be divorced from their genetic environment. It will be recalled that in Chap. 6 genes were treated as if they were independent entities; results such as these studies of *Cepaea* constantly remind us that this is an oversimplification.

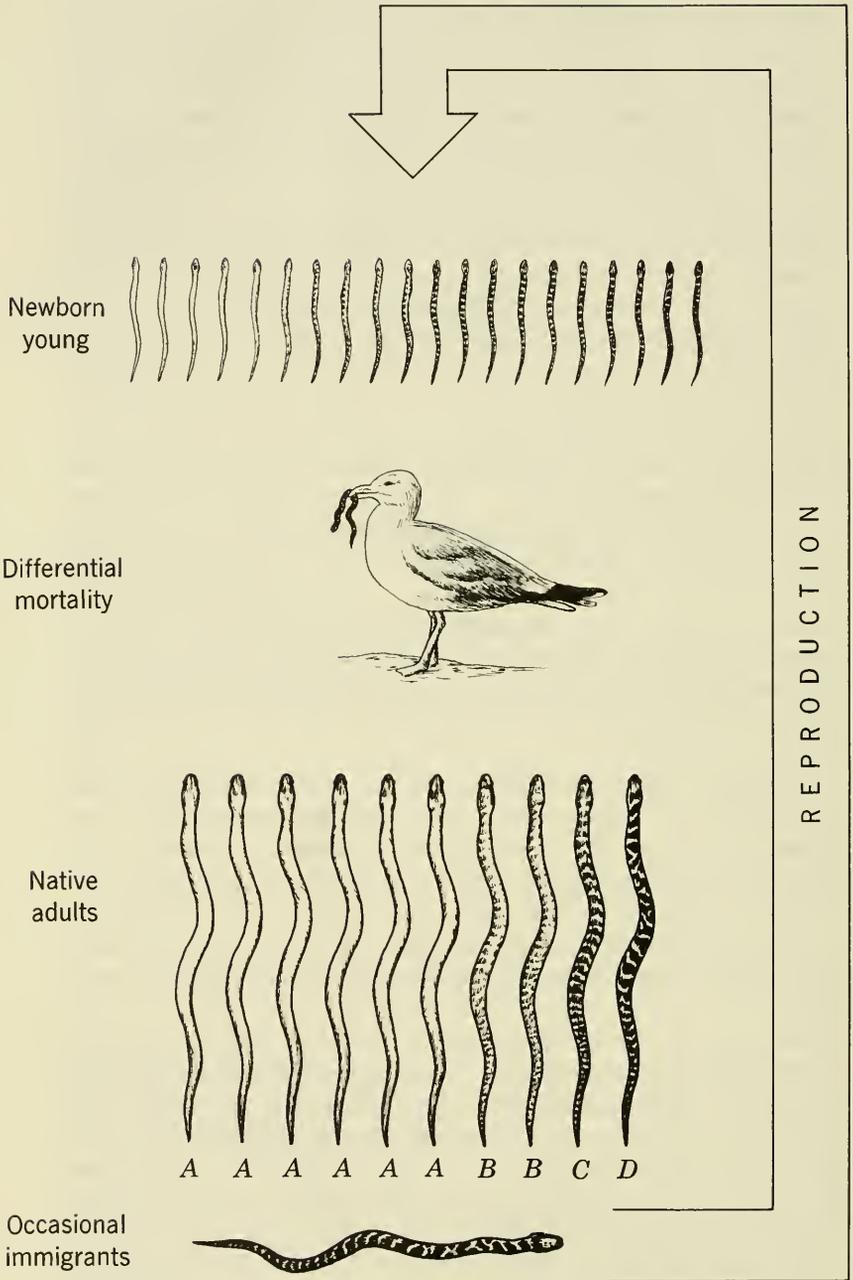
Island Water Snakes

Camin and Ehrlich have studied microevolution in populations of water snakes (*Natrix sipedon*) on the islands in western Lake Erie. The snakes on these islands have variable banding patterns. These have been divided into four classes: A, B, C, D (type A snakes being unbanded and type D snakes being completely banded; see Fig. 7.5). Except in the area of western Lake Erie (and one locality in Tennessee), all known *N. sipedon* populations are made up of type D individuals. Virtually all the snakes taken from the mainland surrounding Lake Erie are type D. On the islands a large proportion of the snakes are of the other types, including numerous individuals that are totally unbanded. The islands have very little inland water, and the snakes are restricted largely to the lake shore. The marginal flat limestone rocks, limestone cliffs, and pebble beaches are the only suitable habitats.

Large samples of adult snakes were taken from the islands, and pregnant females were kept alive until their young were born. The distribution of pattern types in the litters was compared with that of the adults. The distribution of the adult and litter pattern types from one group of islands is shown in Fig. 7.6. In spite of the difficulties of statistical comparison of the cluster-sampled litter population with the random-sampled adult population, it was possible to show a significant difference in banding pattern between the two populations. The percentage of relatively unbanded individuals (A and B) was higher in the adult population than in the litter population.

The observed significant differences between the young and adult populations can be accounted for only by differential elimination of pattern types or by pattern changes in the individual snakes. The evidence is overwhelmingly in favor of the former hypothesis, as snakes kept in the laboratory show no evidence of pattern change in ontogeny. In addition, individuals of all pattern types have been recorded from both adult and litter populations; only the *frequencies* differ.

Evolutionary agencies other than selection are easily disqualified. A high proportion of unbanded pattern types might be maintained by migration from other unbanded populations, but the nearest such population is in Tennessee. To maintain the unbanded genotype by mutation alone would require a mutation rate far above that known for any locus ever studied in any organism, even if it is assumed that color pattern is a single factor trait (which it is not). Nor will genetic drift account for the observed differences. There is no sign that the populations on the islands ever approach a size at which drift is



likely to be a significant factor. Seven collectors once captured 400 snakes on an island in 5 hours, and three collectors at another time took 234 snakes in 4 hours. The juvenile-adult shift is toward unbanded individuals on all the islands studied, indicating a systematic pressure rather than random drift. Therefore, by a process of elimination, selection seems most likely to be responsible for the change in pattern-type frequencies.

To prove that selection has taken place, one does not have to discover its mode of operation. However, it is interesting to speculate on the factors producing the observed situation. To the human eye, unbanded snakes are cryptically colored on the flat limestone rocks of the island peripheries and banded individuals are very conspicuous. It is likely that banding would help to break up the outline of the snakes in their more typical, less uniform swamp habitat. There are visual predators present which will eat snakes (gulls, herons, hawks, etc.), and man kills many with firearms.

The selective force is obviously very strong. If the pattern spectrum is divided arbitrarily into two halves (banded and unbanded), the snakes in the banded half have only about 25 percent of the chance of survival of the unbanded half (s for the banded phenotype equals approximately .75). This raises the question why, with such heavy selection, any banded individuals at all remain in the population. The answer appears to be that migration brings a steady influx of genes for banding into the gene pools of the island populations. Snakes have been observed swimming far from land on many occasions, and the distance from the shore to the islands is not too great to be spanned by migrating individuals. Thus the mainland populations form a reservoir of banded individuals, some of which periodically reach the islands. The resultant interaction between selection and migration has produced a situation unusually amenable to analysis.

Chromosomal Polymorphism in *Drosophila*

Classic examples of microevolution are found in the work pioneered by Dobzhansky on inversion frequencies in some 30 species of *Drosophila* that show polymorphism in chromosome type. This type of

Fig. 7.5 | (see opposite page) Natural selection in water snakes on the islands of Lake Erie, as shown by the differential in frequencies of banding types in young and old snakes.

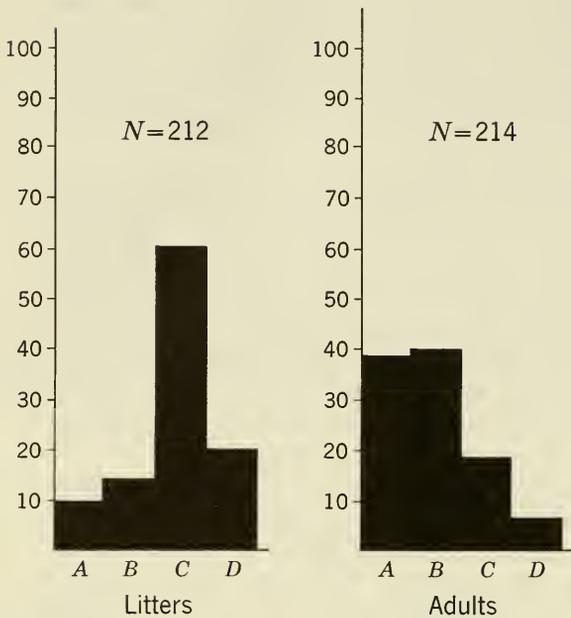


Fig. 7.6 | Comparison of *Natrix sipedon* litters and adults from the Bass complex of islands in Lake Erie. Ordinate, percent in class; abscissa, banding type. A, least banded; D, completely banded. (From Camin and Ehrlich, 1958, *Evolution* 14.)

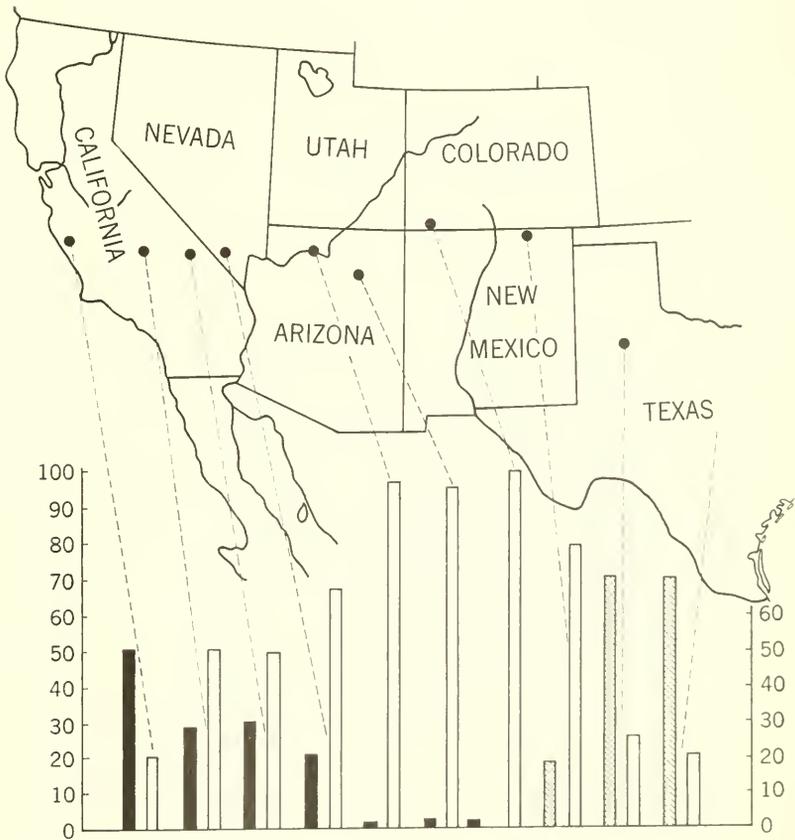
investigation is possible in *Drosophila* because of the giant polytene chromosomes found in the salivary glands of the larvae of these fruit flies. These chromosomes show the close pairing usually associated with the zygotene stage of meiosis. Their size and this somatic pairing make them very useful tools for research. Inversion heterozygotes in *Drosophila* may be detected by examination of the salivary chromosomes for the characteristic inversion loops (Fig. 3.2).

Vernacular names have been given to the different sequences of the banding in the very variable third chromosome of *D. pseudoobscura*. The three most widely discussed inversions in evolutionary literature are Standard (ST), Arrowhead (AR), and Chiricahua (CH). When two different kinds of chromosomes occur in the same population, three types of individuals will be present: two inversion homozygotes and one inversion heterozygote. For example, where

only Standard and Chiricahua chromosomes are present, the three different kinds of individuals are the two homozygotes (ST/ST and CH/CH) and the heterozygote (ST/CH). The homozygotes can be distinguished only by progeny testing or careful study of the pattern of banding, while the heterozygote is easily recognized by the inversion loop.

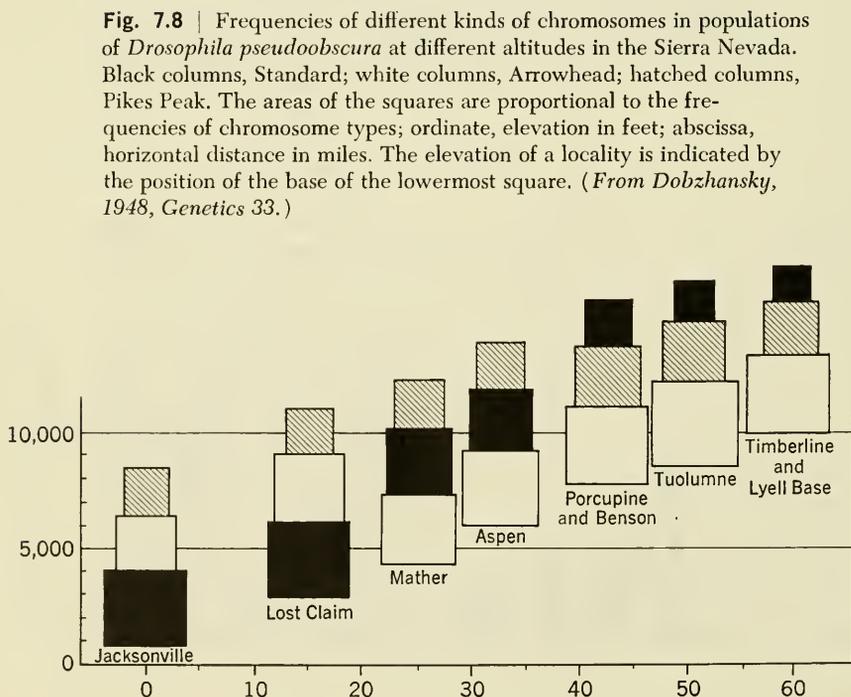
The different kinds of chromosomes in *D. pseudoobscura* have different geographic distributions, apparently because of their varying adaptive values in different habitats. Figure 7.7 shows the geo-

Fig. 7.7 | Frequencies (in percent) of different kinds of chromosomes in populations of *Drosophila pseudoobscura* in southwestern United States. Black columns, Standard; white columns, Arrowhead; hatched columns, Pikes Peak. (From Dobzhansky, 1947, *Evolution* 1.)



graphic variation in frequencies of three different chromosome types in a series of localities transecting the southwestern United States. The chromosomal frequencies also change with altitude, as can be seen in Fig. 7.8, which shows the proportions of three different types at different elevations in the Sierra Nevada of California. Superimposed on this geographic variation is a seasonal variation in frequency. For instance, in the Sierra Nevada, the Standard gene arrangement is commonest at lower elevations, becoming progressively less common with increasing altitude. Arrowhead, on the other hand, has a frequency that is positively correlated with altitude, being greatest in the subalpine zone (about 10,000 feet) and least at the base of the mountains (850 feet). However, in general, Standard chromosomes tend to increase in frequency as the season progresses, whereas Arrowhead chromosomes tend to decrease in frequency. Thus the frequencies of these chromosomes in late summer populations at high elevations tend to approach the frequencies of spring populations at lower elevations.

These changes may best be explained as the result of rather strong selection pressures. Dobzhansky has tested this hypothesis in



a series of experiments in which he reared *D. pseudoobscura* in population cages. His experimental populations were started with known frequencies of chromosome types, and then he repeatedly sampled them to determine what changes in frequency, if any, had occurred. He found that in populations maintained at 16.5°C there was no change in the chromosome frequency. However, in populations maintained at temperatures above 20°C the frequencies change, usually arriving at an equilibrium point at which all the original types are still present but in frequencies quite different from the initial ones.

The data from one population cage experiment are given in Fig. 7.9. The cage colony was constituted on March 1, 1946, with individuals selected so that the population had 10.7 percent ST and 89.3 percent CH chromosomes. Throughout the remainder of the year the percentage of ST chromosomes increased, at first rapidly and then more slowly, until at the end of the year (some 15 generations later) it had leveled off at about 70 percent. This pattern of increase and the establishment of an equilibrium strongly suggested a selective advantage of the structural heterozygotes (ST/CH) over both homozygous types. From the standpoint of population genetics, this would be comparable to overdominance for fitness at a single locus. Similar results could be obtained, however, by negative assortative mating (unlikes mating). This latter possibility was ruled out by taking a sample of eggs from the population cage and raising the larvae under optimum conditions so that almost all survived. The different genotypes proved to be present in the expected Hardy-Weinberg frequency, demonstrating that mating was random and that differential fecundity or fertility was not involved. Samples of adult flies taken from the population, however, showed the following deviations from Hardy-Weinberg frequencies:

	ST/ST	ST/CH	CH/CH
Observed number	57	169	29
Expected number	78.5	126.0	50.5
Deviation	-21.5	+43.0	-21.5

These results, along with the establishment of equilibrium at about 70 percent, clearly indicate that there is differential elimination of the homozygous types between the egg and adult stages. It has been demonstrated that in eggs laid by wild flies there is no significant deviation from the expected Hardy-Weinberg frequencies but

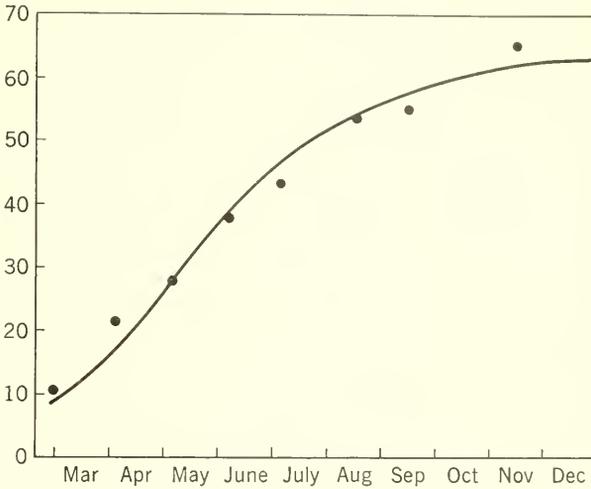
that in adult males heterozygotes are significantly more common than one would expect in a population in Hardy-Weinberg equilibrium.

An extreme case of selective advantage of structural heterozygotes occurs in a population of *Drosophila tropicalis* where there are two common chromosome sequences. Both types of structural homozygotes die early in development, and only the heterozygotes survive to breed. Although only half of the zygotes formed are viable, this population flourishes.

Long-term changes in inversion frequencies have been reported. In California before 1941 only four Pikes Peak (PP) chromosomes were found among 20,000 chromosomes studied. In 1957 PP chromosomes were found in all 10 localities sampled in the state, the mean frequency being about .08 (a 400-fold increase). This increase occurred at the expense of CH chromosomes. The agent behind the change is not known, but it is almost certainly selection. Since 1941 the PP chromosomes have continuously predominated in populations found on the eastern slope of the Rocky Mountains and in Texas. The California increase could not be due to migration from this reservoir of PP chromosomes, as geographically intermediate populations in Arizona and Utah did not change significantly between 1941 and 1957. The source of selection pressure is not known, but widespread drought and increasing smog are two of the more obvious factors which might be considered.

The above is only a brief outline of some of the highly interesting work done on the genetics of natural populations of *Drosophila*. There can be little doubt that the different gene constellations or supergenes in the inversion chromosomes (remaining together as rather stable blocks because of the effect of the inversions in suppressing the results of crossing-over) have different adaptive values under different conditions. Many examples of chromosome frequency changes correlated with environmental changes have been elucidated. Less success has attended attempts to determine when advantages and disadvantages occur in the life cycle. Describing the exact nature of these adaptive changes also has proved difficult. It is impossible to reproduce natural conditions in the laboratory, and very little is known about the life history and ecology of the various *Drosophila* species. Studies of *D. pseudoobscura* and *D. persimilis* breeding in "slime fluxes" (yeast- and bacteria-infected sap exudations on trees) in the Sierra Nevada, and laboratory studies of many species, have yielded valuable information. Much more work is needed. The complexity of the problem may be appreciated by considering the factors determining pupation site in

Fig. 7.9 | Frequency of Standard-type chromosomes (in percent) in different months in a single population cage. (From Dobzhansky, 1947, *Evolution I.*)



D. melanogaster, a characteristic known to be of considerable selective importance in laboratory populations. Among other things, temperature, humidity, moisture content of the medium, larval density, and length of larval period all affect the place in which the larva chooses to form the pupa. The ecogenetics of *Drosophila* will supply a fertile field for research for a long time to come.

Examples from Man

As one might expect, natural selection plays an active part in shaping the genetics of populations of our own species. An outstanding example of this is the selective control of the frequency of the so-called "sickle-cell" gene. Individuals who are homozygous for this recessive gene show distortion of their erythrocytes, accompanied by severe anemia and general, serious and painful disability. The condition is usually fatal. Heterozygous individuals may be detected by the distortion (sickling) of their red blood cells, which occurs when the oxygen concentration of the blood is reduced. Sickle-cell heterozygotes, however, apparently are protected to some degree against malaria and thus are favored by selection in malarial areas. Allison found that the frequency of sickle-cell heterozygotes was

higher in adults than in young children, indicating that this genotype is at a selective advantage. The advantage of the heterozygotes is about of the magnitude theoretically necessary to maintain the frequency of the sickle-cell gene (about .20). This advantage appears to be responsible for the maintenance of a balanced polymorphism at the sickle-cell locus throughout much of Africa, in spite of the very low viability of the homozygous recessives.

Glass and his coworkers studied the frequencies of genes controlling a number of characteristics (blood groups, mid-digital hair types, etc.) in a "Dunker" religious community in Pennsylvania where the population was less than 100 individuals. The gene frequencies at several loci deviated strongly from those found in the surrounding population and in the population from which the group was originally derived (western Germany). Drift is tentatively considered to be responsible for these deviations. Interestingly, there was little or no deviation at different loci known to be under rather strong selection (e.g., Rh).

The one known example of selection against heterozygotes involves the Rh locus in man. When an Rh negative mother (double recessive) is fertilized by an Rh positive sperm, the resultant heterozygous fetus runs a high risk of death due to antigenic incompatibilities between it and the mother. This selection is apparently compensated to some degree by a tendency of families with Rh problems to have repeated pregnancies until a number of children are raised successfully. This, however, is not sufficient in itself to account for the continued presence of the polymorphism in the human population. The gene-frequency equilibrium point, although no longer at .5 (see Chap. 6, selection against heterozygotes), is still unstable. It is possible that migration has helped to prevent fixation in the human population as a whole. Fixation of the Rh positive genes may be approached in some subpopulations, and fixation of Rh negative in others. Intermixing of these populations may then reestablish the polymorphism.

Pasture Plants

Unfortunately botanists have found few situations in nature that are amenable to the sort of analysis discussed in the foregoing cases. Kemp in southern Maryland studied pasture seeded with a grass-legume mixture and subsequently partitioned. One half was protected from livestock, while the other was used for grazing. Three years later, plants of bluegrass (*Poa pratensis*), orchard grass (*Dactylis glomerata*), and white clover (*Trifolium repens*) from each half of the pasture were dug up and transplanted to an experi-

mental garden with uniform conditions. It was found that the grazed half yielded a high proportion of genotypes that produced a low prostrate growth. Those from the ungrazed half were erect and showed no tendency to procumbency. This clearly shows that there was a heavy selection in these populations for adaptive growth forms.

Mimicry of Flax

An extremely complex system of mimicry has been found in the genus *Camelina*, plants of the family Cruciferae. Various types of *Camelina* occur as weeds in fields of cultivated flax (*Linum*, family Linaceae). It has been hypothesized that, as the cultivation of flax became more efficient, *Camelina* was subjected to a series of increasingly severe selection pressures. For instance, there was a selective advantage for the *Camelina* seeds to remain with the flax seeds during the winnowing process so that they would be sown along with the flax. Plants that grew were from seeds with the correct aerodynamic properties; the other seeds were never planted. The more thorough the winnowing, the stronger the selection pressure. This selection produced *Camelina* seeds that mimicked flax seeds, not in appearance but in distance blown by a given amount of wind. Similarly, selection favored the production of tall spindly *Camelina* plants that would not be shaded out of existence in the dense stands of cultivated flax. Such selection has produced flax mimics not only in the genus *Camelina* but also in other plants, including *Spergula* and *Silene* (Caryophyllaceae). It should be noted that the evidence for selection here is more inferential than in the preceding examples.

Disruptive Selection in Mimetic Butterflies

When selection favors two or more phenotypic modes, it is said to be *disruptive*. Experimental work with bristle numbers in *Drosophila* has shown that a pattern of selection in which extremes are favored over intermediates can produce a bimodal population with increased variance. Apparent examples of the operation of disruptive selection in natural populations are found in arrays of mimetic butterflies. For instance, the widespread and much-studied African swallowtail butterfly *Papilio dardanus* (Fig. 7.10) has a wide variety of mimetic females, although the males never show mimicry. Presumably this is because “normal” color pattern and wing shape of males are important in making them sexually acceptable to the females. Several different forms of the females commonly occur in the same locality, each one accurately mimicking a different distasteful species of butterflies.

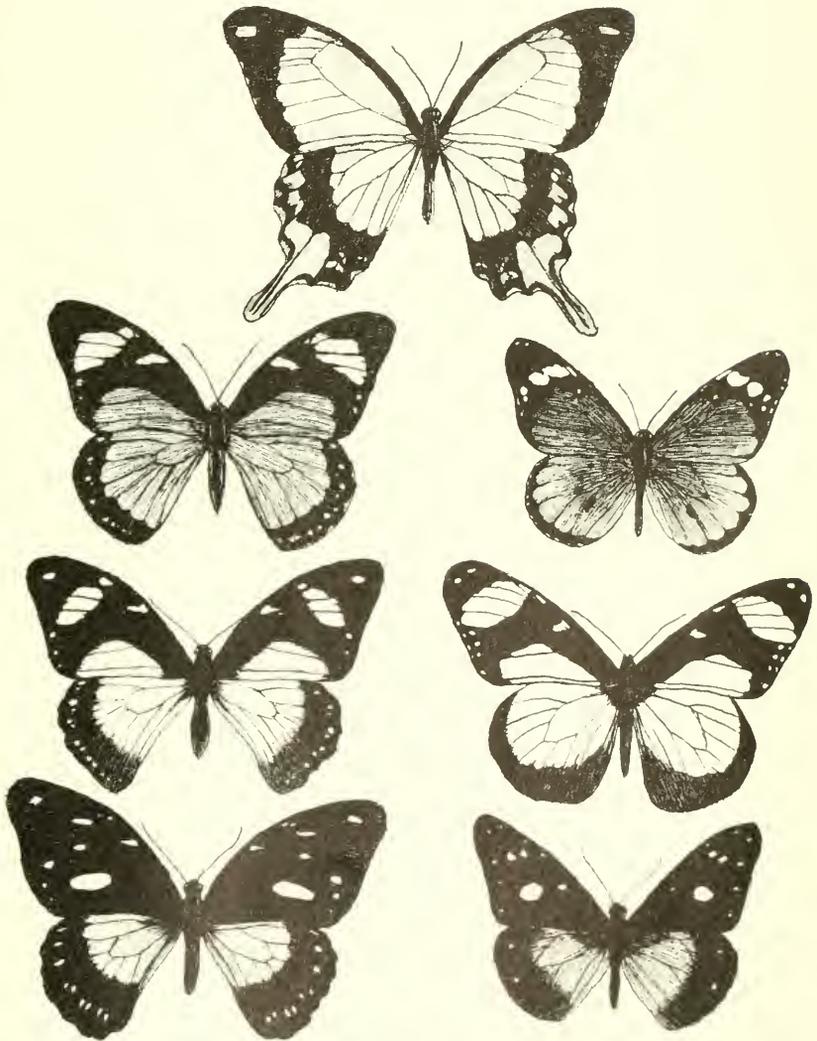
There is evidence (summarized by Sheppard, 1961) that certain combinations of characteristics give the best mimicry of different models and are at a selective advantage. Others do not look like any model and are at a disadvantage. In at least some cases, selection seems to have reduced the possibility of the production of poorly protected combinations by increasing the linkage between the loci concerned in producing the pattern. This permits linked groups of loci (supergenes) to be selected as a unit and the superior combinations to be preserved. (The phenomenon is quite comparable to the holding together of gene constellations in *Drosophila* populations by inversions.) In mimetic butterflies disruptive selection may also operate through the accumulation of modifier genes which further perfect the resemblance. This is supported by hybridization experiments in which supergenes are transferred to a new genetic environment. There they do not produce phenotypes that mimic the model as precisely as before.

Resistance to Antibiotics and Insecticides

No discussion of evolution would be complete without mention of the response of some organisms to man's attempts to reduce their population size or eradicate them. Striking and important examples of the response of natural populations to human endeavors center around the phenomenon of resistance. Indiscriminate application of insecticides to large areas of the earth's surface has constituted a very potent selective force. In the vast majority of cases, the large population sizes of pest insects have contained sufficient residual variability to allow these insects to develop strains resistant to virtually all the compounds that the ingenuity of the organic chemists can produce. The chemists are, of course, limited severely by the survival requirements of nontarget organisms such as man. Even so, there is considerable evidence that man and his domesticated plants and animals have not escaped damage from powerful synthetic pesticides.

It is interesting to note that insects have met the challenge in diverse ways. There have been examples of behavioral resistance in which insects no longer alight on sprayed surfaces and of many kinds of physiological resistance in which the penetration or action of the insecticide is prevented by various mechanisms. Parallel to insecticide resistance has been the appearance of strains of microorganisms that are highly resistant to antibiotics. This has been caused by the overuse of these antibiotics by well-meaning doctors when other treatments might suffice or be better. So far, the increase

Fig. 7.10 | Mimicry involving an African swallowtail butterfly, *Papilio dardanus*. Upper butterfly, male *P. dardanus*; right-hand column, three danaine butterflies (*Danais chrysippus*, *Amauris niavius*, and *Amauris echeria*); left-hand column, forms of female *P. dardanus* mimicking the danaines. (After Punnett, 1915, *Mimicry in Butterflies*, Cambridge University Press.)



of these organisms has been countered largely by a scramble to find new chemical weapons to use against them, rather than by the application of methods that are biologically more sophisticated and infinitely more beneficial in the long run.

Such alternative approaches are well known. Some resistant insects prove to be less viable than their nonresistant relatives when they exist in an environment free of insecticide. In these cases, moratoria on insecticide applications would give time for the forces of natural selection to return the populations to their previously susceptible condition. By intelligent use of insecticides at critical moments, a reasonable level of control may be attained with a minimum danger of creating resistant strains (a danger maximized by "broadcast" application). Where moratoria are not feasible, multiple applications of many different poisons may make it impossible for the population simultaneously to develop resistance to all. Because it is not possible, however, to affect one member of a community without affecting the entire ecosystem, this approach is fraught with unforeseen dangers. It is well known that accumulation and concentration of chemical poisons take place in members of food chains. And, if the target organisms are not eliminated, their predators and the predator's predators may be severely affected.

In addition to this, many pestiferous insects are more readily and economically controlled by interfering with their biology in a non-chemical way than they are by the application of insecticides. For example, the draining of swamps in which mosquitoes breed, the introduction of predators to control imported pests, the releasing of multitudes of sterilized males to compete with wild males for mates, and the dissemination of laboratory-grown pathogens have all proved to be effective. Similarly, classical methods of antisepsis will often deal with highly resistant microorganisms much more effectively than newer and costlier antibiotics.

LABORATORY POPULATIONS

The term artificial selection pertains to man's control of the genotypes that contribute to the gene pool of succeeding generations. Artificial selection is carried out by both plant and animal breeders and also by scientists wishing to study the effects of selection in the laboratory. It may have a purposiveness directed at a single trait, another respect in which it differs from natural selection, which operates on all the phenotypic characters affecting fitness and has no purpose. Nevertheless, even under the most carefully controlled laboratory conditions, natural selection still operates in conjunction

achieved with the first selected line. When selection in this line was relaxed, there was only a slight regression in bristle number. In addition, after some 85 generations in the continuously selected line, further response was achieved.

Artificial selection often produces rapid results at first; then a plateau is reached at which further progress is difficult or impossible, or the viability of the line reaches such a low ebb that either selection must be discontinued (relaxed) or the line is lost. Generally, if selection is discontinued before a plateau is achieved, the relaxed lines regress toward the control level. If selection ends after the population has reached a plateau, there may be little or no regression. Continuous selection of a population that has achieved a plateau often will not produce appreciable results for long periods. However, if selection is continued long enough, progress once again may be made.

One reason for these phenomena presumably is the balance between artificial and natural selection. Although the details are neither clear nor uniform, it appears that natural selection must create a balanced system in which the best possible relationship of characteristics determining fitness is produced. In other words, fitness must be maximized. The available evidence seems to indicate that, especially in animals, a high degree of heterozygosity in the genotype produces a high degree of physiological fitness. It also seems likely that extremes of quantitative characters often are produced by a high degree of homozygosity at the loci concerned. Therefore artificial selection for high or low bristle number may well be countered by natural selection for fitness if the bristle-number extremes are produced by homozygosity at a series of loci.

One might make a crude analogy to an airplane. One could try to improve the airplane by making the motor more powerful, but this would do little good if increased speed would tear off the wings. This problem might be solved by strengthening the fuselage or the structural members of the wings, but this would not help if it made the airplane too heavy to get off the ground. In an organism, as in an airplane, a viable balance of all the various factors that ensure successful functioning must be attained. There is a limit to how much one factor alone can be modified before the "working combination" is seriously disrupted.

Lerner (1954) has produced a mathematical model which might explain the establishment of a plateau below the maximum level of expression of a character under selection. He bases this model on a system in which there is an obligate level of heterozygosity determining fitness. Crossing-over can convert potential genetic varia-

bility to free genetic variability, permitting further selection without loss of fitness. The whole situation can then be looked at in terms of shifting states of balance. Strong selection at one or a few loci places a stress on the balanced genotype. After the expression of the character has been shifted a certain distance, this stress will result in loss of fitness, followed by either extinction or the attainment of a new balanced state. If selection is relaxed before either of these events, the line tends to regress to the control level.

A tremendous volume of literature on artificial selection has accumulated, as work on economic problems (improvement of domestic animals and plants, studies of resistance, etc.) has produced information of great value. Much of our understanding of such diverse problems as the origin of dominance, the integrative properties of genotypes, and the efficacy of selection under varying conditions has been the direct or indirect result of investigations of such prosaic matters as egg laying in chickens, the weight of swine, rust resistance in wheat, the yield of corn and cotton plants, and the productivity of bovine mammary glands. The reader wishing a well-organized introduction to this vast and complex subject is referred to Lerner (1958).

GENETIC HOMEOSTASIS

At this point it would be well to mention an important steady-state property of mendelian populations, the often-observed tendency of populations subjected to directional selection to regress toward the original mean. Lerner has called this phenomenon *genetic homeostasis*. A mendelian population has characteristics above and beyond those of its component individuals. For instance, it would be meaningless to say that an individual is in Hardy-Weinberg equilibrium. Populations tend to retain a genetic composition that produces a maximum number of individuals with a high degree of fitness. In short, there is selection in favor of maintaining the balanced "maximum-fitness" genotype. This is essentially a stabilizing selection operating against deviant individuals. A genotype showing a high degree of fitness is adapted not only to the environment in the classical sense but also to its genetic environment, that is, the gene pool in which the genotype occurs. In other words, the frequency and distribution of genes in the population help to determine the fitness of any genotype within the population. One may summarize the subject of genetic homeostasis by saying that selection organizes the gene pool of a population in such a way that its various components are coadapted and produce a maximum number of highly fit genotypes. Well-

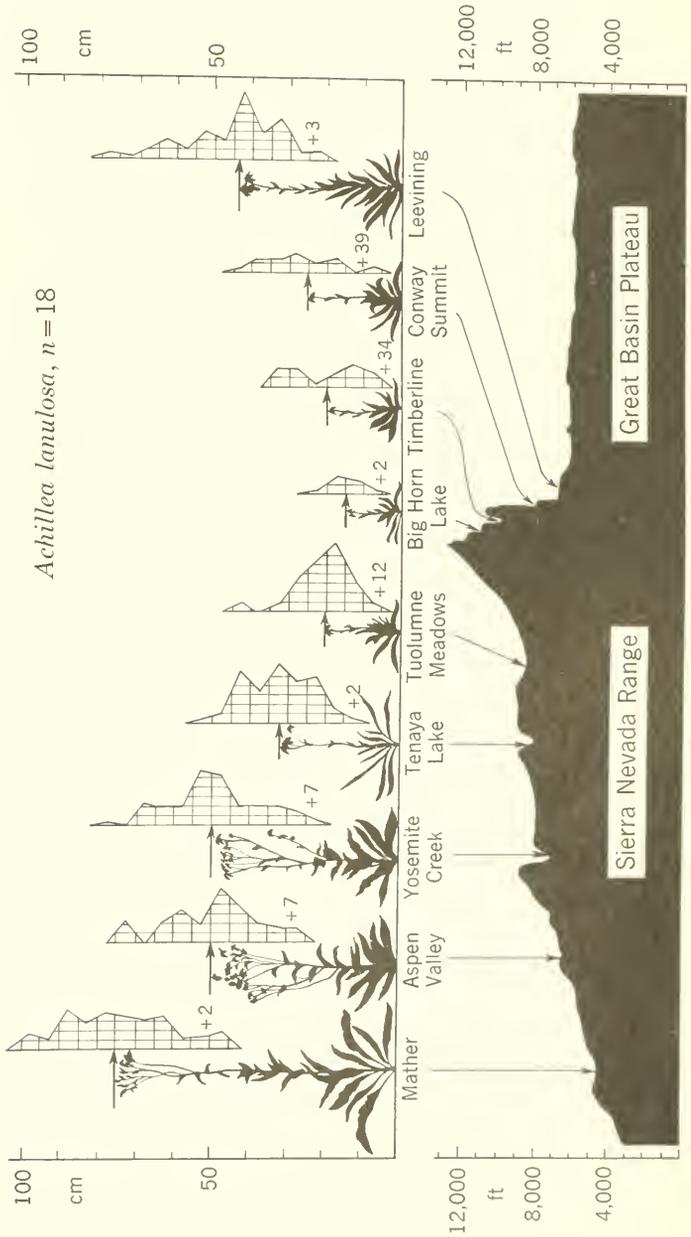
integrated genotypes are "winning combinations," and, as demonstrated in the experiments of Mather and Harrison, selection to change them in order to meet a particular environmental stress is countered by selection favoring the retention of the successful integrated unit. The unusually sharp break between the two kinds of *Maniola jurtina* populations mentioned earlier in this chapter may represent the border between two such highly integrated units. Permanent directional progress is made only when the selective forces operating in favor of change are able to overbalance those operating in favor of retaining the successful combination. There is much to indicate that the phenomenon of overdominance with respect to adaptive value (selective advantage of the heterozygote over homozygotes) is one of the fundamental mechanisms contributing to genetic homeostasis in most animals and many plants. However, the term includes all methods of genetic autoregulation of populations.

GENETIC ASSIMILATION

When individuals of the plant *Achillea lanulosa* (Compositae) were transferred from localities at various altitudes in the Sierra Nevada to an experimental garden at sea level, the plants did not all grow to a uniform height (Fig. 7.12). In the now classic experiments of Clausen, Keck, and Hiesey, plants from the higher elevations were much shorter than those from lower elevations. Since all were grown under roughly identical conditions, those from the higher localities were shown to be genetically dwarfed; that is, they had genotypes that tended to produce short individuals regardless of the environment in which they developed. However, when low-altitude plants were divided (giving genetically identical stocks) and these divisions were grown at sea level and at mid-altitude, the mid-altitude individuals were shorter than their identical twins at sea level. In other words, the low-altitude genotype interacting with mid-altitude environment developed into a plant similar to those with a mid-altitude genotype. Such forms, in which a phenotypic change simulates a genotypic change, have been termed *phenocopies*.

There seem to be many situations in nature where such phenocopying occurs, although rigorous demonstrations of the phenomenon generally are lacking. For instance, many butterflies have spring generations that are smaller and darker than their summer generations, the difference presumably being due to the seasonal variation in the environment. However, in more northern parts of their range, the butterflies have only a single summer generation which is small

Fig. 7.12 | Heights of plants obtained from various altitudes in the Sierra Nevada when grown at Stanford in uniform garden. Illustrated plants represent a population of about 60 individuals. The frequency diagrams show variation in height within each population. Horizontal lines separate class intervals of 5 cm according to the scale on the ordinate, and the distance between vertical lines represents two individuals. Numbers to the right of frequency diagrams indicate nonflowering plants. Arrows point to the mean of each distribution. (From Clausen, Keck, and Hiesey, 1948, *Carnegie Inst. Wash. Publ. No. 581.*)



and dark and resembles the spring generation in southern localities. In the northern populations the individuals are presumed to have genotypes that produce the dwarfing and darkening. Although the critical transfer experiments have not been done, the greater constancy of the northern forms in the face of environmental changes supports these presumptions.

How can one account for the development of the high-altitude races of plants, the high-latitude races of butterflies, and similar phenomena? The environmentally produced changes cannot be directly transmitted to succeeding generations; the Lamarckian idea of the inheritance of acquired characters has long been discarded. A method by which such acquired characters could, *through selection*, become assimilated in the genotype has been proposed by Waddington and is supported by a series of experiments by Waddington and others. This *genetic assimilation* is best explained by a brief example.

A strain of a wild-type laboratory population of *Drosophila melanogaster* was subjected to a high-temperature shock during the pupal stage. A few of the adults emerging from the treated pupae showed an abnormal break in the veins of the wings (the “crossveinless” phenotype). Only those individuals showing the acquired crossveinless phenotype were used as parents for the next generation. After more than a dozen generations, the frequency of crossveinless flies from treated pupae was over 90 percent, and a few crossveinless flies began to appear from untreated pupae of the selected strain. Crossing these latter flies produced strains that had a high frequency of crossveinless phenotypes in the absence of heat shock. It would appear that an acquired character had become heritable. Actually, in this experiment, selection seems to have favored those genotypes that had a low threshold for producing the favored phenotype. Eventually the threshold was lowered to a point at which no heat shock was necessary to move the developmental sequence to the crossveinless end point. Similar results have been obtained in studies of other characters in *Drosophila*.

It is most important to remember that the range of possible viable phenotypes is genetically determined and that selection may alter this range so that phenotypes that previously *could* be induced by the environment become genetically fixed as the *only* possible result of gene-environment interaction. Selection may favor phenotypic plasticity where butterflies face different environments in succeeding generations. It may operate to produce a highly canalized development leading to a “winning” phenotype in situations where the

environmental stresses are highly similar, generation after generation. Developmental aspects of genetic assimilation are discussed in Chap. 4.

ADJUSTMENT TO THE ENVIRONMENT

The diverse and ingenious ways in which organisms meet the problems of survival and reproduction are inferential evidence for the great efficacy of natural selection. This adjustment to the environment is usually called *adaptation*, but for reasons discussed in the final chapter this ambiguous term is avoided whenever possible. One need not go into the details of the evolution of the bird's wing, the giraffe's neck, the vertebrate eye, the nest building of some fish, etc., as the selective origins of these and other structures and of behavioral patterns may be assumed to be basically the same in outline as those, such as industrial melanism, which have already been discussed. Even a slight advantage or disadvantage in a particular genetic change provides a sufficient differential for the operation of natural selection. Thus the property of light sensitivity of unicellular organisms provides a starting point for the development, through selection, of the highly complex eyes found in vertebrates, insects, and certain mollusks.

The old antievolutionist argument that the vertebrate eye would be useless unless present in its modern complexity is nonsense. Many organisms with less complex and less specialized photoreceptors put them to good use, and it is easily seen that even a human being would be better off with a non-image-forming photoreceptor (one which gave information only on the amount of light present) than without any photoreceptor at all. Similarly, any non-detrimental variation in a highly edible butterfly, tending to make it look more like a sympatric distasteful species, puts this deviant at a selective advantage.

The presence today of all degrees of refinement in the phenomena of mimicry and protective coloration argues strongly against the hypothesis that such resemblance must be virtually perfect before it is effective. Experimental evidence at hand indicates that less perfect copies of certain distasteful model butterflies also enjoy a degree of protection, though perhaps not as great as that of the more nearly perfect mimics. It is interesting to note that mimetic forms of various butterflies generally do not occur in areas where the models are absent, indicating that a selection pressure favoring mimicry is required to prevent regression to the wild type. Even

such difficult-to-explain phenomena as the evolution of social behavior in bees are now yielding to investigation (e.g., Michener, 1958). This problem is complicated because the unit of evolution is the colony, not the individual. (Most members of a hive are non-reproductive.) Selection in honeybees consists largely of differential reproduction of colonies rather than of individual genotypes.

Loss of features when they no longer confer selective advantage is one of the most widely observed evolutionary phenomena. Selectively neutral characters presumably are rare. The eye, very useful to most animals, may become an easily injured, infection-prone liability to a cave fish. Body hair, which at one time protected human beings against cold and injury, became a happy hunting ground for lice with the invention of clothing.

SUMMARY

In this chapter has been given a series of examples of studies of evolutionary changes within populations, chosen for the diversity of approach and material. In addition, inferential evidence bearing upon the efficacy of the selective process is discussed. It becomes apparent that, although it is relatively simple to demonstrate changes, it is much more difficult to partition the responsibility for the changes among the various evolutionary forces. The problem is especially complicated because of complex interactions within genetic mechanisms and developmental systems. Most difficult of all to document is the role of genetic drift. It is nearly impossible to "prove" the efficacy of drift in natural populations, as one can always hypothesize the existence of some as-yet-to-be-discovered selection pressure that could account for the observed phenomena. Indeed, there have been several cases, especially in snails, where differences at one time attributed to the action of drift have been demonstrated to be caused by selection. However, the inevitability of drift, together with results of studies of gene frequencies in small populations of *Drosophila*, both in nature and in the laboratory, leads one to believe that drift, interacting with the other pressures, can be an important evolutionary force. Extensive studies still are needed on a wide variety of organisms before broad generalities on the relative contribution of the various forces can be made with real confidence.

REFERENCES

- Allison, A. C. 1959. Metabolic polymorphisms in mammals and their bearing on problems of biochemical genetics. *Am. Naturalist* 93:

- 5-16. Summary paper with extensive bibliography. (Allison, 1956, is the central reference on sickle-cell anemia.)
- Camin, J. H., and P. R. Ehrlich. 1958. Natural selection in water snakes (*Natrix sipedon* L.) on islands in Lake Erie. *Evolution* 12: 504-511. This is the principal paper on selection in *N. sipedon*.
- Clarke, B. 1960. Divergent effects of natural selection on two closely related polymorphic snails. *Heredity* 14: 423-443. The bibliography lists most of the important papers on *Cepaea*, including Sedlmair (1956).
- Dobzhansky, T. 1951. *Genetics and the Origin of Species*. Columbia Univ. Press, New York. The classic work on genetics and evolution in animals. A "must" for every serious student. The early work on chromosomal polymorphism in *Drosophila* is summarized here.
- . 1959. Variation and evolution. *Proc. Am. Phil. Soc.* 103: 252-263. The bibliography of the paper will introduce the reader to more recent evolutionary literature on *Drosophila*. The number of the *Proceedings* containing this paper has many articles of interest to the evolutionist.
- . 1960. Evolution and environment. In Sol Tax [ed.], *Evolution After Darwin*, Univ. Chicago Press, Chicago, vol. 1, pp. 403-428. Contains a good discussion of drift in *Drosophila*.
- Genetics and 20th Century Darwinism*. 1959. Cold Spring Harbor Symposia on Quantitative Biology, vol. 24. See especially Lamotte's paper on *Cepaea* for his side of the drift-selection controversy, and the interesting papers by Carson, Dobzhansky, and Mayr.
- Lerner, I. M. 1954. *Genetic Homeostasis*. Wiley, New York. Highly theoretical and well worth reading (partly out-of-date).
- . 1958. *The Genetic Basis of Selection*. Wiley, New York. This is a comprehensive source on artificial selection.
- Michener, C. D. 1958. Distinctive type of primitive social behavior among bees. *Science* 127: 1046-1047. Evidence of the origin of worker-queen differentiation.
- Sheppard, P. M. 1959. *Natural Selection and Heredity*. Hutchinson, London. An excellent little book covering much of the material in this chapter.
- . 1961. Some contributions to population genetics resulting from the study of the Lepidoptera. *Advances in Genet.* 10: 165-216. See this for further information and references on the Lepidoptera examples and a guide to the literature on disruptive selection.
- Stebbins, G. L. 1950. *Variation and Evolution in Plants*. Columbia Univ. Press, New York. The plant equivalent of Dobzhansky's *Genetics and the Origin of Species*. Summary and references for all plant examples in this chapter—and much more.
- Waddington, C. H. 1961. Genetic assimilation. *Advances in Genet.* 10: 257-293. Summary and discussion of the work and literature.

8

genetic systems I

The cytogenetic mechanisms discussed in the preceding chapters provide for the production of offspring sufficiently similar to the parental types that, barring unduly rapid environmental change, the group survives. They provide also for sufficient variability that, when the environment changes gradually, the organisms change also and thus survive. The persistence of an organism depends on the proper balance between these two phenomena: fitness for the immediate environment and fitness, in the long-range view, for whatever changes take place in the environment in the course of time. It has already been pointed out that the genetic mechanism of most organisms provides for storing variability in unexpressed form, as well as for regulating the release of this variability. Diversity of means of storage and release of variability, which, like other traits, must be under genetic control, implies that these means change in the course of time; in other words, they evolve. The collective ways in which the amount and type of new gene combinations are controlled may be referred to as the genetic system. Thus one may speak of the evolution of genetic systems, which is the evolution of those mechanisms effecting and affecting variability.

In this chapter the various sorts of genetic systems found in plants and animals will be described. In the following chapter several specialized genetic systems which have become important in certain organisms will be discussed in greater detail. Elucidating the interrelationships and ultimate significance of these systems and integrating them into evolutionary theory are among the greatest challenges facing the modern evolutionist.

Although the actual course of evolution of genetic systems is not known, there has been considerable speculation as to the main lines that it may have taken. Here genetic systems will be discussed, starting with the simplest and concluding with the most complex. This does not indicate an evolutionary sequence. The simplest biological phenomena often can be interpreted as reduced to this state from something more complex.

GENETIC SYSTEMS IN MICROORGANISMS

Transformation

Transformation is a phenomenon involving genetic change in some bacteria. For example, studies of strains of pneumococcus bacteria (*Diplococcus*) have shown that the DNA extracted from a strain

with a particular trait can transform a strain lacking this trait into one that possesses it. Virulence in pneumococcus depends on the polysaccharide envelope of the bacterial cell. If a nonencapsulated, nonvirulent strain is grown with purified DNA extract from a virulent strain, virulent cells with a capsule will develop in the culture. Thus the DNA determines the polysaccharide coat. Transformation has been achieved for a large number of traits, and there is an equal probability of transformation in either direction. Linkage of traits in the DNA material also has been found, since in experiments involving differing traits double transformations occur more frequently than would be expected for independent events.

Recombination in Viruses

A rather complex relationship exists between certain bacteria and bacterial viruses known as bacteriophages. A single phage consists of two major structural elements, a tail and an enlarged (often hexagonal) head. A protein coat surrounds a DNA core. When a bacterial cell is infected, the phage attaches itself by the tail to a specific receptor site on the cell wall. During the course of the next few minutes the DNA leaves the phage and enters the bacterium. Within the bacterium, the phage multiplies and the cell eventually breaks open (undergoes lysis), releasing the new phages. During the period of multiplication, new phage DNA is synthesized and new phage protein formed, the result being a hundred or so new phages of the same type as the infector. The original infector has, with its DNA, managed to preempt the synthetic processes of the bacterium and turn them to its own use, that of duplicating the phage.

Since the beginnings of their scientific study, phages with many different traits have been found. It is possible to infect a culture of bacteria with a mixture of phages with different traits. When this is done, recombination of traits occurs in the phage progeny. With some characteristics, recombinants appear with equal frequency; with others there is a reduction in the number of recombinants, indicating that linkage exists between the genetic factors affecting the traits. What has happened then is recombination of the genetic material of the phage in the host cell of the bacterium. Radioactive-tracer studies have shown this genetic material to be the DNA. Such evidence, taken with that from experiments with bacterial transformation, in which the transforming agent is DNA, shows that in these forms the genetic material is DNA. It also shows that, in the

absence of sexual reproduction, recombination of the genetic material can occur during the synthetic processes producing more DNA.

Transduction

The bacteriophages discussed previously are virulent, and the host bacterium is killed as the cell undergoes lysis. However, there are also temperate phages capable of establishing a sort of symbiotic relationship which need not result in lysis of the host bacteria. These are called lysogenic bacteria (for example, *Salmonella*). The noninfectious stage of the temperate phage is called prophage. Reproduction of the prophage and bacterium is so regulated and integrated that there is no detrimental effect. Occasionally, however, at a rate of 10^{-2} to 10^{-5} per generation, lysis of a bacterial cell occurs and the phages released are able to adsorb on other bacterial cells.

In the course of DNA synthesis, the prophage may incorporate some of the genetic material of the host bacterium. If the prophage should convert to the phage stage, the host will lyse. When the phage is released and infects a new bacterium, it carries with it genetic material from the former host. This in turn has a chance of being incorporated into the genotype of the recipient bacterium, a phenomenon known as transduction. The genetic material transferred usually is not a single genetic factor but groups of factors. Transduction thus is a special sort of genetic recombination, again involving not the sexual process but an infectious process. The phage acts as a vector for infectious transfer of bacterial genes. Viruses, including phages, with RNA are also known, but their study is just beginning.

Sexual Recombination in Bacteria

Sexual recombination also occurs in bacteria. Tatum, Lederberg, and others have shown that in *Escherichia coli* conjugation of cells may take place. Genetic material is transferred from one cell to another, one of the conjugating cells being a recipient cell, the other a donor. Recombination of traits from different strains has been studied in some detail. The process of conjugation can be interrupted by separating the cells by agitation, and it can be shown that the amount of genetic material transferred is proportional to time. The genetic material of the bacterium behaves as if it were on a single chromosome. Linkage maps of this chromosome have been

made. Spontaneous breakage of the transferring chromosome also occurs. Hybrids of *E. coli* and *Shigella dysenteriae*, as well as of *E. coli* and *Salmonella typhimurium*, have also been studied.

Microbial Genetics and Evolution

The occurrence and significance of such phenomena as transformation, transduction, and sexual recombination in many microorganisms in nature are unknown. The extent to which these processes are distributed among microorganisms also is largely unknown. It is obvious that population genetics of these forms is apt to be rather different from that known in larger organisms. The possibility of some sort of "genetic" relationship between very small replicating systems and larger organisms is only beginning to be studied. Most of what has been observed in this category has been termed infection. At this level, of course, the distinction between genetics, infection, and development breaks down. Many viruses, particularly the RNA viruses of plants (which may be transmitted by sucking insects), produce morphological effects similar to those controlled by chromosomal genetic material.

Some strains of *Paramecium* are known as killer strains, since they secrete into the medium in which they grow a substance poisonous to sensitive strains of *Paramecium*. It has been found that killer-strain individuals contain particles of DNA called kappa particles. In order for kappa particles to be maintained in the cell, the genotype of the strain must contain a dominant nuclear factor *K*. In the course of asexual fission the kappa particles reproduce in such a way that all members of the resulting clone contain the particles. Should the rate of cell reproduction exceed that of particle reproduction, *KK* individuals lacking kappa may appear. Such individuals are not killers, but sensitives, and can regain kappa particles only by contamination from a cellfree suspension of killer animals. They are not able to initiate the formation of particles despite their chromosomal genotype.

Sexual reproduction in *Paramecium* involves conjugation of cells and cytoplasmic exchange, during which kappa particles may or may not be transferred. In the cross between *KK* and *kk* individuals, the resulting *Kk* paramecia will be killers if conjugation has lasted long enough that kappa particles are transferred. Paramecia that are homozygous for the recessive factor *k* may inherit kappa particles in the cytoplasm, but these are lost during subsequent generations of fission.

It is obvious that there is a resemblance between this situation in

Paramecium and the more variable ones in bacteria and their associated viruses. From the kappa-particle inheritance to the inheritance of differences in chloroplasts in plants is but a short step. Chloroplasts are bodies with genetic continuity in the cytoplasm which may mutate to a different form or color. The variant may then continue to reproduce the altered form. Portions of a plant may be affected, producing a mosaic of yellowish or white areas interspersed with the usual green. Chloroplasts are inherited in the cytoplasm of the egg but not through the pollen. Some mutants are initiated and maintained by chromosomal gene changes; some are initiated by nuclear change but continue in the absence of the chromosomal factor; finally, there are plastid mutants which appear to be independent of nuclear control. If other cellular components, such as mitochondria, could be studied as easily as plastids, perhaps they would be found to exhibit the same behavior. It should be noted that virus infection of plants may simulate the same sort of mutations of plastids that occur spontaneously or can be induced by irradiation with X rays or ultraviolet light.

This digression into what is usually termed cytoplasmic inheritance will serve to illustrate the difficulty of drawing distinctions between nuclear and cytoplasmic inheritance and between genetic recombination and infection at the level of cell and microorganism. It should be reiterated that the evolutionary significance of such phenomena as cytoplasmic heredity and infection is largely unknown, but their importance can scarcely be doubted. There are indications from work with both plants and animals that what have been regarded as genetic traits are the effects of viruses or that genetically determined characters are mediated by the presence of viruses. When these processes are considered in relation to the role of microorganisms in the ecosystem or community, very important relationships may emerge. Bacteria and other microorganisms may be involved in the transmission of genetic information in the ecosystem in diverse ways, in addition to their role as reducers or decomposers.

GENETIC SYSTEMS OF OTHER ORGANISMS

The basic features of the genetic systems in the vast majority of living organisms are the same. There is an alternation of haploid and diploid phases, the result of alternating haploisis (meiosis) and diploisis (syngamy). In the few viruses and bacteria that have been studied, the genetic system is simpler and more variable. Only in

the blue-green algae (Cyanophycophyta) is recombination unknown. In their rather specialized habitats the blue-green algae seem to be a successful and widespread group. One is led to suspect that they must have some mode of genetic recombination at present not detected. Perhaps it is related to that in bacteria, and possibly it involves viruses as well.

Sexuality and Diploidy

The phenomenon of sexual reproduction is so widespread and its evolutionary significance is so immediately apparent that most biologists place its origin very early in the evolution of life. In many groups of plants and animals, every individual produces both female and male gametes. Even so, cross-fertilization is frequently the rule. Where the organisms are not hermaphroditic, the nature of sexual development may be affected by environmental factors such as light intensity, photoperiod, temperature, chemical composition of the medium, etc. It would seem that, in the course of evolution, this rather variable sex determination is replaced with more precise control systems or, at least, have such imposed upon them.

The first question to be considered is the origin of diploidy. It is usually assumed that diploidy has high selective value because of the opportunity it provides for the storage of recessive genes and thus of variability. There seems to be little doubt that diploidy also provides necessary buffering in development and thus greater freedom from environmental effects. One would expect that this would be increasingly important as the complexity of organisms increases. Fusion of free cells occurs spontaneously in tissue cultures and cultures of unicellular organisms with such frequency that it is not difficult to imagine the origin of syngamy. Perhaps the resulting buffering effect in the diploid cell would have immediate selective value.

In many instances, fusion of cells leads to instability which is resolved by division. It was suggested in Chap. 1 that in early protoorganisms a sort of protorecombination might have taken place. Since a great many of the simpler algae and fungi are haploid for most of their lives (the only diploid cell being the zygote which immediately divides), one might conclude that recombination occurring with division immediately after syngamy had high selective value.

Sexual reproduction is a complicated process having many components that must be integrated in function. The stages in its evolution are not known. With the completely unstable genetic

mechanism of protoorganisms, each "individual" would presumably have been different from all others. Fusion would occasionally combine complementary "genotypes," and this may have been the foundation of a selective advantage of fusion. On the basis of the speculations presented in Chap. 1, it may be suggested that the stabilization of the genetic mechanism of early protoorganisms involved loss of superfluous genetic material or its assumption of new functions; association of the DNA nucleotides with protein molecules to form chromosomes; and the restriction of gene function so that expressivity became less variable and control more precise. The variety of genetic systems in plants and animals includes many bizarre and unusual phenomena. Their common features suggest that, in nearly all instances, the advantages of diploidy and of recombination have been combined. Meiosis of the nuclear genetic material and fusion of cells are combined in a life cycle of varying degrees of complexity. This combination appears to have arisen independently in a number of different ways in plants and animals.

Stebbins has concluded that the wide occurrence of haploidy in the flagellates and filamentous algae is a result of their short and simple development and their rapid rate of reproduction, which makes the establishment of complex gene-developmental systems less important. The selective value of buffering and long-term storage of recessives would also be less important. With increasing complexity have come increased length of the developmental period and concomitant lengthening of the life cycle. The build-up of integrated gene complexes with ontogenetic buffering and genetic homeostasis is thus favored, and the diploid state has high selective value.

Diploid Life Cycles and Alternation of Generations

Some groups of Protozoa are predominantly diploid, with complex mating behavior effecting recombination. Certain groups of algae, notably some of the brown algae (Phaeophycophyta), diatoms (Bacillariophyceae), and some green algae (Siphonales), also are diploid during most of their life cycle. Meiosis results in the production of haploid gametes. The Metazoa, of course, have the same sort of genetic system.

Presumably this diploid life cycle arose independently several times from organisms with a predominantly haploid cycle. In addition, there also arose in plants and in fungi life cycles that involve alternation of generations. In these forms there is a regular cycle of haploid individuals that produce gametes and diploid individuals that produce asexual spores. Gametogenesis takes place by mitosis.

Sporogenesis involves meiosis and resultant recombination. In some algae and fungi, the alternating generations are isomorphic (indistinguishable morphologically).

With increasing complexity, there seems to be a tendency for reduction of the haploid gametophyte generation in proportion to the diploid sporophyte. Thus in most ferns the gametophyte is a small thallus, usually a centimeter or less in diameter, whereas the sporophyte may be quite massive. In gymnosperms and flowering plants the gametophytic generation is reduced to relatively few cells (the pollen grain is a male gametophyte) and the sporophyte is the conspicuous stage. In mosses, on the other hand, the gametophyte is the conspicuous stage. It is perhaps better to regard the bryophytes (mosses and liverworts) as a specialized offshoot of ancient terrestrial plants and not on the main phyletic line of the vascular plants.

No process comparable to alternation of generations is known to occur in animals, with the possible exception of some Sporozoa. In other animals the haploid phase is represented by the gametes only. The Coelenterata have the so-called alternating generations of medusae and polyps, but these are morphologically, not cytologically, different.

The fungi, as a group, have a number of distinctive genetic systems of interest here in so far as they shed light on the selective forces involved in the evolution of genetic systems. These highly specialized organisms are poorly understood cytogenetically. The occurrence of somatic crossing-over and systems of multiple-mating types attests to the selective advantage of recombination. The water molds, Phycomycetes, which are filamentous and without cross cell walls, build up numerous haploid nuclei in the common cytoplasm of the filaments or hyphae. Within the mycelium of these fungi genetically different populations of nuclei may arise, producing the so-called heterokaryotic state.

Mushrooms and toadstools (Basidiomycetes), the most complex of the fungi, and some of the sac fungi (Ascomycetes) show an interesting parallel with the evolution of diploidy in plants and animals. Haploid mycelia, often with specific mating types, develop in the soil. The cellular hyphae of different mycelia, coming into contact, may fuse. Eventually a mycelium results in which each cell has two haploid nuclei—one from each haploid mycelium—which do not fuse until reproductive structures are formed. This special sort of diploidy is known as dikaryosis. Just as diploidy is associated with developmental and structural complexity in plants and animals,

dikaryosis appears to be requisite for great morphological complexity in the fungi.

Recombination and Genetic Systems

To recapitulate, when the many different genetic systems that have evolved are compared, certain common features stand out. Except where simple unicellular structure and rapid reproduction are found, it seems that diploidy has had selective value. Simple, rapidly reproducing organisms have great flexibility for these reasons alone, and mutation rate is the chief source of variability. Such organisms as yeast and *Paramecium* are exceptions. With increased complexity, integrated combinations of genes controlling the developmental pathways are built up. The diploid state (or dikaryosis) provides the necessary buffering. It also permits the storage of variability in the form of recessive genes and of polygenes in balanced systems. Meiosis and syngamy produce the release of variability as new gene combinations.

It is usually assumed that, without environmental change, most new gene arrangements will have lower selective value than existing ones. Thus a certain wastage of zygotes occurs in addition to the wastage of gametes in sexual reproduction. Nevertheless, the wastage in diploid outcrossing organisms is surely much less than that in haploid organisms. The wastage of recombinants in the bacteria-bacteriophage systems is probably very much higher still. This suggests that there has been selection, also, for genetic systems that not only provide for buffering and the build-up of gene complexes and for storage and gradual release of variation but also reduce the wastage of biological materials and thus energy in the course of evolution. (It must not always be assumed, however, that what appears to be "wastage" is disadvantageous.)

Reduction of Recombination

In nearly all genetic systems, modifications that reduce the amount of recombination have occurred. The result is reduction of wastage, as immediate fitness is increased. It has been generally assumed that the most primitive organisms were asexual, and these modifications are usually referred to as *reversions to asexuality*. Since recombination mechanisms have been found in nearly all organisms and since the ability to effect recombination appears to be a fundamental

property of DNA, this is perhaps an inappropriate designation. Sexuality and diploidy probably evolved relatively early in time. Reduction of recombination takes many forms. In unicels there may be absence of sexual reproduction. In the more complex multicels, reduction of recombination may occur as a result of reduction or elimination of crossing-over, assumption of specialized mating systems, inbreeding, self-fertilization, or loss of sexuality. As Stebbins has pointed out, such modifications are found most often in pioneer forms whose populations experience pronounced fluctuations in size. Under conditions of environmental change, such forms can exploit newly opened habitats through rapid duplication of closely similar genotypes. Often there is reduction in body size and in developmental complexity, as well as increased reproduction rate. Cytogenetic mechanisms affecting recombination are discussed in Chap. 9; systems of mating will be considered here.

Since the amount of recombination is affected by selection, the genetic system of nearly any organism is always in a state of flux. The simultaneous existence of variable mechanisms producing increase and decrease in recombination provides a system buffered against short-term environmental change but able to respond to long-term change. Most of the mating systems are bivalent in this sense or are combined with other mechanisms to produce this bivalence.

Mating Systems and Recombination

The basic type of mating against which the others may be compared is random mating. If like individuals are more apt to mate than would be expected by chance, the system is said to be positively assortative. If unlike individuals mate more frequently than expected by chance, the system is negatively assortative. The nature of reproductive mechanisms in plants and animals makes it unlikely that truly random mating ever occurs. It is difficult to specify precisely the extent of deviations from randomness. Mating systems do not, of course, fall into discrete classes, and any population in nature may show several of the arbitrarily delimited types. Furthermore, mating-system type is affected by such things as selective advantage of particular characters and population size.

As pointed out in Chap. 6, random mating results in constant gene frequency with no change in variability. With selection, gene frequencies change, but the variance of the population and genetic correlation between relatives are little affected. As the population size reaches lower limits, the effects of sampling error lead to genetic

drift. Small population size also leads to inbreeding and a deviation from randomness of mating when the species is considered as a whole.

Inbreeding Systems

Inbreeding may be referred to as positive genetic assortative mating for it increases the chance of mating by organisms with like genotypes. Mating systems leading to inbreeding result in the break-up of a population into smaller groups that only rarely exchange genetic information. The heterozygosity of the population is reduced as fixation occurs in the subgroups. Genetic variance is increased in the population as a whole unless there is strong selection for particular homozygotes. Morphological and physiological mechanisms leading to inbreeding are common in plants. Their degree of restriction ranges from facultative self-pollination to obligate self-fertilizing types with cleistogamous flowers (see Chap. 9).

Detailed studies by Stebbins, Grant, and others have shown that the degree of restriction of recombination in plants is closely correlated with their growth form and habitat. As is discussed in Chap. 9, populations often combine genetic systems that have opposite effects on recombination. Herbaceous plants, which have short generations and thus more recombination, tend to have low chromosome numbers. Perennial plants with longer generation time have higher chromosome numbers. Plants that occur in ecological communities usually thought of as "closed," i.e., those in which most offspring do not survive to maturity, tend to have genetic systems that promote genetic recombination. Oaks are an example. On the other hand, pioneer organisms, wherever they may occur, are members of "open" communities. In order for zygotes to survive, they must have the proper genotypes; there is no time for the organism to experiment with recombinants. It is not surprising, therefore, to find that plants of desert regions, grasslands, and cleared areas in the tropics generally have genetic systems that result in reduced recombination.

When inbreeding is imposed on populations that are usually outbreeding, a loss of fitness referred to as inbreeding depression occurs. The relationship between fitness, heterozygosity, and outbreeding is not well understood as yet. Many groups of plants have successfully employed inbreeding as a mating system for long periods of time with only occasional outbreeding. It cannot be assumed that all organisms necessarily maintain developmental and genetic homeostasis through outbreeding and heterozygosity.

Outbreeding Systems

Negative assortative mating is the mating of unlike individuals with a frequency greater than that expected under random mating. The differentiation of sexes in animals generally assures that self-fertilization cannot occur. In addition, most animals have developed systems of varying degrees of complexity which influence the degree of outbreeding. These are briefly discussed in Chap. 5. There is evidence that genetically controlled components of dispersal affect outbreeding and gene flow in insects. Behavioral mechanisms in both invertebrates and vertebrates often operate to reduce the frequency of nearest-neighbor matings. In *Homo sapiens* such ethological mechanisms reach their extreme.

A diversity of mating types affects recombination in microorganisms. Dispersal mechanisms in plants, as in animals, make nearest-neighbor matings less frequent than would be expected if chance alone determined the pairings. Flowering plants have floral pollination mechanisms which also function to determine the amount and type of recombination. It is commonly assumed that there has been a general evolutionary trend from open flowers, composed of numerous parts, which are pollinated more or less indiscriminately, to flowers with the few stamens and stigmas positioned in such a way that pollen is precisely applied to and withdrawn from the body of the pollinator.

Other plants have physiological incompatibility systems that ensure outbreeding. Since reproduction in the higher plants requires pollination by male gametophytes, as well as fertilization by male gametes, the process can be interrupted at many steps. A common system has a multiple allelic basis, the gene for incompatibility, *S*, existing in many states. The various possible genotypes affect pollination so that pollen tube growth is very slow in a style with the same allele of *S* as is found in the male gametophyte. Other more complex incompatibility systems have been studied in the flowering plants.

SUMMARY

Recombination is a basic property of nucleic acids. Viruses and bacteria show simple, variable genetic systems producing recombination with great wastage of recombinants. In flagellates and filamentous algae, the life cycle may be predominantly haploid with a diploid

zygote that divides by meiosis immediately after formation. From this situation, diploid life cycles and cycles with alternation of generations seem to have evolved independently a number of times in plants and animals. In the fungi, specialized mechanisms producing recombination and diploidy have developed. The selective advantage of diploidy and sexuality seems to lie in their provision for developmental buffering and the storage and release of variability, as well as in the reduction of the amount of gamete and zygote wastage. Recombination may be modified in multicellular organisms by mating systems leading to predominantly inbreeding or predominantly outbreeding individuals.

REFERENCES

The references are given at the end of Chap. 9.

9

genetic systems II

As has been seen in the consideration of evolutionary change in the quantitatively measured characteristics of organisms, recombination is a factor more significant than mutation as a source of variability. Since the genotype of an organism evolves under conditions determined, among other things, by the constitution and organization of its chromosomes, the investigation of the chromosomal mechanism is particularly important in evolutionary studies. The basis of variation lies in the genetic code, but changes in the structure and number of the chromosomes bearing the code may directly or indirectly affect the amount of recombination of the code.

Genes are defined here as those regions of the chromosome between the closest points of crossing-over. They are therefore the smallest units of recombination in higher organisms. Larger units of recombination may involve particular portions of the chromosome in which crossing-over or its effects are restricted; these may be called supergenes. There are whole chromosomes, e.g., the sex chromosomes, which behave as recombinational units. The entire nucleus is the unit of transmission and recombination in organisms that reproduce asexually (some kinds of apomictic organisms).

The cytological mechanisms that determine, in part, the amount of recombination in a population are an important aspect of the genetic system of the organism. Often they are visible in the phenotypic appearance of the chromosomes, the karyotype. However, structural and genic changes may occur without any obvious changes in the karyotype. The cytological mechanisms about to be discussed usually are referred to as *aberrations* or *mutations*. Since they appear to occur with measurable frequency in most organisms and since they become characteristic of entire populations or taxonomic groupings of animals and plants, they are best thought of as aspects of the cytogenetic repertoire of organisms. As with any other characteristic, they arise spontaneously and are maintained by selection as long as they confer an advantage.

MEIOTIC DRIVE

In a variety of organisms, all alleles of a locus do not have an equal chance of inclusion in the gametes. This phenomenon has been called meiotic drive, since one allele is favored or driven. It is part of the genetic system, as it reduces the amount of recombination. Cytogenetic mechanisms that affect the distribution of alleles have been studied in some detail in *Drosophila melanogaster*. It is obvi-

ous that, with meiotic drive, an allele might increase in a population even if it had a deleterious effect. In such a case, selection presumably would result in the accumulation of factors that reduce the effect of the gene responsible for meiotic drive. It is possible that meiotic drive might result in the spread of a beneficial gene. The extent to which this has occurred in nature is unknown.

CHANGES IN CHROMOSOME STRUCTURE

The usual cytological mechanisms of haploid and diploid organisms already have been described. The student should review the material on chromosome behavior in Chap. 3 before reading the following discussion of derivative genetic systems, those in which cytological changes operate to increase or (more often) to decrease what usually is thought of as the standard amount of recombination.

Inversions

Chromosome inversions are structural changes that can lead to supergene formation. Here a section of the chromosome is in reverse sequence as compared with a standard. Upon synapsis in meiosis, one of the pairing chromosomes must become twisted, and a characteristic loop is formed in an organism heterozygous for an inversion. As has been seen, crossing-over and recombination are profoundly affected. Single crossing-over within the loop of a paracentric inversion (one that does not include the centromere) leads to the formation of a dicentric chromatid and a chromosome segment without a centromere. At anaphase I, these appear as a bridge connecting the daughter nuclei and a fragment which does not move to the poles (Fig. 3.2). Depending upon the number of the cross-overs and the chromatids involved, all or a portion of the gametes are unbalanced genically and therefore nonviable. Thus the genes within the inversion remain together as a supergene that is the length of the inversion. The gametes containing recombinations of the genetic code within this supergene may not survive, or the resultant zygote may be inviable. One way or the other, recombinants are not produced.

In a long inversion, more than one crossover may occur; the results depend upon whether the same or different chromatids are involved in the second as were concerned in the first. If the same chromatids are affected, the second crossover will compensate for the first and there will be no detectable cytological effect. If a new pair cross over, a double bridge and two fragments are found at anaphase I.

Various other configurations may occur, depending upon the number and position of crossovers. Should an inversion be pericentric (i.e., include the centromere), a supergene will be formed, but the inversion is not detectable by a bridge and fragment as with paracentric inversions.

The evolutionary effect of inversions depends upon whether they are relatively long or short. Short or moderately long inversions frequently are found "floating" in populations of plants and animals where they appear spontaneously. They reach high frequency when they become associated by chance with a favorable combination of genes. The genus *Drosophila* provides numerous examples of this (see Chap. 7). It has been found that, concomitant with inversions regularly associated with certain chromosomes, there may be marked increase of crossover frequency in other chromosomes. Thus the effect of the inversion must be to form supergenes rather than simply to reduce the amount of recombination. For if selection were operating to reduce recombination generally, the increase in crossover frequency in other chromosomes probably would not be observed.

When individuals from geographically isolated populations or from different species are crossed in the laboratory, they are often found to differ by very long inversions (perhaps of an entire arm). Several such inversions prevent the formation of fertile offspring; thus they may be thought of as isolating mechanisms. Their importance in nature is not as clear-cut as that of shorter inversions. It seems clear that spontaneously occurring inversions might rather rapidly differentiate karyotypes of populations that become separated. When they occur with regularity, as in *Drosophila* and *Sciara*, they seem to be playing a special role.

Reciprocal Translocations

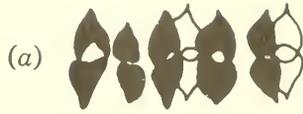
Reciprocal translocations likewise may function in setting up supergenes in populations heterozygous for the change. If the interchanged segments are short, usually only two competent combinations can be formed in a heterozygous organism. Should crossing-over occur between the centromere and the point of interchange, only two of the four chromatids associated at any one place may be separated as competent combinations (see Chap. 3). With more than one interchange between the same two chromosome pairs, rings of more than four chromosomes are formed at meiosis. In some organisms, such as the plant *Rhoeo* and several species of *Oenothera* (evening primrose), all the chromosomes exchange segments and all are

united, forming one great ring at meiosis (Fig. 9.1). Directed alternate disjunction may occur in these specialized types. Since synapsis is very precise, homology determines that each chromosome has its own place in the ring which can be changed only by further structural changes.

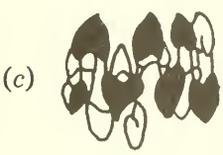
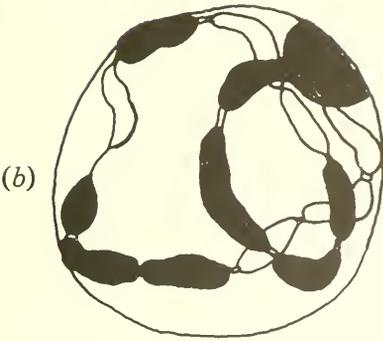
When more than one interchange has occurred, a new type of chromosome segment is set apart. The homologous chromosome arms are called pairing segments, and the portion of the chromosome between the point of interchange and the centromere is the interstitial segment. The new area, which is associated with the central part of a chromosome with which it is not paired terminally, is the differential segment which may or may not include the centromere. In this area, crossing-over occurs rarely; when it does, the interchanges are modified, and the arrangement of the chromosomes or the number of rings may change. The study of reciprocal translocations requires careful and painstaking analysis of crosses between many different individuals so that the homology of the pairing segments can be determined.

Floating translocations occur in a large proportion of diploid plants (e.g., *Campanula*, *Paeonia*), as well as in scorpions and cockroaches. In many invertebrate animals translocations are involved in the sex chromosome mechanism. When an XX female and XO male chromosome mechanism exists, one of the autosomal chromosomes may become translocated to an X. This leaves one of the autosomes with its homologue as part of a modified sex chromosome (which may be called a neo-X). This autosome subsequently behaves as do Y chromosomes or heterochromatic regions of chromosomes in general. It is said to have become heterochromatized and is called a neo-Y. Apparently this process has occurred in several grasshoppers and mantids, as well as in other invertebrates. Presumably some readjustment of gene function takes place. The genes in the autosome translocated to the X are now present in half their previous number in the males. This is because heterochromatization presumably results in their loss in the homologous autosome (the neo-Y). Multiple sex-chromosome mechanisms (with several X's and

Fig. 9.1 | (see opposite page) Chromosome behavior in two species of *Oenothera*. *a*, seven bivalents in *O. hookeri*; *b*, ring of 14 in meiotic prophase of *O. biennis*; *c*, ring of 14 in alternate disjunction at anaphase I in *O. biennis*. (After Cleland, 1936, *Bot. Rev.* 2, and after Abrams, 1951, *Illustrated Flora of the Pacific States*, Stanford University Press.)



Oenothera hookeri



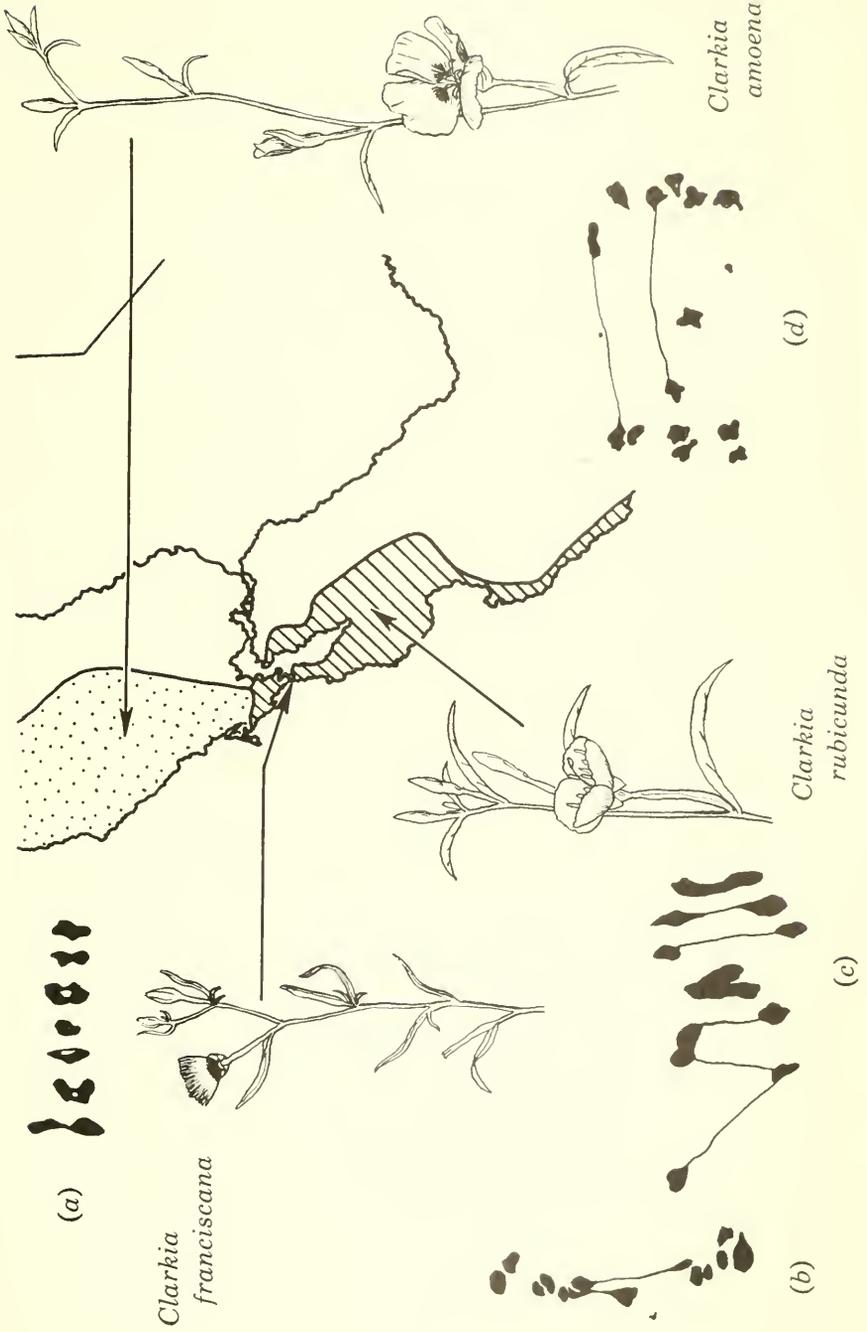
Oenothera biennis

Y's) may evolve by this process, as has been the case apparently in *Drosophila miranda*. Karyotype evolution in the *Drosophila virilis* group also involves translocations between autosomes and sex chromosomes. An extreme case of multiple sex-chromosome mechanisms is found in the Palestinian beetle *Blaps polychresta*. In the males there are 12 X chromosomes and 6 Y chromosomes. The females have 24 X chromosomes.

Genetic systems based upon regularly occurring structural hybridity for reciprocal translocations are characteristic of a few groups of plants. The behavior of translocation systems in nature is not well understood for most plants, although rings are reported for a number of genera, for example, *Rhoeo*, *Paeonia*, *Datura*, *Hypericum*, and many Onagraceae. Progress toward an understanding of such mechanisms in natural populations of *Clarkia* and *Oenothera* is being made by Lewis, Raven, and their associates. *Clarkia* has been studied in some detail cytologically. Species invariably differ by chromosome rearrangements, and interspecific hybrids are often highly sterile. It has been estimated that in many species of *Clarkia* more than 20 percent of the plants in nature have rings of chromosomes, indicating the presence of translocations. Such rearrangements form a part of the genetic system and may characterize whole populations.

An interesting example of evolution involving chromosome rearrangements is *Clarkia franciscana*, studied by Lewis and Raven. This largely self-pollinated plant is restricted to an area of serpentine rock in San Francisco which is within the geographic range of the closely related *C. rubicunda*. Apparently *C. franciscana* is also related to *C. amoena*, a northern species. Studies of meiosis in hybrids show that *C. franciscana* differs from *C. amoena* by at least two translocations and two paracentric inversions. It differs from *C. rubicunda* by at least three translocations and four inversions (see Fig. 9.2). (*Clarkia amoena* and *C. rubicunda* differ by at least three

Fig. 9.2 | (see opposite page) Evolution involving chromosomal rearrangements in *Clarkia*. *a*, seven bivalents in *C. franciscana*; *b*, anaphase I showing two bridges and two fragments in cross between *C. rubicunda* and *C. franciscana*; *c*, anaphase I showing chain of five chromosomes, a chain of three chromosomes, and three bivalents in cross between *C. rubicunda* and *C. franciscana*; *d*, anaphase I showing two bridges, two fragments, and a lagging chromosome in a cross between *C. amoena* and *rubicunda*. Map shows distribution of three species in San Francisco Bay area. (After Lewis and Raven, 1958, *Evolution* 12, *Brittonia* 10; and Lewis and Lewis, 1955, *Univ. Calif. Publ. Bot.* 20.)



translocations and two inversions.) Lewis and Raven have concluded that *C. franciscana* has originated relatively recently from *C. rubicunda* and that it may have been the result of a rapid repatterning of the chromosome set, producing many differences in a relatively short time. It also seems likely that *C. rubicunda* may have arisen from *C. amoena* at an earlier time.

Some plants, such as *Oenothera*, subgenus *Euoenothera*, have evolved translocation systems of amazing complexity. The development of these systems seems to have involved selection for hybridity. This group is well known through the work of Cleland and others. Indeed, the "mutation hypothesis" of De Vries was based upon studies of *Oenothera erythrosepala* (*O. lamarckiana*). Some species of the subgenus, for example, *O. hookeri*, have seven pairs of chromosomes (Fig. 9.1) or small rings (floating translocations). In others, such as *O. biennis*, all their chromosomes are in a ring of 14 at meiosis (Fig. 9.1). In addition to the reciprocal translocations that involve all the chromosomes, there are balanced sets of lethal genes, the R enner complexes, which prevent the survival of homozygous offspring by acting to produce nonviable gametes or zygotes. (As mentioned above, there is directed alternate disjunction.) The ring-forming species have small flowers and are largely self-pollinated (in contrast to *O. hookeri*, for example). They consequently form a very large number of highly heterozygous, mostly true-breeding, and partially isolated races. Occasional outcrossing between the races leads to the origin of new ring systems and new racial types. The great number of such races, which are the primary evolutionary units in the ring-forming *Oenotheras*, makes the taxonomy of the group very difficult.

As Cleland has pointed out, these ring-forming *Oenotheras* illustrate that various types of "mutations," which individually might be considered harmful, may, in combination, produce a workable genetic system. They form a widespread and even weedy group. Reciprocal translocations (which usually lead to sterility), lethal genes, and self-pollination combine to form a system in which heterozygosity of all the chromosomes is preserved and the plants are highly fertile. There are what appear to be disadvantages of such a genetic system. Recombination is reduced, and there may be wastage of gametes and zygotes. The failure of any part of the system destroys the whole. Polyploidy apparently is excluded since it is incompatible with a complete ring system and lethal gene complexes.

Changes in Chromosome Size and Shape

By their nature, inversions and translocations also change the size and appearance of the chromosomes. Pericentric inversions may

change the position of the centromere and thus alter the relative length of the arms. Unequal reciprocal translocations also may change the chromosome length. Since the number of crossovers is proportional to the length of a chromosome arm, there may be a change in the amount of recombination simply as a result of size changes. As is discussed below, if a chromosome is very small, for example, because of translocation, and does not pair properly, it may be lost and the basic chromosome number changed.

Changes in Chromosome Number

One way of expressing the amount of recombination afforded by the genetic system is to use the recombination index of Darlington. This simple measure is equal to the haploid number of chromosomes plus the average number of chiasmata. The larger the recombination index (R.I.), the greater the number of new gene combinations formed by recombination and segregation. The index does not take into account the existence of supergenes formed as a result of structural changes or apomixis, but its use leads to interesting comparisons.

An increase in the basic number will increase the R.I.; for this reason, chromosome-number change may be regarded as an aspect of the genetic system related to the balance between immediate fitness and long-range flexibility. Stebbins has made an analysis of the distribution of R.I. as indicated by chromosome number in flowering plants. In woody plants (trees and shrubs) the basic gametic number is significantly higher than that of herbaceous genera. This suggests that among long-lived plants a high recombination index has been favored by selection. In short-lived rapidly reproducing organisms, the genetic system usually seems to favor immediate fitness at the expense of flexibility. There is, however, a certain amount of flexibility inherent in a short life cycle with its rapid turnover of genes. Within strictly cross-pollinated herbaceous flowering plants, Stebbins finds that annual species tend to have a lower recombination index than perennials. Most of these annual species are either cross-pollinated with a low R.I. or predominantly self-pollinated, with a high R.I. They appear to be specialized for rapid occupation of uniform habitats.

POLYPLOIDY

The basic chromosome number clearly appears to have had selective value. How are changes in the basic number accomplished? The minimum number of chromosomes, though all different, that function as a harmonious and integrated unit is a *genome*. For purposes of discussion, the genomic number may be symbolized as x . The

total number of chromosomes in any nucleus is its chromosome complement. It is easy to see that the complement may include one or more genomes or parts of genomes. In discussing the regular alternation of gametic and zygotic chromosome numbers, it is convenient to use a different symbol n . The haploid and diploid numbers of all organisms are n and $2n$. Organisms that have experienced an increase in chromosome number are called *polyploid*. Here n includes more than one x or portions of x . In polyploid organisms n and $2n$ usually are called haploid and diploid, even though in a tetraploid, for example, $n = 2x$ and $2n = 4x$. The commonest type of change is eupolyploidy, which is irreversible increase by whole genomes. The oldest members of a eupolyploid series are those with the lowest numbers. Thus if a plant is found to have $2n = 22$ ($x = 11$) chromosomes, its closely related tetraploid derivative would have $2n = 44$ ($x = 11$). The number of chromosomes in one genome may also change, leading to aneupolyploidy. Strictly speaking, an aneupolyploid series is a series of numbers, such as 11, 12, 13, 15, not a series of organisms; aneuploidy is reversible and may arise in several ways.

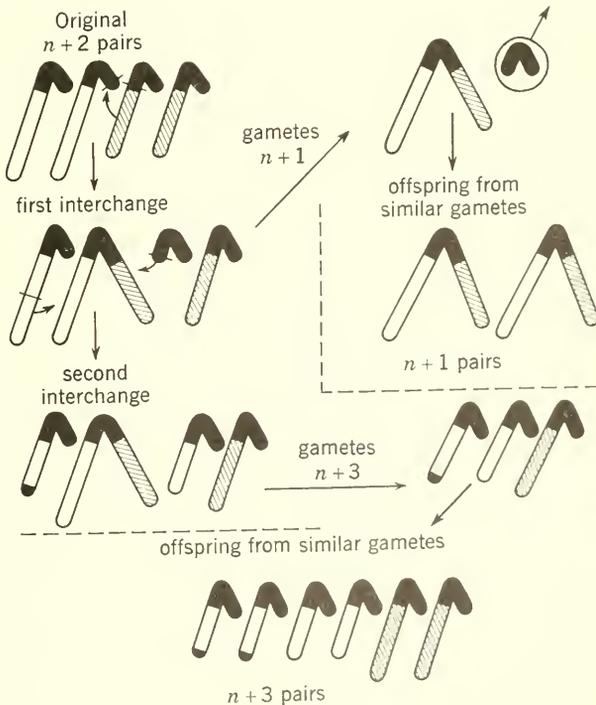
Aneupolyploidy

There is cytogenetic evidence that centromeres do not arise anew in populations in nature. Nor can genetically active chromosomes be added or subtracted from the genome. Nevertheless, conditions favoring the loss or gain of chromosomes can be brought about by unequal reciprocal translocations. In many organisms the region of a chromosome adjacent to the centromere is genetically inert (heterochromatic). Darlington has suggested that, if the active euchromatic arms are translocated to other chromosomes, the remaining heterochromatic centric fragment usually will not pair properly and may be lost. Thus a chromosome is removed from the genome, but the same amount of genetic material remains (Fig. 9.3). The resulting offspring is isolated cytogenetically from its parent; if it forms a new population, further differentiation may be expected to occur. On the other hand, a second translocation might apportion some active material back to the centric fragment, dividing the genetic material of another chromosome. Again pairing will be upset and a variety of gametes will be produced. A zygote that has an extra chromosome added to its genome may be formed. The original amount of genetic material must be present or the combination will not be viable.

Aneuploid change in chromosome number has been studied extensively in plants. Generally a decrease in basic chromosome number

is involved. In *Crepis* (false dandelion, Compositae) the chromosomes may be recognized individually. Species considered to have retained primitive characteristics in other features of the phenotype have $x = 7$, 6, or 5. The most specialized species have $x = 4$ and $x = 3$. The correctness of the above-described model of Darlington has been shown by Tobgy, who demonstrated that *Crepis fuliginosa* ($n = 3$) was derived from *C. neglecta* or its ancestor ($n = 4$). One arm of the C chromosome of *C. neglecta* apparently is inert, and the other arm was translocated to the A chromosome. This is shown by pairing behavior in the F_1 hybrid between the two species.

Fig. 9.3 | Diagram showing how basic chromosome number can be increased or decreased by reciprocal translocation of unequal chromosome segments. Nonhomologous chromosomes are white and hatched; black indicates supposedly inert segments. (From Stebbins, 1950, *Variation and Evolution in Plants*, Columbia University Press, and after Darlington, 1937, *Recent Advances in Cytology*, Blakiston.)



Similarly, *C. kotschyana* ($n = 4$) was derived from an $n = 5$ form close to *C. foetida*.

There are numerous examples suggestive of progressive increase in chromosome number but unfortunately little experimental evidence. The genus *Clarkia* apparently is one in which chromosomes have been added to the genome. This increase may be associated with the formation of supernumerary chromosomes (see below). Aneuploidy that simulates progressive increase may result when loss or gain of one chromosome is followed by amphidiploidy (doubling of the chromosome number following hybridization of two diploids). Part of such a series has been produced in *Brassica* (mustard) where $x = 8, 9,$ and 10 may represent a phylogenetically ascending series. The numbers known in nature or experimentally produced are $n = 17, 18, 19, 27,$ and 29 . The genus *Carex* (sedges) has the most extensive aneuploid series known. Haploid numbers ranging from $n = 6$ to $n = 56$ have been reported, and every number from 12 to 43 is represented by one or more species. Presumably structural changes and polyploidy have produced some of the numbers in this series.

Structural rearrangements in which two acrocentric chromosomes give rise to a large metacentric chromosome and a minute fragment, which subsequently disappears, are common in *Drosophila*, grasshoppers, and reptiles. The process is known as centric fusion and represents a special sort of reciprocal translocation. In many families or genera, the number of long arms remains constant while the relative number of acrocentrics and metacentrics fluctuates. Many examples could be given. An interesting one is the cricket genus *Nemobius*. *Nemobius fasciatus* has a metacentric X chromosome and seven acrocentric autosomes. Other species have additional metacentrics and fewer acrocentrics, presumably the result of structural rearrangements.

In addition to the basic number of chromosomes in the genome, both plants and animals may have extra chromosomes called supernumeraries. Ordinarily extra chromosomes are not tolerated, for they cause genetic unbalance and upsets in meiosis, as in experimentally produced trisomics, tetrasomics, etc. This is why, in general, only reciprocal translocations can change the basic number. The genetic material remains the same; only its distribution among the centromeres is changed. When supernumerary chromosomes are found, it is evident that they must be neutral in some sense or have a special function. Often they are variable in number from cell to cell, or individual to individual. Nevertheless, it seems unlikely that they are completely inert, since they may in some cases remain in the population.

These supernumerary chromosomes in plants commonly are called B chromosomes, and they are surprisingly frequent. In general, the B chromosomes are smaller than the others, and they pair only among themselves. In most instances they are heterochromatic. They vary in number among individuals, they may be in odd or even numbers or absent, and their presence usually cannot be detected in the phenotype of the plant. B chromosomes may have physiological effects, however, the evolutionary importance of which is unknown. In *Clarkia*, supernumeraries probably have arisen as the result of structural changes in the chromosomes. These plants often have ring or chain arrangements of chromosomes in translocation heterozygotes, and unequal separation may lead to the formation of trisomics. For some reason, in this genus extra chromosomes do not disturb the genetic balance or reproduction.

Supernumerary chromosomes are found among many invertebrates. They appear to be largely heterochromatic. Some are mitotically stable; others show nondisjunction. Perhaps related to these supernumeraries are the so-called "limited" chromosomes of some Diptera. These chromosomes are limited to the germ line, where they often show bizarre cytological behavior. The fungus gnat *Sciara coprophila*, for example, has seven chromosomes in somatic cells of males and eight in somatic cells of females (Fig. 9.4). Cells in the germ line that will produce gametes contain 10 (sometimes 9 or 11) chromosomes; this group includes the four pairs of somatic cells plus a pair of large chromosomes never found in cells other than the germ line. These are the limited (L) chromosomes. In meiosis female flies produce eggs with a full haploid set including an L. Meiosis in males is unusual, in that synapsis does not occur and at the first division a unipolar spindle is formed. The L's and one of each of the other chromosomes proceed to the pole of the spindle, while the others (which genetic evidence shows are all *paternal* chromosomes) are eliminated as they go in the opposite direction and are cut off in a small bud. During the second division a bipolar spindle forms and the chromosomes behave normally except for the X, which divides but sends both daughters to the same pole. Only the spermatid that receives the X's matures; therefore only one sperm is formed at each meiosis. It contains 2 L's, 2 X's, and one of each autosome; except for the L's, these chromosomes come originally from the maternal parent.

After fertilization, which results in a zygote with three pairs of autosomes, 3 X's, and (usually) 3 L's, a series of cleavage divisions takes place in which the L's and X's are selectively eliminated from cells. Eventually the chromosome numbers and distribution

that began the cycle are restored. In embryos that will become males the X's from the father are eliminated, whereas in embryos that will become females one of the paternal X's is also eliminated and degenerates in the cytoplasm. There are many fascinating details not included in the above description and many problems of interest to geneticists, embryologists, and evolutionists that have not been solved. One cannot help but be impressed by the very large number of phenomena observed by cytogeneticists which are unknown variables in an overall picture of the evolutionary process.

Eupolyploidy

Eupolyploidy as a genetic system occurs very frequently in plants but seems to be quite rare in animals. It has been suggested that increase in chromosome number in animals would upset the sex-determination mechanism and for this reason it has been selected against. Only in parthenogenetic animals are there polyploid series comparable to those in plants. Chromosome numbers have been sampled, however, for relatively few organisms, and conclusions about the occurrence of polyploidy are dangerous. On the basis of available numbers in plants, polyploidy appears to be most common among the vascular plants. For this reason, the following discussion will be limited to that group.

The study of chromosome numbers and behavior in wild forms and in hybrids made in the laboratory usually enables one to identify polyploid organisms. It is even sometimes possible to synthesize in the laboratory a species recognized in nature. If the diploid hybrid can be made, chemicals, such as colchicine, which upset the spindle mechanism can be employed to double the chromosome number. If a plant has a high chromosome number and is impossible to cross with other forms, one can only infer its polyploid nature. If pairing is perfect in such a plant and if its fertility is high, it must be assumed that it has become functionally diploid. Only the techniques of comparative morphology (including comparisons of proteins) offer hope of deducing its origin.

In discussing this sort of genetic system it is customary to draw a

Fig. 9.4 | (see opposite page) Chromosome cycle of *Sciara coprophila*. Discussion in text. (Modified from White 1954, *Animal Cytology and Evolution*, 2d ed., Cambridge University Press, and after Metz, 1938, *Am. Nat.* 72.)

distinction between polyploids in which all the genomes are alike, or autopolyploids, and polyploids in which the genomes are different, allopolyploids. In practice, this distinction may be difficult to draw. Clearly, organisms are autopolyploid when they are the result of somatic doubling of chromosome number (unless the parental organism is a diploid hybrid). Usually plants resulting from the fusion of haploid or polyploid gametes of the same species are regarded as autopolyploids. The genomes, if not the genes, are presumably much the same. The difficulty arises when wider crosses are involved or when hybrids experience doubling, leading to complex combinations of autopolyploidy and allopolyploidy.

Among the higher plants, sporophytic haploids with the gametic number of chromosomes (where $n = x$) in their somatic tissues are unknown in natural populations. They may be produced in culture and are of great interest cytogenetically but they are not known to be of direct evolutionary significance.

Strict autopolyploids also are rare in nature. The presence of more than two similar genomes in an autotriploid ($3x$) or autotetraploid ($4x$) organism leads to difficulties at meiosis: Only two homologous chromosomes can synapse at any one point. Instead of the usual bivalents, multivalents and/or univalents may be found, depending upon chance and the length of the chromosomes as related to chiasma number. Although numerous autopolyploid organisms may show enhanced "vigor" or other physiological properties considered advantageous by the plant breeder, they ordinarily are unable to reproduce sexually and are selected against in nature unless they acquire an efficient mode of asexual reproduction (see below). The reduction in fertility may not be complete (it may be very slight); furthermore, most of the higher plants have one or more modes of vegetative propagation. Many of the most important horticultural and pomicultural plants are triploids (such as most bananas, many apples, some cherries, Japanese iris, tiger lilies, tulips). In addition, both autotriploids and autotetraploids occasionally occur spontaneously in animals (e.g., in certain salamanders). Autopolyploids rarely become established as populations in nature, however.

Allopolyploidy, on the other hand, is known in virtually every phylum of the plant kingdom. Well-known and often-discussed examples are the allotetraploid of radish and cabbage, *Raphanobrassica*, and the allotetraploid of two horticultural species of primrose, *Primula kewensis*. The first involves a cross between different genera, the second different species; therefore the two genomes in the hybrid would most certainly be different.

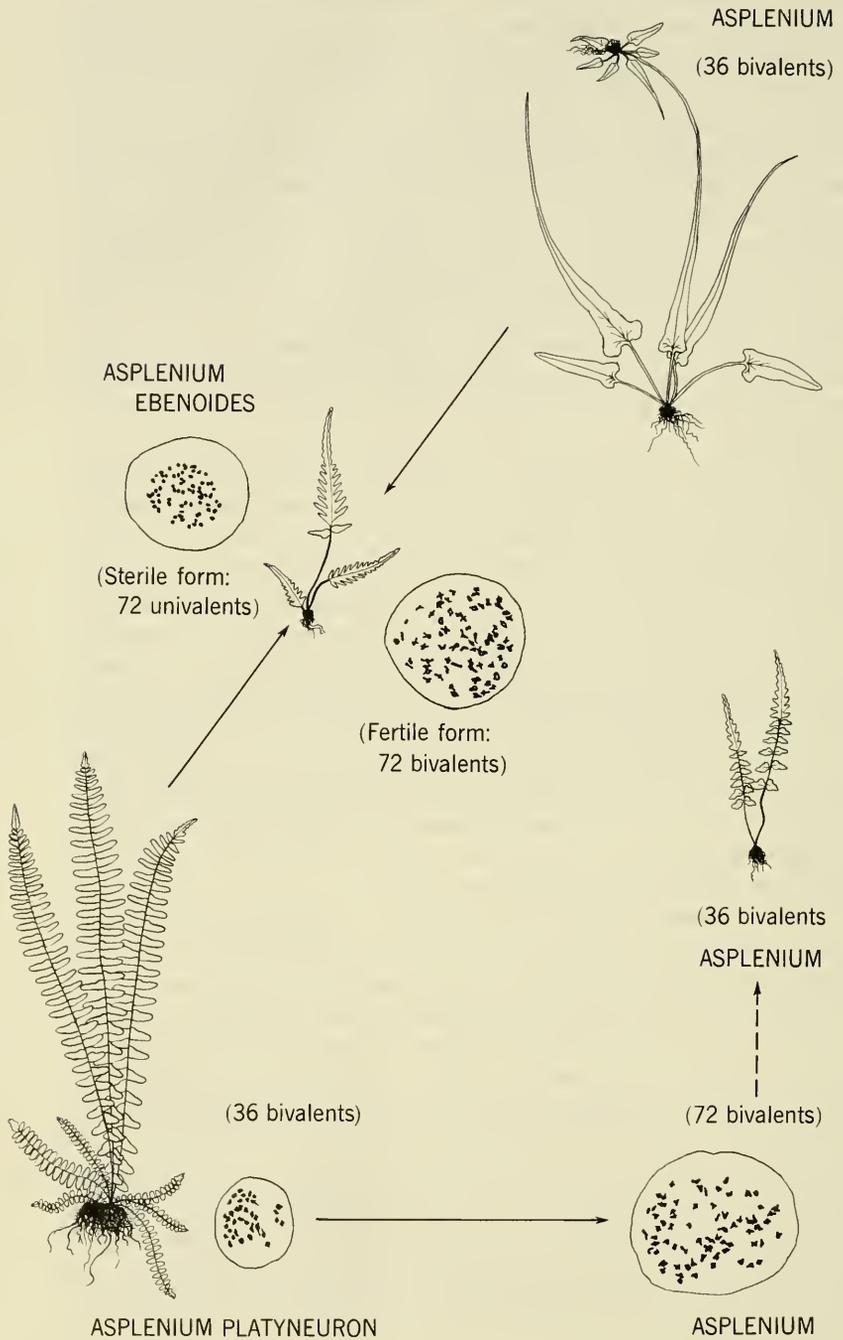
In diploid hybrids between species and genera, chromosome be-

havior is variable. For example, in *Raphanobrassica*, there seem to be so many small differences between the chromosomes of the parental species that pairing does not take place and only univalents are found at meiosis. The same is true of the cross between *Allium fistulosum* (scallion) and *A. cepa* (onion). The univalents are distributed at random, and only rarely will cells with balanced chromosome complements be produced. At the opposite extreme, in the *Primula* example and in the cross between *Festuca pratensis* (meadow fescue) and *Lolium perenne* (perennial rye), bivalents are formed in the diploids. This suggests that there are fewer differences between the genomes involved. Nevertheless, following disjunction, the diploid hybrids are sterile. Doubling of the chromosome number provides the chromosomes of each genome with the appropriate homologues at meiosis. Bivalents are formed and fertility is restored.

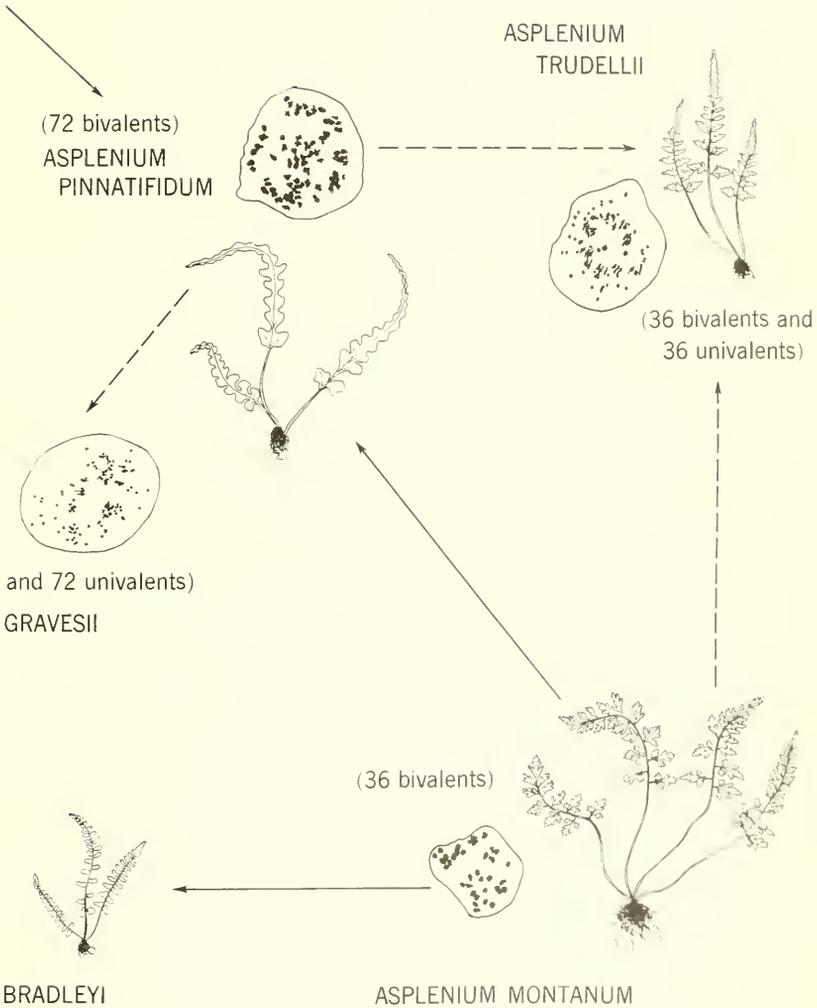
The resulting allotetraploids are sometimes referred to as amphidiploid since, in effect, they are diploid for each parent. That is, $2n = 2x_1 + 2x_2$. Allotetraploids of this sort occur in nature. Observation of the chromosomes of artificial hybrids between the suspected tetraploid and its possible parents will suggest the relationship involved. In a backcross to a genuine parent, a mixture of bivalents and univalents occurs. It is apparent, however, that there is an evolutionary disadvantage inherent in the make-up of a strict allotetraploid. The genomes may be so differentiated that, when they are combined in the fertile tetraploid hybrid, genome recombination does not occur. The parental genomes presumably continue to exhibit the same amount of recombination as they did in the diploid. Because pairing is perfectly normal, genes of different genomes cannot be recombined and segregated.

Probably more common in nature is a tetraploid in which the genomes are partly differentiated but are still sufficiently similar that multivalents are found in which crossing-over between chromosomes of the two parents may occur to produce genetic recombination. This is referred to by Stebbins as segmental allopolyploidy, because only some segments of the chromosomes are different. While segmental allopolyploids are of the greatest significance for evolution, they are difficult to recognize in nature. They may result from hybridization of morphologically similar parents, and because of multivalent formation, they simulate autopolyploids. Furthermore, as a result of their partial sterility, they are unstable. Selection, acting to increase fertility, may tend to favor further chromosome differentiation. Bivalents may be formed and a strict allopolyploid result.

Fig. 9.5 | Polyploid complex in the fern genus *Asplenium*. Discussion in text. (Original and after Wagner, 1954, *Evolution* 8.)



RHIZOPHYLLUM



There are many groups of plants in which the major evolutionary differentiation has involved allopolyploidy. One of the best examples is the fern genus *Asplenium* (spleenwort), studied by Wagner and his associates. As shown in Fig. 9.5, there are three primary species with $n = 36$. Meiosis is regular, and 36 bivalents are formed in each. By a study of morphology and by analysis of chromosome behavior in other species, it could be shown that *A. bradleyi*, *A. ebenoides*, and *A. pinnatifidum* are allotetraploids involving the primary species in pairs. It is interesting that the sterile diploid hybrid of the same parentage as *A. ebenoides* is known; in it there are 72 univalents, instead of 72 bivalents. *Asplenium trudellii* is a backcross of *A. pinnatifidum* to one of its parents, for it shows 36 bivalents (*montanum* genome) and 36 univalents (*rhizophyllum* genome). *Asplenium gravesii*, on the other hand, is a hybrid between two different allotetraploids that share *A. montanum* as a parent. This is revealed by the behavior of the chromosomes also, for the two *montanum* genomes form bivalents, while the *platyneuron* and *rhizophyllum* genomes remain unpaired (36 bivalents plus 72 univalents).

In other groups, much more complicated polyploid complexes are known. The diagram of Stebbins (Fig. 9.6) shows the combinations of genomes and of autopolyploidy and allopolyploidy that may occur (although higher levels have been found). In some groups, allotetraploids are able to form partially fertile hybrids with autopolyploid forms of either of their parents. In plants, particularly those with any degree of vegetative propagation, the result may be to blur or obliterate the morphological limits of the taxa originally involved. A group of different degrees of ploidy and varying morphology, as well as ecological preferences, may arise. Only by cytological analysis can such complexes be resolved and then sometimes only partially. The situation may be further complicated if the plants reproduce apomictically, perpetuating individuals that are sexually quite sterile (see below).

It is difficult to specify the general importance of polyploidy as a genetic system. It has been estimated that up to one-half of the flowering plants are of polyploid origin. Similarly, the ferns and their allies show much polyploidy, as do the algae and mosses. Only the fungi form an exception and they have been very poorly sampled cytologically. Unfortunately very little is known of tropical species, so that the sampling is far from thorough or representative. Whole families or subfamilies (e.g., Pomoideae of the Rosaceae, the apples and their relatives), as well as genera, have numbers that suggest a polyploid origin. Despite the existence of regular progressions of chromosome number in animals, polyploidy generally

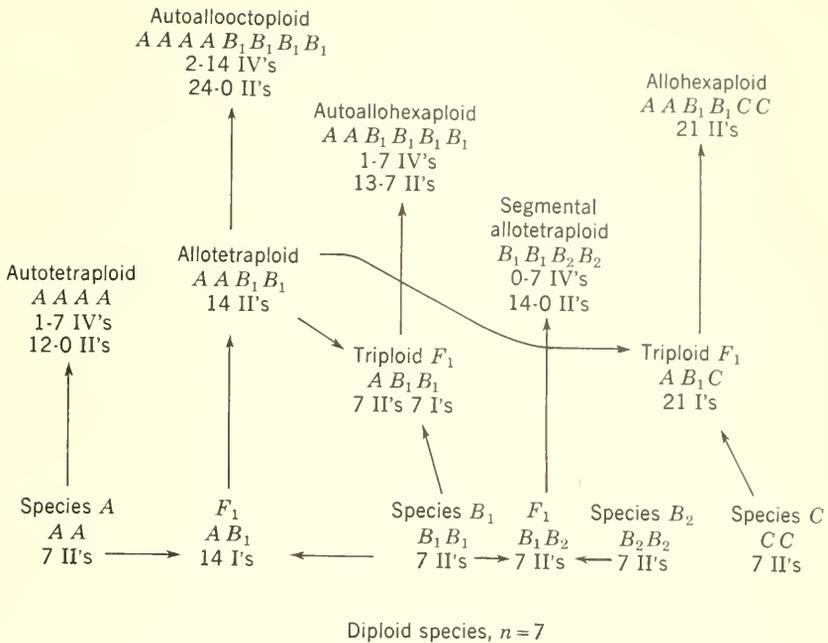


Fig. 9.6 | Diagram showing various levels and types of polyploidy, their genome constitution, and their mode of origin. Letters represent genomes; roman numerals indicate pairing behavior, e.g., I = univalent, II = bivalent, etc. Thus 24-0 II's = 24 to 0 bivalents. (From Stebbins, 1950, *Variation and Evolution in Plants*, Columbia University Press.)

is not invoked in explanation. As has been seen, centric fusion is thought to be the cause.

The effects of polyploidy as a genetic system are varied and at times opposed. For example, autopolyploidy may severely restrict or eliminate genetic recombination in one organism, only to act as a bridge between an allopolyploid and one of its parents. A strict amphidiploid is limited in recombination potential to that of its parents, but in segmental allopolyploidy recombination of the parental characteristics, including ecological preferences, may occur. In general, one might say that polyploidy may act to increase the scope of evolutionary units, enhancing the occasional interbreeding through time. The situation resembles that postulated by Wright for most

rapid evolution: subunits partially isolated in space which occasionally exchange genetic material. It makes possible further exploitation of the advantages of hybridization at the diploid level.

APOMIXIS

The ultimate in the restriction of recombination is the elimination of sexual reproduction altogether. In extreme cases, recombination is completely eliminated. This appears to be relatively rare, and there are many types of asexual reproduction with varying amounts of recombination. The term apomixis describes all types of asexual reproduction, that is, those types of reproduction that tend to replace or act as substitutes for sexual reproduction. The classification of the types of apomixis is exceedingly complex, since a variety of situations intermediate between sexuality and obligate apomixis may occur. In most plants, either the gametophytic or the sporophytic generation or both may be involved. Terminology relating to apomixis also has become unfortunately complex; it will be simplified as much as possible in the following account.

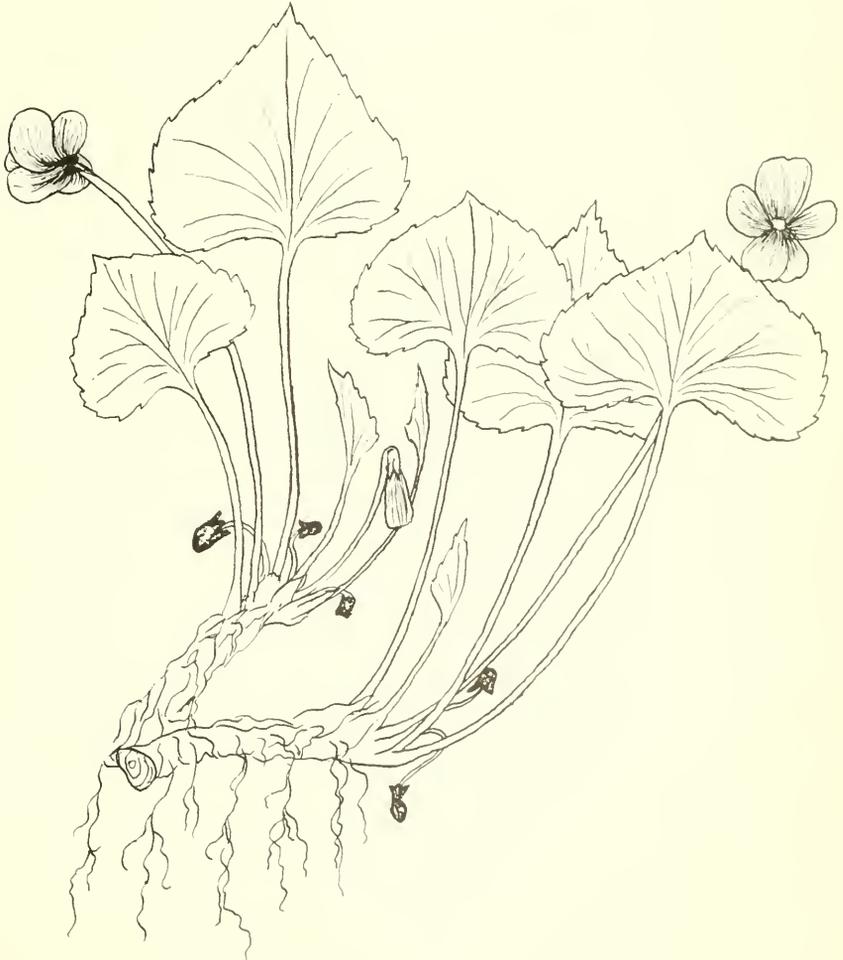
Apomixis may be facultative or obligate. Some organisms reproduce sexually at times and asexually at other times, usually under different environmental conditions. However, in animals, a regular cyclic change from sexual to asexual reproduction is not strictly facultative apomixis, since the asexual portion of the cycle is obligate.

The simplest sort of apomixis is vegetative reproduction; it may function as the only mode of reproduction. For example, some aquatic plants are known to reproduce only asexually in northern Europe (e.g., *Elodea*, where only pistillate plants are found) and sexually in other parts of their range. The self-sterile triploid day lily (*Hemerocallis fulva*) reproduces asexually in America. The effect of such vegetative propagation, whether by rooting and further growth of broken-off branches or by the production of specialized propagules such as gemmae or bulbils (which are modified branches or buds), is to create a population of genetically identical organisms. Such a population is called a *clone*. Clones may be formed by animals that reproduce by fission (Protozoa) or budding (Coelenterata, Annelida, etc.). From the standpoint of genetics, the population is one genetic individual. Since they usually eventually separate from one another, members of a clone are individuals physically and play the role of individuals ecologically.

Among both plants and animals, vegetative reproduction may occur in individuals that also reproduce sexually and thus have a

dual breeding system. This usually is not referred to as apomixis, except where it assumes the entire reproductive function during a portion of the life cycle. Ordinarily, as in some species of *Viola* (violets), sexual reproduction and asexual reproduction occur at the same time (Fig. 9.7). For example, individual plants of *Viola* produce runners or stolons at the base; these eventually produce a series of new rosettes which may become separated from the parent plant. Typical violet flowers also occur; they are pollinated by insects, producing heterozygous seeds. At the same time, however, cleistogamous flowers may be formed. These flowers, close to the

Fig. 9.7 | Violet (*Viola*) showing typical flowers, cleistogamous flowers, and vegetative propagation (creeping underground stems).



ground among the leaves, never open and are self-pollinated within the bud. Seeds from these flowers, virtually sown at dehiscence, produce plants genetically similar to the parents. Thus three modes of reproduction, providing different amounts of genetic recombination, occur in the same plant at the same time.

Somewhat more cryptic sorts of vegetative reproduction, without the formation of seeds, also are known. These include some instances of so-called "vivipary" in plants. That is, the propagules are tiny bulbils which occur in the inflorescences and may replace the flowers. Some species of *Allium* (onion, Fig. 9.8), for example, as well as some *Poa* (bluegrass) species reproduce in this fashion. From a developmental point of view, one may say that the indi-

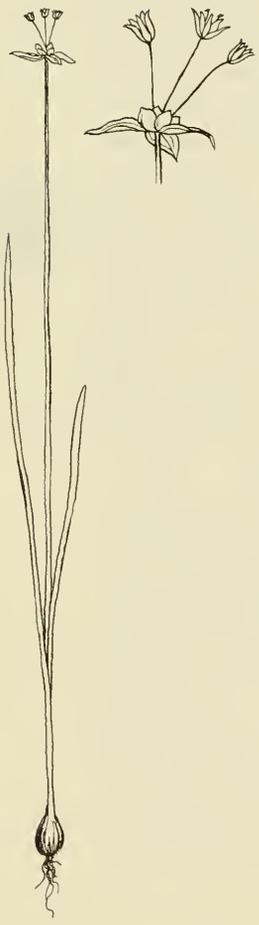


Fig. 9.8 | Onion (*Allium*) showing some flowers in inflorescence replaced by bulbils.

vidual flowers, which are modified spore-producing branches, develop into specialized vegetative branches that fall from the plant, subsequently to root and grow. Clone formation is the result.

Besides these relatively simple modes of apomictic reproduction, there are sorts involving seed production whose complexity is amazing and whose effects are greatly puzzling. They are known collectively as *agamospermy*. Considering only the higher plants as examples, one must first remember that their life cycle has a gametophytic period which separates meiosis and fertilization and which alternates with the sporophytic generation. The gametophyte may consist of only a few cells (e.g., eight in many flowering plants), or it may be a relatively massive multicellular plant, physiologically independent of the sporophyte (as in most ferns). In either event, apomixis may occur in this generation if the egg develops without fertilization. The four basic types of apomixis in which the gametophytic generation is involved are known collectively as *gametophytic apomixis*; this includes forms in which cells other than the egg may develop to produce a new sporophyte. Development of the egg without fertilization is called *parthenogenesis*, while the term *apogamety* refers to the production of a sporophyte from other cells of the gametophyte. Ordinarily the products of either type of development are diploid; haploid parthenogenesis and haploid apogamety are not of evolutionary significance in vascular plants.

Some upset of meiosis in the preceding sporophytic generation has taken place, or meiosis may have been eliminated altogether. Thus the resulting spores, and the gametophytes they produce, are diploid. This may occur in two ways. The cells of the sporophyte that would ordinarily undergo meiosis (e.g., in the ovule) may undergo mitotic or only partly meiotic divisions; this is known as *diplospory*. In some plants somatic cells of the reproductive structures may, through mitotic divisions, produce a gametophyte. This process, *apospory*, likewise results in a diploid gametophyte. The further development of such a gametophyte may involve parthenogenesis or apogamety, as seen above.

Development may be dependent upon the influence of a pollen tube or on nutritive tissue (itself a product of fertilization), called endosperm, that surrounds the apomictically produced embryo sporophyte. Thus *pollination* is necessary, but *fertilization* of the egg does not take place. This is called *pseudogamy* and is generally one of the most difficult forms of apomixis to detect.

Apomixis in the higher plants may progress to the point that the gametophytic generation is suppressed completely. A variety of agamospermy known as *adventitious embryony* results. Here cells

of the integument or nucellus of the ovule produce the new sporophyte by mitotic divisions. Thus sporophytic tissue gives rise directly to a new sporophyte that is enclosed in the usual seed coats and is superficially indistinguishable from the usual situation. Adventitious embryony also may be pseudogamous.

It will be seen from the above that apospory and adventitious embryony produce plants genetically identical with their parent. Since diplospory may involve divisions that are partly meiotic, the possibility of genetic recombination exists. The nature and possible results of partial recombination of this sort are discussed below under thelytoky in animals.

Just as apomixis in the higher plants is complicated by the existence of alternation of generations, so is it complicated in higher animals by sex. In a number of groups of animals, males arise from unfertilized eggs and are haploid. Females are produced from fertilized eggs and are diploid. This type of apomixis, known as *haplo-diploidy*, haploid parthenogenesis, or arrhenotoky, obviously may be a means of sex determination. Apparently haplo-diploidy has arisen about seven times in the Metazoa (among the insects, arachnids, and rotifers). In the insects, the Hymenoptera as an order are characterized by this form of apomixis and sex determination, which also is known in the Homoptera, Coleoptera, and Thysanoptera.

In haplo-diploidy, no true meiotic division occurs in the male, the sperm being produced by a mitosis or a simulated meiosis and thus genetically identical (except for mutation) with the parental genotype. The evolutionary genetics of haplo-diploid organisms is by no means well understood. For example, it can be seen that recessive genes must be immediately expressed in males of species with this genetic system, unless some special mechanism prevents this. It has been suggested that, by virtue of some sort of "repeat" mechanism of gene duplication, the organisms may be functionally diploid. It is well known that most highly differentiated tissues of an organism are endopolyploid (often to a high degree); this might protect the soma from harmful mutations. On the other hand, haploid males could act as a sort of screen for recessive lethals.

A rather different mode of apomixis in animals is called thelytoky; it is a kind of parthenogenesis in which females are produced from unfertilized eggs. It appears to have arisen in most major animal groups, including the vertebrates, under natural conditions. In some organisms thelytoky is complete: Males are very rare or unknown and every individual arises from unfertilized eggs. More common is cyclical thelytoky where there is an alternation, usually in an annual cycle, of sexual and asexual generations. This mode is found

in aphids, gall wasps, cladocerans, many parasitic worms, and rotifers.

As in plants, reduction division may be entirely suppressed, and the divisions resulting in the egg are mitotic. The egg is then diploid. On the other hand, meiosis may occur essentially as normally, but doubling takes place at a later stage, restoring the diploid condition (Fig. 9.9). This is comparable to the results of diplospory in plants. The usual products of meiosis are four haploid cells. In the higher plants these would be megaspores, and in animals an egg and two (or three) polar bodies. If the first division of meiosis occurs, crossing-over may take place and the basis for recombination established. Should the daughter cells, following the second division, fuse in pairs, then only two cells are formed, and meiosis and recombination are partially suppressed. In animals this may be the result of the fusion of the egg nucleus with that of the second polar body. The resulting cells are diploid, and a limited amount of recombination may have occurred.

White has pointed out that, since no segregation can occur in ameiotic thelytoky, recessive mutations and structural rearrangements of the chromosomes tend to accumulate. Daughters will resemble their mothers, but the line will tend to become more and more heterozygous. This may account for the vigor with which some apomictic organisms are endowed. On the other hand, in partially meiotic thelytoky where segregation can occur, existing heterozygosity will be reduced in time, without the fusion of gametes to restore it.

The effects of apomixis on the organism are varied and complex. In both plants and animals, apomixis commonly is associated with both hybridization and polyploidy, although there is no reason to infer a causal relationship among the three. If a major factor in the relative absence of polyploidy in animals is the sex-determination mechanism, it is clear that thelytokous animals are free to become polyploid. Also, the various cytological components of apomixis are controlled by a large number of genes that are largely of negative selective value when separated. For example, mutations leading to upsets in spindle formation would be deleterious unless combined with mutations leading to the formation of restitution nuclei and to the development of eggs without fertilization. Hybridization may serve to bring these genes together in a functional system. It has been suggested also that some sort of buffering may take place if the organism is polyploid.

In those plants in which apomixis has been adopted as a genetic system, a common effect is the origin of what are called agamic

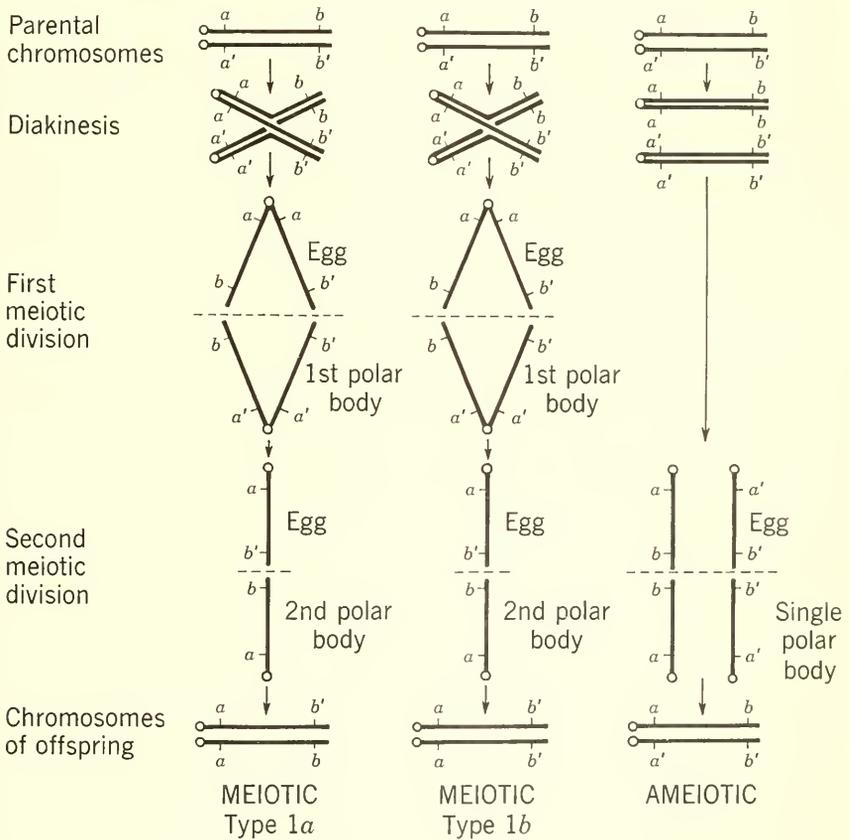
complexes, which are the despair of the taxonomist and the cytogeneticist alike. The genera *Rubus* (blackberries and raspberries) and *Poa* (bluegrass) are familiar examples in which relationships are so blurred as to prevent any clear understanding of the group as a whole. The American species of *Crepis* (false dandelions) form the only agamic complex of size that has been studied in its entirety from both the systematic and cytological points of view. It is interesting that, of the 196 species of *Crepis* (which have been grouped into 27 sections), apomixis and polyploidy are known only in five species of the section *Pyramaches* in southeastern Asia and in nine species of the section *Psilochaena* in America.

The ten North American species of section *Psilochaena* make up a group more heterogeneous than any other. Their basic chromosome number, $x = 11$, is not found in any other section, and it may have originated as a result of interspecific hybridization of Asiatic species with $n = 7$ and $n = 4$, or with $n = 5$ and $n = 6$. *Crepis runcinata* is the only member of the section that shows neither apomixis nor polyploidy, having a chromosome number of $2n = 22$. Seven of the remaining species each have a 22-chromosome diploid with which are associated numerous polyploid apomictic forms. The other two species include only polyploid apomictic types derived by hybridization between two or more of the above-mentioned seven.

Thus there are seven primary diploid types involved in polyploidy and apomixis. Five have greatly restricted geographic distribution and very different ecological preferences. No localities are known in which two diploids occur together, and no diploid hybrids have been found. The polyploids, with chromosome numbers of 33, 44, 55, 77, and 88, show combinations of characteristics of two or more of the diploids and all are apomictic (some facultative). In general, the apomicts exceed in geographic area their diploid ancestors.

The analysis of this agamic complex may serve as a case study for such problems in general. The unveiling of relationships and the construction of a useful classification were dependent upon recognition of the primary sexual diploids. Around these could be grouped the derivative autopolyploid, and allopolyploid asexual forms. Although the variation at first appears baffling and overwhelming, it can be made sensible; in so doing, interesting facts are revealed. For example, diversity is greatest in the regions where the sexual species are found and is less in the peripheral areas of the range occupied only by apomicts. The latter appear to have radiated, subsequent to their formation by hybridization and polyploidy, from the more central area of their sexual ancestors.

Fig. 9.9 | Diagram of three types of parthenogenesis and their genetic consequences. Type 1a, somatic number restored by fusion of second polar body nucleus with egg nucleus; type 1b, somatic number restored after cleavage division of egg by fusion of cleavage nuclei; ameiotic type, divisions resulting in egg are mitotic. (From White, 1954, *Animal Cytology and Evolution*, 2d ed., Cambridge University Press.)



Agamic complexes in plants other than in *Crepis* are less well known. They may be quite small or exceedingly large and complex. The chromosome numbers may become very high and unbalanced. Study of other genera has proved to be quite difficult where the ancestral sexual diploids have become extinct (*Rubus*) or where there may be several agamic complexes in one genus (*Poa*).

Large agamic complexes are less common in animals. The case of *Artemia salina* (brine shrimp) with sexual diploids and thelytokous triploids, tetraploids, pentaploids, octaploids, and decaploids is well known. In the Curculionidae (weevils) and Lumbricidae (earthworms) larger complexes have been found; these may include diploids, triploids, tetraploids, and pentaploids, or even hexaploids and decaploids. In the weevils there is reason to believe that occasional fertilization of parthenogenetically developing eggs by sperm from bisexual races or species takes place.

Thirteen species of thelytokous earthworms have been studied cytologically; all are polyploids ranging from triploids to a possible decaploid. Some sexual species are polyploid as well. Since the Lumbricidae generally are hermaphroditic, thelytoky involves modification or loss of the male organs. Oögenesis is complex, there being chiasma formation and bivalents even in odd-numbered polyploids. The apparent success of these forms, if their wide geographic distribution is to be a criterion, may be accounted for by postulating heterosis as a result of allopolyploidy.

Apomixis has been reported in the vertebrates, but its extent and evolutionary importance are virtually unknown. Some subspecies of the European lizard *Lacerta saxicola* are parthenogenetic. Several species of the American lizard *Cnemidophorus* may consist only of females, since no males have ever been collected; this suggests that parthenogenesis may occur. An interesting situation has been studied in some detail in the fish genus *Mollienesia*. Several populations of *M. formosa* have been sampled in southern Texas, where they occur in streams and drainage ditches. The fishes have also been raised in the laboratory and their genetic similarity studied by means of tissue transplants. Grafts of donor tissue are rejected by the host fish (because of the presence of tissue antigens produced by the host genes) in a period of time roughly proportional to the degree of genotypic similarity between the host and donor.

Mollienesia formosa is parthenogenetic, but eggs do not develop without the stimulation of sperm. Since males of *M. formosa* are exceedingly rare in nature, sperm from related species (in this instance *M. latipinna*) is necessary to initiate development. This mode of reproduction, in which the genetic information of the sperm is

not incorporated into the zygote, is known as gynogenesis. As in other instances of apomixis, the genetically identical progeny of a female form a clone. Tissue-transplant studies have shown that two clones of *M. formosa* make up about 80 percent of the population in one drainage ditch near Olmito in the valley of the Rio Grande. The remainder belong to a third clone or cannot be identified. Clones sampled in 1961 were the same as those found in 1960.

In 1954, several dozen *Mollienesia formosa* were taken from the Olmito ditch and released in the San Marcos River some 250 miles to the north. The species has become established, as has *M. latipinna* which was introduced into the area many years earlier. The San Marcos population thus was available for comparison with the Olmito fishes; it was also sampled in 1960 and 1961. Only two clones were found; these were the common clones at Olmito. Thus the clones of these Mollienesias probably have remained relatively unchanged (within the limits of tissue-transplant discrimination) for at least a decade and possibly for much longer.

There remains to discuss only cyclical parthenogenesis, a peculiar genetic system found in aphids, gall wasps, Cladocera, and rotifers. The cytological mechanisms differ from group to group, but we may single out a species of aphid as an example. In *Tetraneura ulmi*, which produces galls on elm leaves, there is a sequence of generations which have been given names descriptive of their behavior: fundatrices, emigrantes, exules, sexuparae, and sexuales. In the spring, females of the *fundatrix* generation become adults within the elm leaf galls. There each produces, parthenogenetically, female offspring which later develop wings and fly away to feed on the roots of grasses. They are the *emigrantes*, which produce, also parthenogenetically, several generations (females) of *exules*. Eventually the *exules* give rise to the *sexuparae*, winged females which fly back to the elm and there parthenogenetically produce both males and females called *sexuales*. The latter pair, and from fertilized eggs appear once more the female fundatrices, the gall-making generation.

Cytological investigation shows that female sexuales have $2n = 14$, while males have $2n = 13$; there is evidently an XX:XO sex-chromosome system. The fundatrices, emigrantes, and exules types of thelytokous females have a diploid set of 14 chromosomes. There is a single maturation division in oögenesis. The eggs produced are diploid because the division is not reductional and they develop into females that are identical genetically except for mutation. The sexuparae produce eggs of two kinds. In those eggs that will be female-determining, all the chromosomes split, as in mitosis. In those

that will give rise to males, the chromosomes behave similarly, except for the X chromosomes, which pair and are reduced as in meiosis. One X remains in the egg; the other goes into the polar body.

In spermatogenesis of the male sexuales, the X chromosome is apportioned to one of the secondary spermatocytes in normal fashion. However, those cells without the X chromosome eventually degenerate and only X-containing cells produce sperm. Thus the sexuales males can have only daughters, which complete the cycle as fundatrices.

Other aphids have similar cycles in which the number of generations may differ, in which there are two kinds of sexuparae: male-producing and female-producing, etc.

In such complexes as those described for plants and animals, the usual concept of species is very difficult to apply. The sexually reproducing diploids may be comparable to species in other organisms. But the autopolyploids and allopolyploids that combine the characteristics of two or more diploids in asexually reproductive and therefore very fertile organisms break down the utility of criteria based upon morphological intergradation, gene exchange, and geographic distribution. Combining the classic techniques of taxonomy with the methods of cytogenetics, however, the biologist may be able to identify the major evolutionary units within the complex. To these he customarily gives the rank of species, while the multitude of apomictic forms may be described, with or without formal taxonomic recognition, as appears most useful.

Aside from greatly complicating the work of the biologist, what are the effects of apomixis as a genetic system? It is obvious that apomixis makes possible the survival of many genotypes that are vigorous and well-adapted but sexually sterile for one reason or another, e.g., in unbalanced polyploids. Apomixis also permits the building up of large numbers of genetically similar individuals for the rapid colonization of newly available habitats. One finds apomixis often to be the genetic system of weedy or pioneer organisms and of those in habitats subject to frequent or regular catastrophe, such as sand bars, lawns, etc.

It is also true that apomixis limits the genetic variability of the organisms that have adopted it as their sole mode of reproduction. For this reason, it generally is found to be an alternative or secondary genetic system. Apomixis usually is not combined with other systems that reduce the long-range flexibility of the organism for the sake of immediate fitness (e.g., self-fertilization). It is interesting that, even in those groups, such as *Poa*, where apomixis and high

polyploidy are carried to what appear to be extremes, the situation is not, as usually described, "dead end." The pollen of obligate apomicts may be functional, and pollination of an apomict may occasionally result in the segregation that leads to an escape from asexuality.

SUMMARY

Populations of plants and animals often exhibit cytogenetic mechanisms controlling the amount and nature of genetic recombination. These mechanisms, along with others previously mentioned, make up the genetic system of the population that determines how many new gene combinations are produced in a unit of time. They range from inversions and translocations, which produce relatively small groups of linked genes, through polyploidy with its diverse and variable effects, to apomixis, in which recombination is eliminated. Such mechanisms are often considered disadvantageous in the very long-range view. However, they are extremely common in both plants and animals and must result in a selective advantage. The bizarre and complicated genetic systems of some organisms discussed are poorly understood and have not been satisfactorily integrated into evolutionary theory.

REFERENCES

- Darlington, C. D. 1958. *The Evolution of Genetic Systems*. 2d ed. Basic Books, Inc., New York. A remarkable attempt to unify cytology and genetics in evolutionary terms.
- Sager, R., and F. J. Ryan. 1961. *Cell Heredity*. Wiley, New York. This is a recent source for material on the genetic systems of microorganisms.
- Stebbins, G. L. 1960. The comparative evolution of genetic systems. In Sol Tax [ed.], *Evolution After Darwin*, Univ. Chicago Press, Chicago, vol. I. *The Evolution of Life*, pp. 197-226. A thorough recent account of the problem, together with speculations concerning answers.
- White, M. J. D. 1954. *Animal Cytology and Evolution*. 2d ed. Cambridge Univ. Press, New York. The standard reference for genetic systems in animals, though now somewhat out-of-date. Other references to animals will be found in *Evolution After Darwin*, vol. I, cited above.

3

populations: differentiation

The process of evolution is sometimes divided into microevolution (changes within populations) and macroevolution (the origin of major variation patterns). Where to draw the distinction is an arbitrary decision, which we prefer not to make. In the preceding section we have considered primarily changes within populations. In this section the ways in which evolving populations change and interact to produce the diverse life forms on the earth are presented.

Chapter 10 deals with the basic splitting process of evolution: the ways in which a single evolving entity becomes two or more entities. This subject is discussed first by comparing different patterns of diversification which have been observed and then attempting to explain how they might have come about.

Chapter 11 is concerned with the patterns produced over long periods of time by populations evolving and dividing and also becoming extinct. No special factors are postulated to account for the evidence derived from a study of the fossil record, which is accepted as fragmentary and biased in various ways. The same processes that produce elaboration of different populations across a diversified habitat are viewed as being responsible for the elaboration of populations through time. The apparent problem of how "higher" taxonomic categories arise is considered an artifact created by the taxonomic method applied to situations where much extinction and loss of data have occurred.

10

the differentiation of populations

It is obvious to anyone observing the variation of living things in nature that organisms do not vary continuously. Variants of one type of organism may be arranged in a continuum, but there are gaps in the variation from continuum to continuum. Plants and animals, viewed by our usual techniques of studying organisms, seem to be aggregated into discrete or nearly discrete clusters usually called species. Certainly the living world may be structured by the scientist in many ways different from this customary taxonomic one; some of these may be of considerable interest to the evolutionist. In the last chapter of this book some of the problems involved in perceiving and describing structure and pattern in nature are discussed. Nevertheless, it is possible to recognize taxonomic units and to classify them; this has led biologists to attempt to understand the origin of such units in nature. This generally has been studied from the point of view of how a single supposedly interbreeding population can differentiate into discrete clusters. The processes presumed to be involved make up what is frequently referred to as *speciation*.

Elucidating the mechanisms of speciation often has been regarded as the central problem of evolution. Darwin's classic work was entitled *The Origin of Species . . .*, and many monographs in both botany and zoology in recent years have emphasized the so-called species level of recognizable biological difference. This emphasis may have had the effect of obscuring some exceedingly important and interesting problems usually thought of as falling within the province of ecology (for example, the nature and evolution of communities of plants and animals). However, in discussing here the question of how recognizable aggregates of similar organisms arise in nature, we for the moment shall accept the commonly used analyses and designations.

One usually gains the impression from even a casual study of living things that there is a spectrum of degree of similarity among organisms. Some forms appear to be very distinct from all others; some appear to intergrade almost imperceptibly with others that are closely similar. In approaching the problem of how populations become differentiated, it will be useful to consider the nature and size of the gaps in variation between clusters of similar organisms. In this chapter, examples from the spectrum of variation will be discussed, examples in which the degree of differentiation is relatively small. To put it another way, we shall examine situations that seem to be close to branch points in the evolutionary tree—organ-

isms that seem to be on the verge of fragmenting into multiple entities, and multiple entities that appear to be of rather recent origin. A series of examples is presented first, to give the reader some "feel" for the types of patterns that occur. The probable causes of these patterns are then discussed, illuminated with further brief examples. The very distinct forms will be dealt with in Chap. 11.

In what follows, the term character will denote any trait that varies in the overall group under discussion. Thus the presence or absence of plastids is a character when one considers all organisms. For any given organism one can determine whether or not it possesses plastids. Their presence or absence is not a character in roses for they are uniformly present. Femur length is a character in man because it varies within the group and can be measured for any individual. Femur length is also a character when adult mice and adult men are compared, but the ranges of observed variation in this character are not overlapping. Such discontinuities in variation (in single characters or in constellations of characters) are here referred to as gaps.

EXAMPLES OF DIFFERENTIATION

Continuous Geographic Variation

In many instances, variation is sufficiently continuous so that no dividing lines between segregates are obvious. Variation in some characters may occur in gradients. These gradients in single characters are called *clines*, and the variation is then called *clinal*.

Color, Pattern, and Size Variation in Animals. Geographic variation in color, pattern, and size is one of the most widely studied of all biological phenomena. This variation is often of the sort already described in the previous chapter (*Biston*, *Cepaea*, *Natrix*) in which populations differ primarily in the frequency of different types of individuals present. Another example is the North American tiger swallowtail butterfly, *Papilio glaucus*, some populations of which are composed of yellow and black striped (tiger) males and females, and other populations of tiger males, tiger females, and uniformly dark-brown females. In southern Canada and the extreme northern United States the populations of *P. glaucus* are composed only of tiger individuals. In south central Florida the proportion of dark-brown females is very low (6 to 8 percent), and in southern Florida dark females may be completely absent. In most of the southern United States, however, populations show high frequencies (up to 50 percent) of dark-brown females.

In many cases, variation is not in *frequency* of types (partially intrapopulational). Individuals within a given population may all be closely similar (little intrapopulational variation), but color or pattern may change from population to population in broad geographic trends. Among mammals and birds the tendency for populations in colder, drier parts of the range to be lighter than those in the warmer, more moist parts is so common as to have been dignified as Gloger's rule. Other so-called "ecological rules" deal with variation (not necessarily continuous) in size and shape. One (Bergmann's) states that homoiothermal vertebrates in warm areas tend to be smaller than those from cool areas. Another (Allen's) states that all projecting parts (wings, legs, noses, etc.) tend to be shorter in cooler areas than in warm ones.

Ecotypic Variation in Plants. Botanists have attached more importance than have zoologists to the local population as a basic unit, perhaps because of the greater ease with which the less motile plants may be studied. The work of Clausen, Keck, and Hiesey over many years has been directed to an analysis of the variation within and between populations of plants widely distributed in California. Making use of field growing stations at Stanford (sea level), Mather (4,600 feet), and Timberline (10,000 feet), they have been able to separate, to a large extent, environmental and genetic components of variation. Perennial plants that can be propagated vegetatively may be grown at all these locations and their physiological responses to environmental factors thus investigated. In effect, the same genetic individual may be studied simultaneously in three different ecological situations. Studies such as these have led to recognition of the ecological race or ecotype of plants.

The genus *Achillea* (yarrow) in the sunflower family has already been mentioned. By means of transplant studies, Clausen, Keck, and Hiesey have analyzed the *A. millefolium* complex in some detail. The plants are found throughout the Northern Hemisphere, where they grow from sea level to timberline. There is continuous morphological variation, from plants some 6 feet high in the San Joaquin Valley to alpine plants only a few inches in height. Other morphological traits also intergrade from population to population, so that taxonomic distinctions are difficult to determine.

Adjustment of *Achillea* plants to their environment depends on the proper integration of many physiological processes, such as rates of photosynthesis and respiration, resistance to cold, and time of dormancy and other periodic phenomena. Each local population is composed of many different genotypes. Depending upon the level of study, these can be viewed as aggregated into groups of varying

size. Clausen, Keck, and Hiesey concluded from transplant studies along a 200-mile transect of California that the genotypes and local populations are arranged into at least 11 physiological races. Two taxonomic species are represented along this transect, where they occur in different habitats. *Achillea lanulosa*, of the higher elevations, is primarily a species of continental habitats, whereas *A. borealis* occurs at lower altitudes and is a coastal species, in the main. It is interesting to note that in the northern portion of its range, where *A. lanulosa* comes to the coast, it has developed coastal ecotypes that mimic those of *A. borealis*.

It may well be that plants, being rooted, become adjusted to the local conditions with a precision that would not be of selective value in animals.

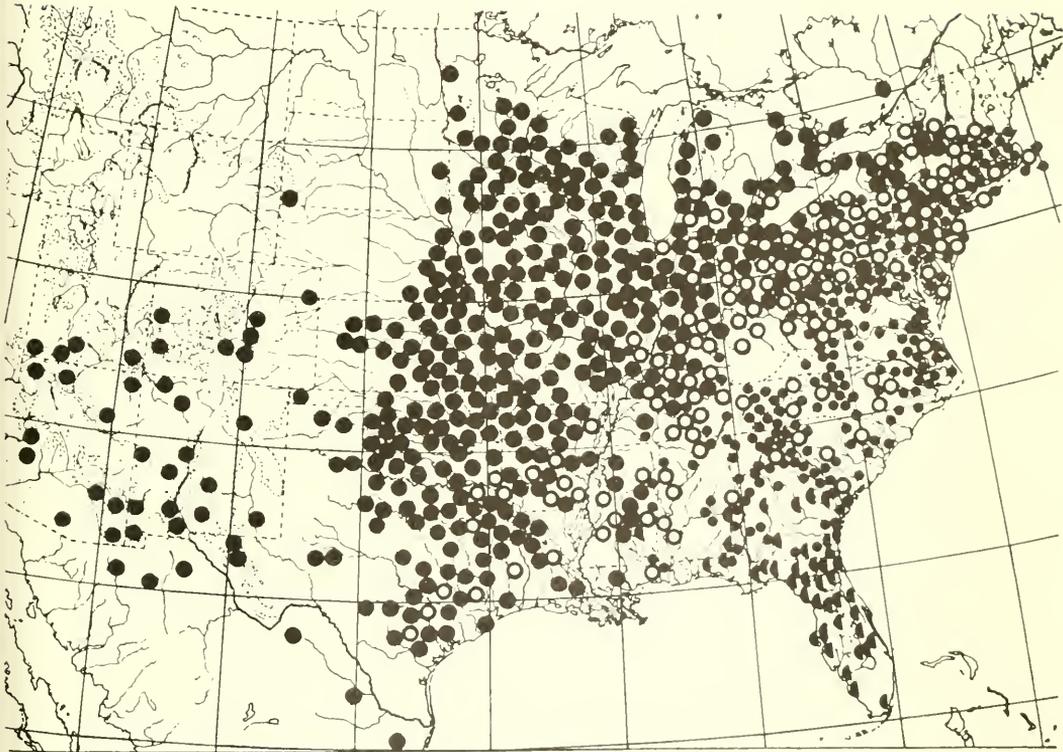
Clinal Variation in Plants. The butterfly weed (*Asclepias tuberosa*) also shows geographic variation, but it has been studied in a very different manner. The subspecies occurring in the eastern two-thirds of the United States have been studied in great detail by Woodson. The distribution of these subspecies is shown in Fig. 10.1. Only *A. tuberosa tuberosa* and *A. t. interior* will be discussed here. In most parts of their range these subspecies can be distinguished by the shape of the leaf. Fortunately, two important components of leaf shape can be quantified and the change in shape studied geographically. These components are angle *A*, a measure of the taper of the apex of the leaf, and angle *B*, which measures the shape of the base of the leaf. The two subspecies meet along a broad front in the eastern United States, and there is a zone of intergradation, as can be seen in Fig. 10.1. Woodson has studied geographic variation by dividing a map of the country into equal-area quadrats and measuring the herbarium specimens collected in these areas. He has also studied local-population samples and has measures of variation within and between individuals and colonies.

By comparing the measurements of specimens collected in 1946 along a 1,200-mile transect from Kansas to Virginia with the available herbarium specimens from the quadrats in which the transect falls, Woodson was able to study the effect of time. The herbarium specimens, collected over a period of many years, represent a sample which is, on an average, older than the 1946 transect. It was clear that characteristics of *A. t. interior* were moving eastward, while those of *A. t. tuberosa* were moving westward but at a much slower rate. When, in 1960, samples were once again collected along the transect, the changes that had occurred in the 14-year interval could be accurately measured. Apparently reciprocal diffusion of the

eastern and western genotypes of both $\angle A$ and $\angle B$ has occurred. Woodson interprets the eastern subspecies to be in the process of genetic submergence by the western one, since its western movement is proportionately less. Nevertheless, its effects on the western leaf shape can be clearly seen.

Clinal Variation in Animals. In some cases, although the geographic variation is continuous, experimental evidence indicates that a considerable amount of differentiation has occurred. Variation in the leopard frog, *Rana pipiens*, is extensive and discordant. The

Fig. 10.1 | Map showing distribution of *Asclepias tuberosa*. Each symbol represents a county record. Large dots, *A. t. interior*; small dots, *A. t. tuberosa*; hollow circles, putative hybrids between subsp. *tuberosa* and subsp. *interior*; half-circles, *A. t. rolfsii*. (From Woodson, 1947, *Ann. Missouri Bot. Gard.* 34.)



variation in 12 characters is summarized in Table 10.1. No overall pattern of variation is evident; indeed, many of the characters seem to vary completely independently. Moore's detailed studies of variation in developmental processes have yielded abundant provocative data. For instance, northern and southern populations of *R. pipiens* show different temperature-tolerance ranges for normal embryological development (Fig. 10.2). These differences parallel those found between northern and southern frogs belonging to clearly distinct clusters. (For example, the northern *R. sylvatica*, which ranges from the subarctic to the central United States, can develop normally between 2.5 and 24°C, whereas *R. catesbiana*,

Table 10.1 | Population Formulas for Meadow Frogs of Eastern North America

Quebec	A	B	C	D	E	F	G	H	I	J	K	L
Maine	A	B	C	D	E	F	g	H	I	J	k	L
Vermont	A	B	C	D	E	F	G	H	I	J	K	L
N. New York	A	B	C	D	e	F	G	H	I	J	K	L
Massachusetts	A	b	C	D	E	F	G	H	I	J	K	L
Rhode Island	A	B	C	D	E	F	G	H	I	J	K	L
S. New York	A	b	c	d	E	f	g	h	i	J	k	l
New Jersey	A	b	c	d	e	f	g	h	i	J	k	l
Maryland	a	B	c	D	e	F	g	h	i	J	k	l
North Carolina	A	b	c	D	e	F	G	h	i	J	k	l
South Carolina	—	b	—	D	e	f	g	h	i	J	—	—
Georgia	a	b	c	d	e	f	g	h	i	J	k	l
Florida	a	b	c	d	e	f	g	h	i	j	K	l
Ontario	—	B	C	D	E	F	G	H	I	J	K	—
Michigan	—	B	C	D	e	F	G	H	I	J	—	—
Wisconsin	A	B	C	D	E	F	g	H	i	J	K	L
Minnesota	—	B	C	D	e	F	g	H	i	J	K	L
South Dakota	A	B	C	D	e	F	g	H	i	J	K	L
Nebraska	—	B	C	D	e	F	g	h	i	J	k	L
Indiana	A	B	C	D	e	F	g	H	i	J	k	l
Kentucky	a	B	c	D	e	F	g	H	i	J	—	—
Illinois	a	B	C	D	e	F	g	H	i	J	k	l
Missouri	A	B	C	D	e	F	g	H	i	J	k	L
Kansas	A	B	C	D	e	F	g	H	i	J	k	L
Arkansas	A	B	c	D	e	F	g	H	i	J	k	l
Oklahoma	a	B	C	D	e	F	g	H	i	J	k	l
Mississippi	a	b	c	D	e	F	G	h	i	J	k	l
Louisiana	a	B	C	d	e	F	G	h	i	J	k	l
Texas	a	B	C	D	e	F	g	H	i	J	K	L

After Moore, *Bull. Am. Mus. Nat. Hist.*, 82, 1944.

Definition of Symbols

A, Head width/head length 0.92 or greater	a, Head width/head length less than 0.92
B, 50% or more with tibia bars	b, Less than 50% with tibia bars
C, Average number of tibia bars (when present) 1.4 or greater	c, Average number of tibia bars (when present) less than 1.4
D, 50% or more without femur bar	d, Less than 50% without femur bar
E, 50% or more without tympanic spot	e, Less than 50% without tympanic spot
F, 50% or more with light reticulum	f, Less than 50% with light reticulum
G, Number of dorsal spots less than 13	g, Number of dorsal spots 13 or more
H, Number of lateral spots 12 or more	h, Number of lateral spots less than 12
I, More lateral than dorsal spots	i, Lateral spot number equal to, or less than, dorsal spot number
J, 50% or more without lateral reticulum	j, Less than 50% without lateral reticulum
K, 50% or more of males with oviducts	k, Less than 50% of males with oviducts
L, 50% or more of males with no, or poorly developed, external vocal sacs	l, Less than 50% of males with no, or poorly developed, external vocal sacs

living from southern Canada to Mexico, has a range of 15 to 32°C; where these two overlap, *R. sylvatica* breeds in the early spring, *R. catesbiana* in midsummer.)

Laboratory crosses of individuals from different populations of *R. pipiens* produce normal offspring when the parents are drawn from populations that are geographically adjacent (e.g., central and southern Florida) or lie at roughly the same latitude (e.g., Texas and central Florida). However, the greater the north-south gap separating the home populations of the parents, the greater also is the proportion of defective (inviable) offspring. Eggs from Vermont females fertilized by New Jersey or Wisconsin males do not differ in development from those fertilized by Vermont males. If the spermatozoa that fertilize the eggs come from a Louisiana male, some abnormal development occurs, but there is no significant increase in mortality. Texas-Vermont hybrids have many developmental difficulties, and mortality may reach 100 percent. In a single cross between a male from an eastern Mexican population and a Vermont female most of the hybrid embryos died in the gastrula or neurula stage. Thus, the *R. pipiens* situation might be considered analogous to that of *Ensatina* discussed below. In the

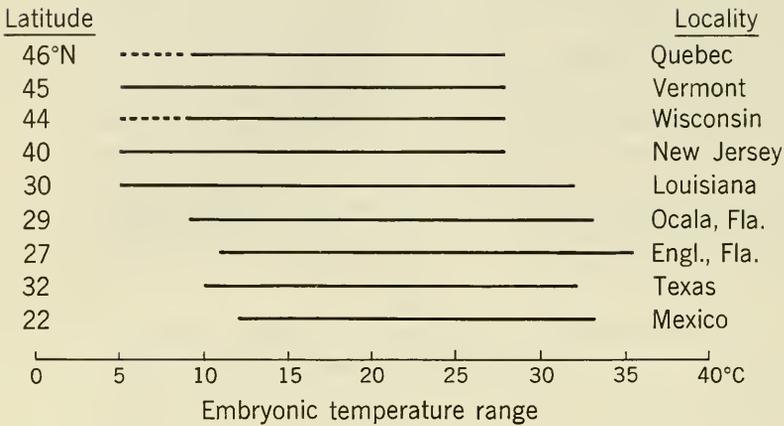


Fig. 10.2 | Temperature tolerance ranges for normal embryological development of *Rana pipiens* from different localities. The lower limit for Quebec and Wisconsin has not been determined but is believed to be identical with Vermont. (From Moore, 1949, *Evolution* 3.)

Rana case, however, the distribution does not form a ring, and the terminal populations of the series do not occur together in nature.

The British satyrine butterfly *Coenonympha tullia* shows a pattern of differentiation reminiscent of *Rana*. Crosses between individuals from widely separated populations resulted in some broods in which a number of “females” were intersexual, indicating some genetic incompatibility. (This result follows Haldane’s rule that inviability or sterility in hybrids will most likely appear in the heterogametic sex, in this case the females.) In crosses between less distant populations no abnormalities were found. However, this butterfly has not been as intensively studied as the gypsy moth, *Lymantria dispar*, for which Goldschmidt has described many degrees of intersexuality in crosses between populations of various levels of differentiation. For those interested in details, this work is well summarized by Dobzhansky.

The First Stages of Genetic Isolation. Populations of some animals that are connected by long series of intermediate forms may occur together and remain distinct. For instance, an interesting pattern of variation has been described in the plethodontid sala-

manders of the genus *Ensatina*. These animals live along the western coast of North America from southwestern British Columbia to southern California. In California they are confined to coastal areas, the Sierra Nevada, and southern interior mountain ranges. There is considerable geographic variation in color pattern and, to a lesser extent, in size (Fig. 10.3). The coastal populations are brown or reddish-brown above, while the Sierra and interior populations become progressively more spotted with yellow, cream, or orange as one travels southward. In the Sierra Nevada, at the latitude of San Francisco Bay, there is an enclave of populations similar to those of the coast, and individuals intermediate between the Sierra Nevada and coastal types are also found. In the characters studied (and with the exception just mentioned) there seems to be rather continuous north-south variation, although taxonomists have broken the continuum into a series of "subspecies" and "zones of intergradation." However, where the southern coastal and inland types meet south of the Central Valley, there is a rather sharp discontinuity in the variation. Strikingly different uniformly colored and blotched forms have been found within 0.2 mile of each other in habitats on the southeast side of Mount Palomar.

In Mill Canyon, above Banning, California (about 50 airline miles north of the Palomar locality), in 1962 R. C. Stebbins¹ and C. W. Brown discovered both forms living together, as well as one apparent hybrid and several possible backcross individuals. Whether or not hybrids will also be found where the two forms meet on the slopes of Mount Palomar remains to be seen.

A similar situation has recently been reported for neotropical fruit flies, *Drosophila paulistorum*. In this case, the pattern is more complex than that described for *Ensatina*, there being three areas where two groups occur together without interbreeding. In these areas not only is hybridization not detected, but in laboratory tests where the forms were denied the opportunity of mating with their own kind, not even cross-insemination (let alone the production of viable hybrids) was found. However, in laboratory tests it was possible to exchange genetic information between these forms by using a series of intermediate "bridging" cage populations sampled from other geographic areas. How much actual exchange takes place in nature through such bridging populations is an open question. Such complex situations are found in more and more organisms as detailed studies are made.

¹ We are deeply indebted to Dr. Stebbins for keeping us informed of the progress of this most interesting work.

Closely Related Isolates

Species Swarms in Fishes. The east African lakes, Victoria, Tanganyika, and Nyassa, support a large number of closely related fish species of the family Cichlidae. For example, in Lake Victoria are found some 70 endemic and 6 nonendemic species of the genus *Haplochromis* living in three different ecological zones. One group consists of deep-bodied forms with short snouts, horizontal mouths, equal jaws, and bicuspid outer teeth (Fig. 10.4). These fish are found inshore and are bottom feeders. The cichlids of a second group have more slender bodies and longer snouts, their mouths are slightly oblique, their lower jaws prognathous, and their outer teeth conical and caniniform (Fig. 10.4). The members of this group are fish-eating predators, hunting the middle depths of open and inshore waters. A third group of *Haplochromis* are slender and long-snouted. They have very oblique mouths (in two forms almost vertical), extreme prognathism of the lower jaw, and caniniform outer teeth (Fig. 10.4). These are predaceous surface feeders, eating principally other fish and insects.

There is only a moderate amount of diversity in this large complex of closely related distinct clusters. Although some of the forms are virtually indistinguishable morphologically, they have been found to be ecologically differentiated and to have distinctive breeding coloration. The greatest morphological variation is in the teeth and structures of the head, which is hardly surprising in view of the diverse feeding habits within the group.

Sibling Species of Alpine Butterflies. In some cases, superficial similarity may disguise a rather large amount of diversity. Lorkovič has shown that the holarctic butterflies of the *Erebia tyndarus* group, although very much alike in outward appearance, have wide divergence in chromosome number ($n = 8, 10, 11, 15, 24, 25, 51,$ and perhaps 52) and (to a lesser extent) in the morphology of the male and female genital structures. Such outwardly similar forms are often called sibling species. In the western Alps (Fig. 10.5) two forms, *Erebia cassioides* ($n = 10$) and *E. nivalis* ($n = 11$), occupy two barely overlapping ecological zones, the former in the subalpine (1,400 to 2,400 meters) and the latter in the alpine (2,300 to 2,700+ meters). Although *E. cassioides* and *E. nivalis* share a narrow border strip, there is little evidence of gene flow between them. Only 2 of 400 specimens examined were not unequivocally assignable to one species or the other. The two forms have quite distinct life cycles, *E. cassioides* completing its development in one year, *E. nivalis*

Fig. 10.3 | *Ensatina* in western North America. Discussion in text.
(After Stebbins, 1949, *University of California Publications in Zoology* 48.)

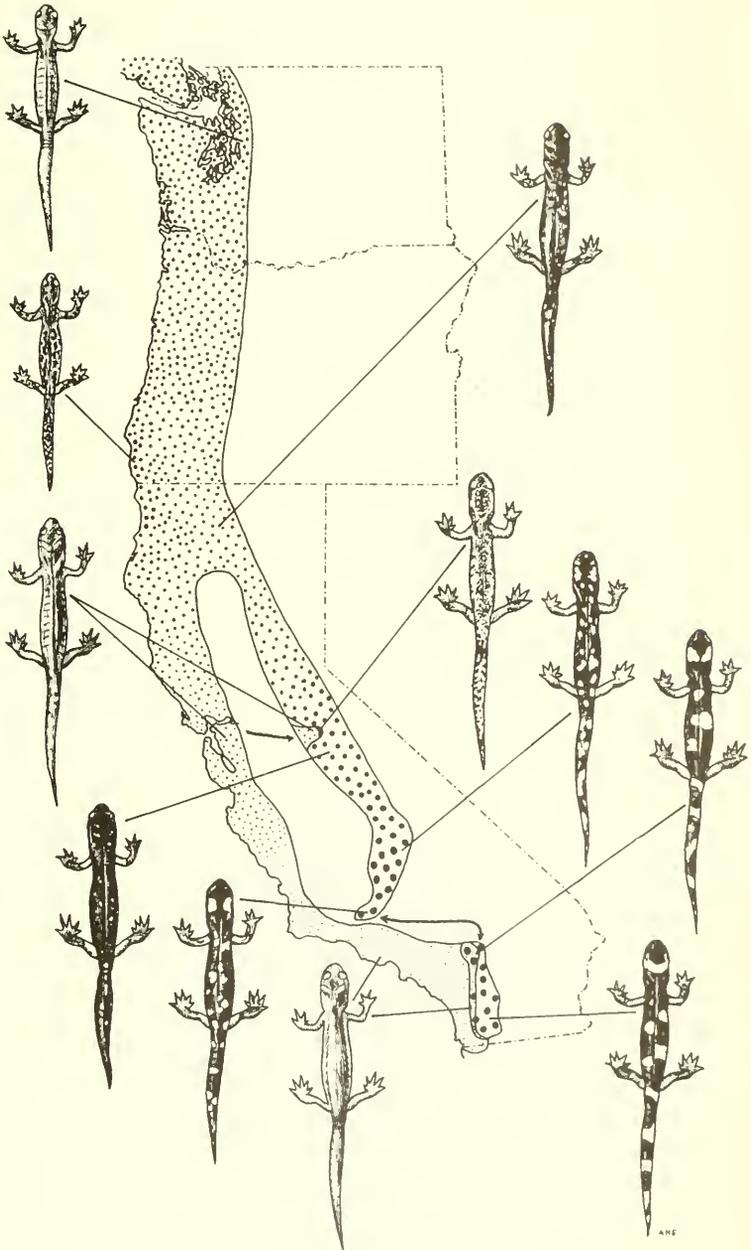
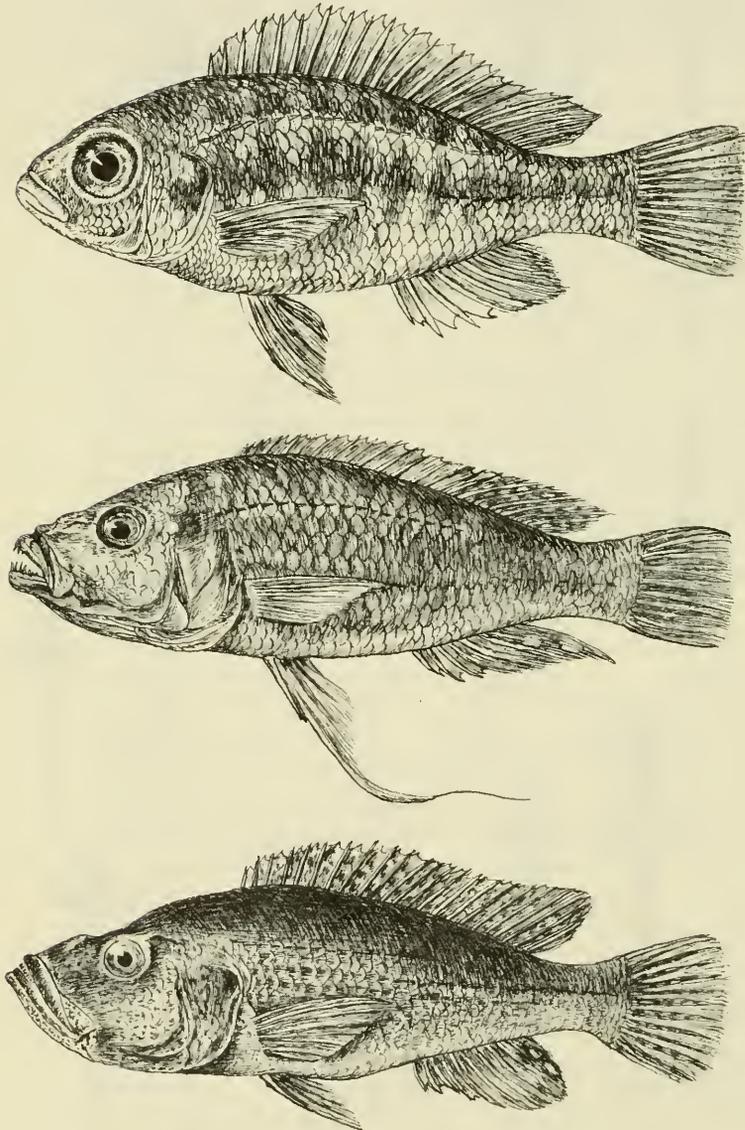


Fig. 10.4 | Cichlid fishes (*Haplochromis*) from Lake Victoria, Africa. Top, *H. macrops*; center, *H. bayoni*; bottom, *H. cavifrons*. These fishes are approximately 100, 180, and 145 mm long, respectively. [After Boulenger, 1915, *Catalogue of the Fresh-water Fishes of Africa in the British Museum (Natural History) III.*]

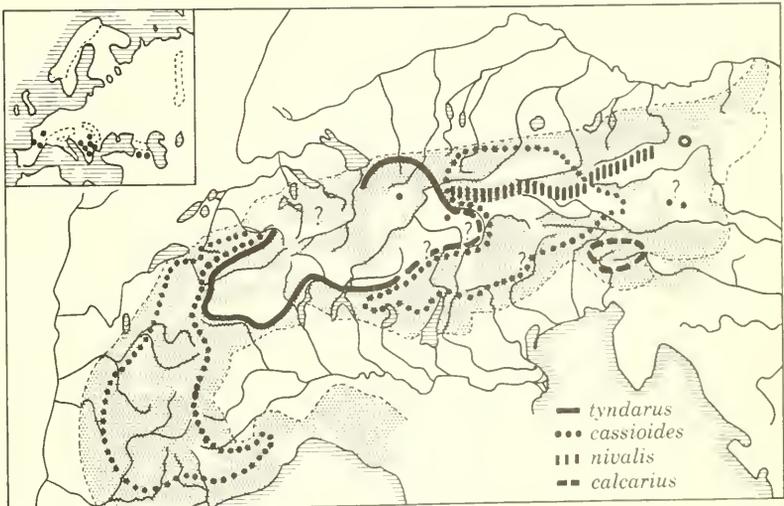


requiring two. Laboratory crosses indicate strong behavioral isolation (females not responsive to males of the wrong form; copulation, when induced, abnormally brief), and hybrids, when produced artificially, are wholly sterile and unlike any individuals found in nature. In short, the two forms seem to be completely isolated from each other genetically.

Erebia cassioides, however, has a wider geographic distribution than *E. nivalis*, and in regions where *E. nivalis* is absent it extends to altitudes as high as those occupied by *E. nivalis* where both are present. Conversely, in some areas where the mountains do not reach great heights, *E. nivalis* lives at lower elevations, with *E. cassioides* correspondingly lower or absent.

Erebia tyndarus ($n = 10$) occurs in essentially the same life zone as *E. cassioides*, but as one can see from Fig. 10.5 the two are not sympatric. *Erebia tyndarus* occurs in the central Alps, with *E. cassioides* on the east and west. Experimental crosses (*E. tyndarus* females \times *E. cassioides* males) showed little behavioral isolation, and about 15 percent of the eggs from these crosses hatched with 25 percent survivorship among the young larvae. Although the ranges of *E. tyndarus* and *E. cassioides* adjoin very closely, both in

Fig. 10.5 | Map showing distribution of butterflies of the *Erebia tyndarus* group in central Europe. (From Lorkovič, 1957, *Biološki Glasnik* 10.)



the east and west, there seems to be no significant overlap. Indeed the three species, *E. tyndarus*, *E. cassioides*, and *E. nivalis*, show a striking aversion to coexistence. A fourth alpine species, *E. calcarius* ($n = 8$), is found in the Julian Alps, but its exact spatial relationship with *E. cassioides* is not known at this time.

The Galápagos Finches. A large cluster of distinct closely related groups is found in the subfamily Geospizinae of the finch family (Fringillidae). These birds, known collectively as Darwin's finches, are restricted, with a single exception, to the Galápagos Islands. One member of this group is found on Cocos Island. First studied by Darwin, they have been the subject of brilliant monographs by Lack and Bowman. There are some 14 distinct kinds of finches, considered by ornithologists to represent six genera. Table 10.2 lists these species.

The 14 species are distributed in various patterns over the islands, individual islands within the Galápagos having between 3 and 10 species each (Fig. 10.6). The birds differ primarily in size and in the form of the beak and in other structures related to their feeding habits (Fig. 10.7). There is almost a complete continuum in the amount of differentiation. The cluster known as *Platyspiza crassirostris* is distributed over eight of the islands but shows almost no inter-island differences in the characters studied. The warbler finch, *Certhidea olivacea*, is found on all the Galápagos and shows considerable variation in color from island to island. For instance, the upper parts of both sexes vary from gray-brown (James Island) to very pale gray (Barrington Island). Superimposed on this is variation in the amount of olive tinge. The under parts range from pale

Table 10.2 | Species of Darwin's Finches (Geospizinae)

Name	Description and Habits	Number of Islands on Which Species Is Permanent Resident
<i>Geospiza magnirostris</i>	Large; forages on ground and in bushes and trees. Feeds on small variety of very hard, generally large seeds.	14
<i>Geospiza fortis</i>	Medium; habits as above. Feeds on large variety of moderately hard, small to large seeds.	12
<i>Geospiza fuliginosa</i>	Small; forages on ground more than <i>G. fortis</i> or <i>magnirostris</i> .	

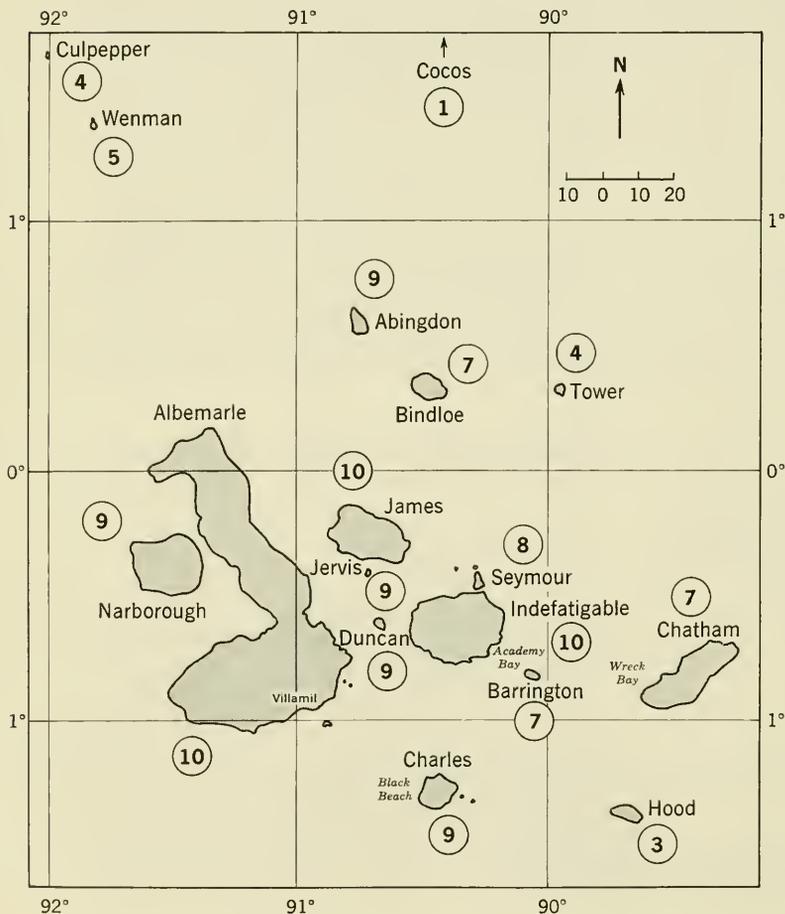
	Feeds on large variety of soft, generally small seeds.	14
<i>Geospiza difficilis</i>	Medium; forages on ground. Presumably takes soft seeds.	7
<i>Geospiza scandens</i>	Medium; rests mostly on <i>Opuntia</i> cactus. Feeds on a small variety of moderately hard seeds, also soft plant tissues and nectar.	11
<i>Geospiza conirostris</i>	Large; habits poorly known but similar to <i>G. scandens</i> .	3
<i>Platyspiza crassirostris</i>	Large; mostly in dense brush and high trees. Feeds mainly on fleshy fruits, soft to moderately hard seeds, young leaves, and flowers.	10
<i>Camarhynchus psittacula</i>	Medium; forages in trees, brush, and occasionally on ground. Primarily insectivorous, excavating fairly deeply into woody tissues, usually on larger branches.	11
<i>Camarhynchus pauper</i>	Same as <i>C. psittacula</i> , which it replaces on Charles Island.	1
<i>Camarhynchus parvulus</i>	Small; forages in trees, brush, on cactus, and on ground. Primarily insectivorous, excavating less deeply than <i>C. psittacula</i> , usually on smaller twigs and in lichens.	12
<i>Cactospiza pallida</i>	Medium; tanager-like habits. Probes with stick or cactus spine; primarily insectivorous.	7
<i>Cactospiza heliobates</i>	Medium; habits poorly known, primarily insectivorous. Restricted to coastal mangroves.	2
<i>Certhidea olivacea</i>	Small; warbler-like. Forages at all levels in trees, occasionally at ground level. Takes only animal food, especially small larvae.	16
<i>Pinaroloxias inornata</i>	Medium; reported feeding on ground and in trees. Presumably takes insects, nectar, and some fruits.	1

Source: Modified from Bowman (1961).

olive-buff (James Island) and wash-brown (Culpepper, Wenman, Charles Islands) to white (Barrington Island).

The peripherally distributed *G. conirostris* is, except for size, quite similar to the central *G. scandens*, the two forms being completely allopatric. Three ground finches (*G. magnirostris*, *G. fortis*, and *G. fuliginosa*) are widely sympatric and differ superficially in overall size and relative beak size. Where the three forms occur together

Fig. 10.6 | Map of Galápagos Archipelago showing main islands. Numbers give the total of different kinds of Geospizine finches recorded from each island. (After Bowman, 1961, *University of California Publications in Zoology* 58.)



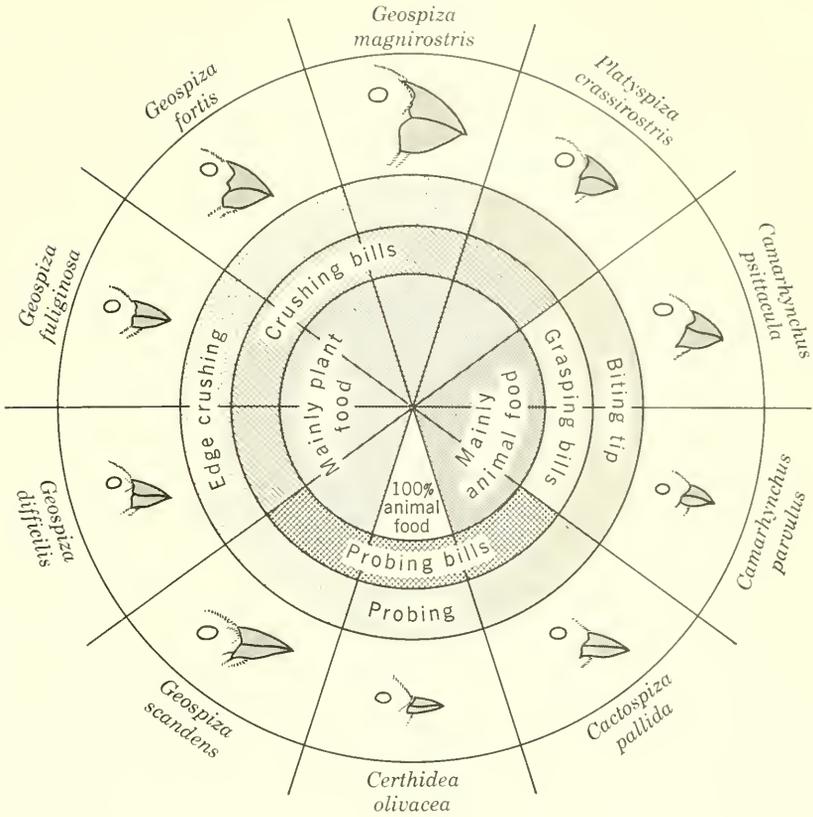


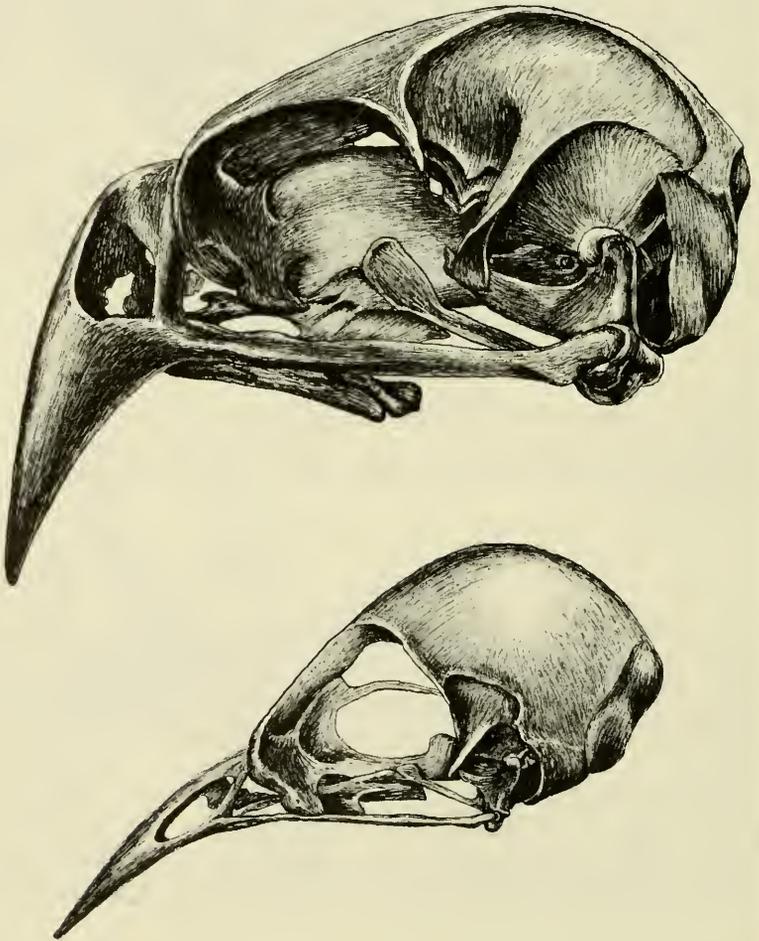
Fig. 10.7 | Schematic representation of the relationship between bill structure and feeding habits in 10 species of Geospizinae from Indefatigable Island. (From Bowman, 1961, University of California Publications in Zoology 58.)

there is almost no overlap in measurements, and observations indicate that individuals recognize and mate only with members of the proper form. The three forms sometimes take the same food; their feeding habits are overlapping but not congruent, as shown in Table 10.2.

The two members of the genus *Cactospiza*, *C. pallida* (the tanager-like finch) and *C. heliobates* (the mangrove finch), are very similar. Both forms are primarily insectivorous, *C. pallida* having the unique habit of excavating for beetles and other insects with its

beak and then probing the excavations with a cactus spine or twig. This remarkable behavior compensates for the lack of a long tongue to use as a probe and is one of the few instances of birds using a "tool." On the only island occupied by both *C. pallida* and *C. heliobates* (Albemarle Island) their ecological differences isolate them (*C. heliobates*, in the coastal mangrove belt; *C. pallida*, inland).

Fig. 10.8 | Extremes of differentiation in skulls of Galápagos finches. Upper, *Geospiza magnirostris*; lower, *Certhidea olivacea*. (After Bowman, 1961, *University of California Publications in Zoology* 58.)



Therefore they are allopatric, although in one case they both live on the same island. The extremes of differentiation within the genus can be seen (Fig. 10.8) by comparing the skulls of the broadly sympatric *Geospiza magnirostris* (the large ground finch) with *Certhidea olivacea* (the warbler finch).

Darwin's finches show a pattern of differentiation opposite to that found in most groups of birds. The most closely related forms of these finches differ primarily in the size and shape of the beak, whereas closely related forms of other birds are usually differentiated most strongly by plumage color. The very closely related Asiatic nuthatches, *Sitta tephronota* and *S. neumayer*, are clearly differentiated by plumage pattern as well as bill length but only where they are sympatric (Fig. 10.9). Where their ranges are separate they are almost indistinguishable. This exaggeration of differences in an area of sympatry is an example of character displacement, a phenomenon common in birds. Other instances have been described in ants, beetles, crabs, fishes, and frogs. Two kinds of termites have been reported to swarm at the same time of day where they are allopatric and at a different time of day where their ranges overlap. Possible causes of character displacement will be discussed in the second half of this chapter on pages 242–244.

Host Preference in Parasitic Organisms

Differentiation in host preference is widespread among parasitic organisms. This phenomenon has been studied in such diverse organisms as cuckoos, human lice, and nematodes. Cuckoos have developed an unusual form of differentiation. They show what has been called "brood parasitism"; that is, they lay their eggs in the nests of other kinds of birds. In most cases the cuckoo egg is incubated by the foster parents, and the voracious cuckoo hatchling crowds its pseudosiblings out of the nest, eventually monopolizing the food brought by its adopted parents. Usually the egg laid by the cuckoo bears a remarkable resemblance to that of the host bird (Fig. 10.10). Cuckoo species seem to be subdivided into groups, each of which tends to lay its eggs in the nests of only one kind of host bird. These subdivisions, called *gentes*, are not geographically isolated from each other, individuals of one being found in close proximity to individuals of one or more of the others.

There are two distinct forms of human lice (*Pediculus humanis*), head lice and body lice, which differ strongly in their "ecology" but are nearly identical morphologically. Head lice, as the name implies, are found primarily in the relatively fine hair of the head. Their eggs are glued to hair. Body lice, on the other hand, live in the clothes,

sucking blood where the clothes are in contact with the body. Body lice attach their eggs to the clothing.

The common human nematode parasite, *Ascaris lumbricoides*, is morphologically and serologically indistinguishable from the pig parasite, *A. suum*, but in most cases eggs from one will not develop properly in the host of the other.

DISCUSSION OF OBSERVED PATTERNS

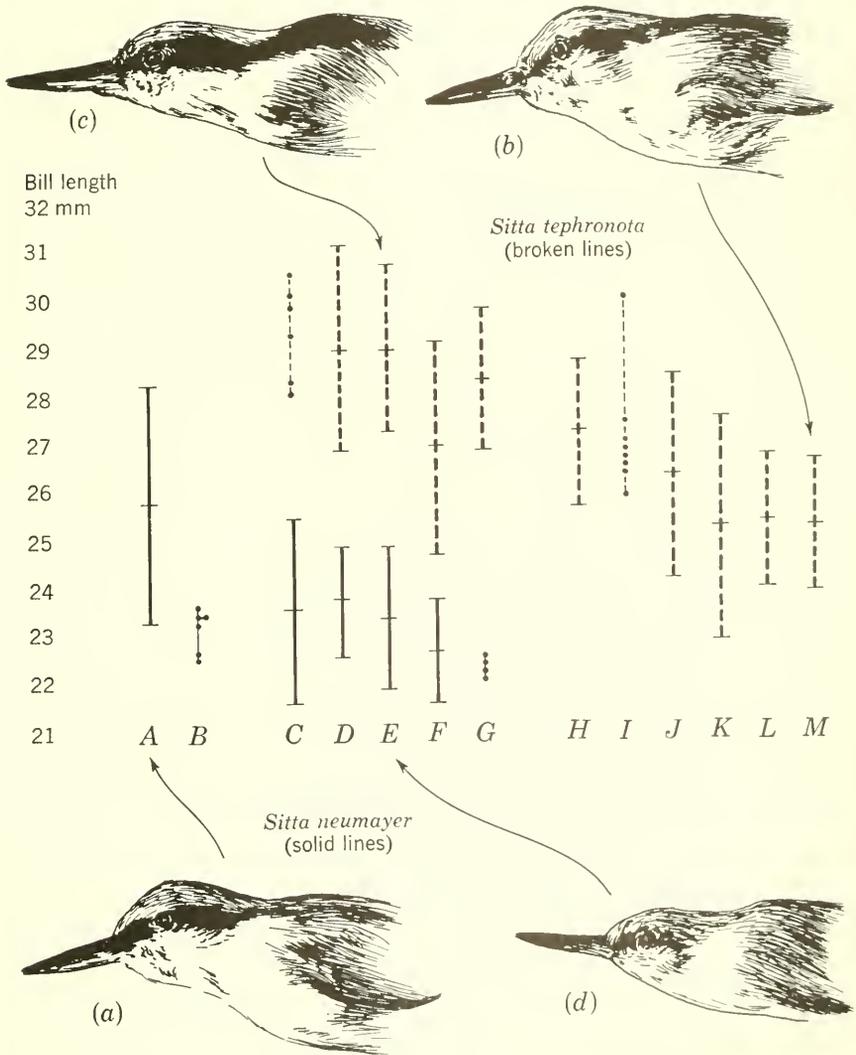
The basic reason for the diverse patterns of differentiation described in the preceding section is that the physical environment is, and always has been, heterogeneous. This heterogeneity has meant that evolutionary forces, especially selection, have operated differentially. In turn, this has produced a heterogeneous biotic environment and further differentiation in the forces operating in any portion of that environment.

It is all too easy to fall into the mistake of assuming that differentiation of populations into genetically isolated forms is somehow the "goal" of evolution. Differentiation often takes place, but usually those instances where incipient species become submerged again are unrecorded. When morphological divergence of two populations has progressed to a certain point, often we no longer say that they interbreed, we say that they hybridize. This implies that they have somehow or other made a "mistake." The fact that occasional genetic interchange enriches the variability of both populations is forgotten. Differentiation is not necessarily a step toward the formation of isolated populations. It is merely one of the many things that happen to populations in nature.

Geographic Variation in Selection Pressures

Geographic variation, in most cases, may be attributed primarily to the different selection pressures prevailing in different areas. Thus *Achillea* growing at high altitude is under selection pressure that favors dwarfed forms physiologically adjusted to rigorous mountain-top conditions. Lowland *Achillea* are not subjected to the same pressures but to others. *Natrix sipedon* populations have adjusted both to "normal" swamp habitats and to the special conditions present on the Lake Erie islands. *Cepaea* populations face selection pressures partially determined by local vegetation types, and *Biston* populations to pressures varying with the relative presence or absence of industrial pollution. The frequency of the so-called "sickle-cell" gene in human populations varies geographically; it is high in regions where malignant tertiary malaria is present, low elsewhere.

Fig. 10.9 | Character displacement in Asiatic nuthatches. Bill length and facial stripe in the two species are very different in areas where they occur together but are quite similar where they occur alone. Populations west of the zone of overlap (*Sitta neumayer*): A, Dalmatia and Greece; B, Asia Minor. In the zone of overlap: C, Azerbaijan and Northern Iran; D, Kermanshah; E, Luristan and Bakhtiari; F, Fars; G, Kirman. East of the zone of overlap (*S. tephronota*): H, Persian Baluchistan; I, southern Afghanistan; J, Khorasan; K, north-central Afghanistan north of the Hindu Kush; L, northeastern Afghanistan (Pamirs); M, Ferghana and western Tian Shan. (After Vauric, 1950, *Am. Mus. Novitates* 1472.)



Biologically sophisticated readers will be familiar with myriad examples in which differences due to different selective pressures (due to different environments) have been inferred. For the student a very few more are added. Arctic foxes (following Allen's rule) have short ears and snouts, whereas tropical foxes have long ears and snouts, presumably because the low surface-volume ratio in the former helps conserve body heat, whereas the high ratio in the latter permits the heat to dissipate more rapidly. Indeed, both Allen's and Bergmann's rules seem to be simply functions of the surface-volume ratio problems concerned with heat retention and dissipation. A great many homoiotherms show clinal variation in conformance with these rules, but physiological work to support their validity is mostly lacking.

Populations of *Papilio glaucus* have high frequencies of dark females in certain areas, supposedly because these dark-brown females resemble the *Aristolochia* swallowtail (*Battus philenor*), which is also found in these areas. *Battus philenor* has been shown to be distasteful to birds, and birds have been observed feeding on adult *P. glaucus* in the field. Selection apparently favored the development and maintenance of the mimetic form of *P. glaucus* in these areas.

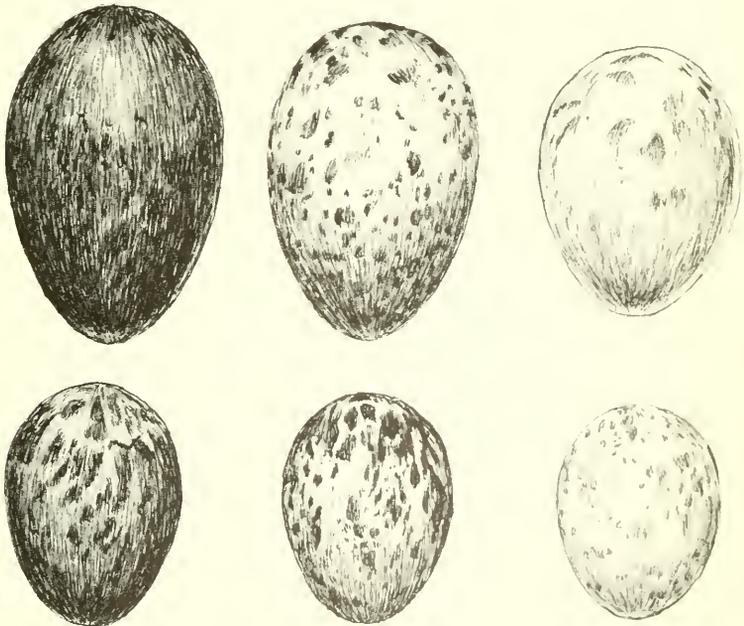
In the high Sierra Nevada of California two forms of the butterfly *Oeneis chryxus* are found, a light form in areas of granite rock and a dark form in areas of basaltic rock. The selection pressure involved has not been discovered, but the correlation suggests the work of an as-yet-undetected visual predator. Similar examples of geographic variation in color and in the habitat of many groups of animals have been reported and could be multiplied indefinitely—geographic variation is ubiquitous, and selection has been shown to play a major role in differentiating most populations that have been studied thoroughly. It is a truism to state that populations of organisms in different places will, under most circumstances, be genetically different.

The variation described in *Asclepias* seems attributable to a combination of differing selection pressures and genetic drift. *Asclepias tuberosa* is a long-lived perennial growing in colonies of several to many plants. The effective population size is estimated to be less than the median census size of 11 plants. One would expect that, in populations of this small size, genetic drift would become an important factor in evolution, and the data suggest that it is. Nevertheless, there appears to be a strong selective component in the changes that have occurred along the transect during the 14 years. It is not possible to discuss these in detail, but it is clear that the western genotypes for $\angle A$ and $\angle B$ are selectively better off than the com-

parable eastern genotypes. In *A. tuberosa interior* the genotype for $\angle B$ has a selective value about three times that for $\angle A$. During the 14 years there has been a decrease of about 30 percent in variability for both $\angle A$ and $\angle B$.

In both years, about midway along the transect there appeared to be a zone of heterozygosity expressed as greater variability as well as greater size and apparent vigor. It is probable that hybridization between these subspecies, which were separated from one another during the Pleistocene glaciation and which have subsequently come together, has resulted in an increase in vigor and an extension of range. This study is one of the few in which populations have been investigated over a period of years. Unfortunately, however, *Asclepias tuberosa* is not a good subject for genetic studies. The cytogenetic bases for the phenomena that have been detected bio-

Fig. 10.10 | Egg mimicry. Upper row, eggs of Asiatic crows, *Corvus coronoides*, *C. splendens insolens*, and *C. s. protegatus*; lower row, eggs of the cuckoo *Eudynamis scolopacea* laid in the same nests as the three crow eggs. (After Baker, 1923, *Proc. Zool. Soc. Lond.*)



metrically are not known. Many other interesting aspects of variation in this species of *Asclepias* also are poorly understood but are being studied by Woodson. These include the apparently centrifugal variation of *A. tuberosa interior*, which has resulted in a concentrically distributed peripheral subspecies in the western and northern parts of the range, and an interesting variation pattern with respect to color of the flower (which can be studied biochemically).

Exchange of Genetic Information

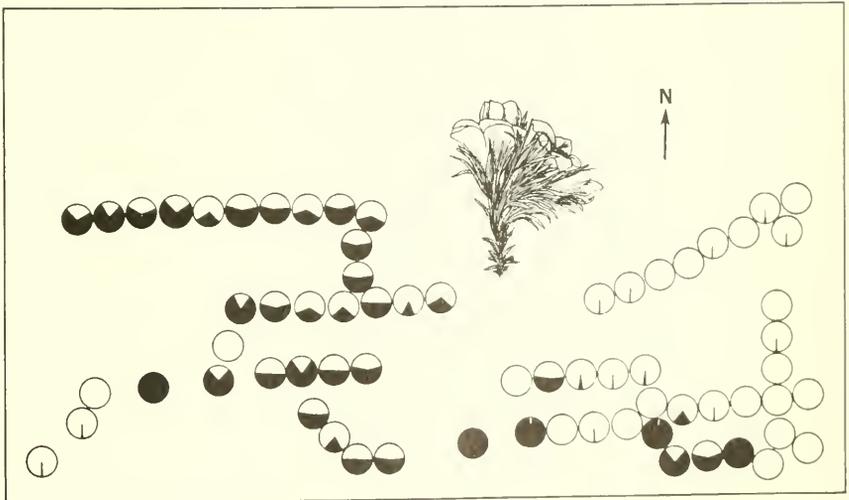
In organisms with relatively continuous distributions, exchange of genetic material among populations will limit the amount of differentiation that can take place. The "mixing" effect of recombination is most pronounced in adjacent populations, which, because of the relative similarity of their environments, are less subject to differentiation through selection. The situation is reversed for widely separated populations in a series. A certain amount of genetic information is passed back and forth through the intervening populations, but the ability of this weakened gene flow to swamp out genetic differences is greatly reduced. In most instances these more distant populations have been subjected to quite different selection pressures, enhancing the trend toward differentiation. This is well illustrated by the *Rana pipiens* and *Coenonympha tullia* cases, in which distant populations are strongly differentiated but pairs of adjacent populations show little differentiation.¹ A classic example of isolation by distance is found in populations of a single species of a California desert plant. Around the southern and western edges of the Mojave Desert a small annual, *Linanthus parryae* (Polemoniaceae), shows an interesting pattern of variation. With good rainfall, the plants form an essentially continuous carpet over large areas. In 1941 *L. parryae* was studied intensively between Palmdale and Lucerne Valley, where it had developed a practically continuous population over some 700 square miles. In most areas investigated, the plant samples consisted of white-flowered forms, but in three isolated sections samples with varying numbers of blue-flowered individuals were collected. The composition of the samples taken from the westernmost of these areas between Palmdale and Llano is shown in Fig. 10.11. The central variable area is separated from

¹ It is possible that gene flow between distant populations of some series is so slow that the migration effect might be practically indistinguishable from mutation as a source of variability.

the western one by a 25-mile gap and from the eastern one by an 8-mile gap.

The frequency of blue-flowered individuals in samples from these "variable areas" is shown in Fig. 10.12. This frequency distribution of *phenotypes* is reminiscent of the theoretical gene-frequency distributions in small populations subjected to some selection pressure (see Fig. 6.9). The curve in Fig. 10.12 cannot be fully interpreted because the genetic bases of the observed variation are unknown. However, the U shape is strongly suggestive of populations sufficiently small for considerable random fixation and loss of genes producing blue flowers to have occurred. It seems likely that selection, drift, and isolation by distance all interact to produce the observed pattern of variation in *Linanthus*. Some unknown selective factor probably gives a small advantage to blue-flowered plants in the "variable areas," while the small effective population size (calculated by Wright to be 14 to 27 plants) permits considerable drift. In addition, the usual desert year (much drier than 1941) would

Fig. 10.11 | Map showing composition, with respect to flower color, of samples of *Linanthus parryae* from an area in southern California. Black sectors, blue flowers; white sectors, white flowers. (From Epling and Dobzhansky, 1942, *Genetics* 27, and after Abrams, 1951, *Illustrated Flora of the Pacific States*, Stanford University Press.)

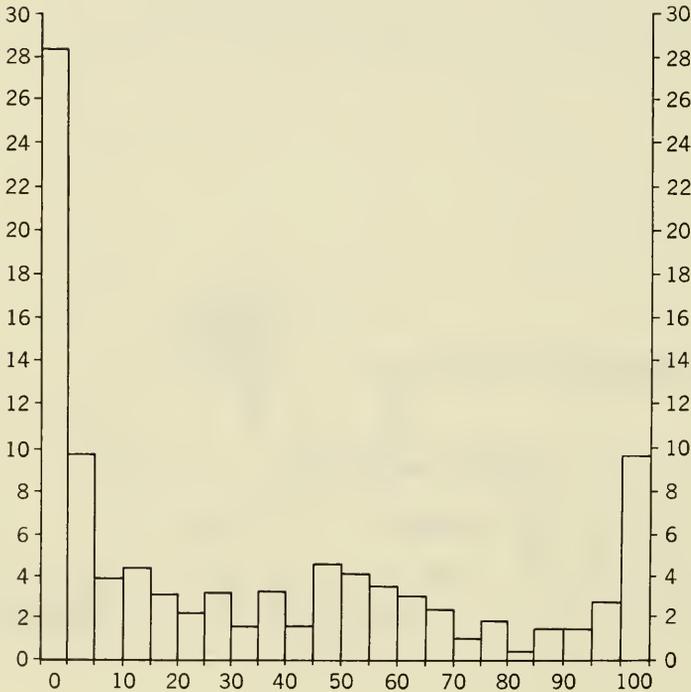


produce only scattered *Linanthus* populations. This, combined with a possible low gene flow in the species (caused by pollinators transferring pollen mostly between nearby flowers), would help to maintain the established pattern.

Cessation of Gene Exchange

When the distribution of an organism becomes broadly discontinuous, exchange of genetic information between populations (or groups of populations) may cease entirely. Such situations may develop in many ways. Emerging land may divide a marine habitat. The Isthmus of Panama has been repeatedly submerged through geologic time. With each new emergence some populations of

Fig. 10.12 | Frequency of samples of *Linanthus parryae* containing different proportions of plants with blue flowers. Ordinate, percentage of samples; abscissa, percentage frequency of blues. (From Epling and Dobzhansky, 1942, *Genetics* 27.)



marine organisms, previously more or less continuously distributed, become isolated. There is considerable evidence that glacial advances during the Pleistocene repeatedly fragmented the ranges of many organisms. Repeated changes of continental seaways (Fig. 10.13) have isolated and reconnected portions of the continents, causing manifold changes in the continuity of the distributions of organisms.

Climatic changes have profound effects on the distributions of plants and animals. Trends toward aridity produce desert or steppe barriers to the passage of organisms requiring high humidity or dense plant cover. Drought may cause large lakes to divide into numerous smaller lakes and rivers to be reduced to isolated series of pools. Increasing rainfall, on the other hand, tends to reunite isolated bodies of water, encouraging gene exchange in aquatic organisms while forming barriers for terrestrial organisms. Belts of high humidity form barriers for desert and steppe organisms.

It is interesting to note that discontinuities in the distribution of an animal are not necessarily the result of barriers which the individuals are *unable* to cross. In many cases behavior patterns prevent dispersal across areas that could easily be traversed if the attempt were made. Thus rivers may serve to isolate bird populations on opposite banks, or a narrow strip of woods may effectively separate two meadow populations of butterflies.

Isolation

Whatever its cause, physical isolation permits the differentiation of populations of sexually reproducing organisms. Isolation is often referred to as if it were the *cause* of differentiation. It is not, of course; recombination between isolates is prevented, so that each isolate responds only to the selection pressures of its own environment. If an organism is continuously distributed along a humidity gradient, the establishment of populations at the ends, which are adjusted to high and low humidity, will be hindered by the transfer of genetic information back and forth along the gradient. If the middle of the continuum is destroyed, differentiation can continue without such interference. By definition, the environments in which two newly isolated fragments of a population find themselves cannot be identical. Thus the two isolates are subjected to different selection pressures. Because of sampling error, the two new isolates will be of different sizes and will have gene pools that are not identical, so that evolutionary forces will be operating in unlike genetic environments. Since mutation is a random process, it is not to be expected that identical mutations will show up in the two isolates. Thus,

through physical isolation, a single evolving unit may become two or more evolving units. As long as such evolutionary units remain isolated, they are free to respond independently to evolutionary forces. However, should circumstances permit such units to regain contact, numerous possibilities are presented.

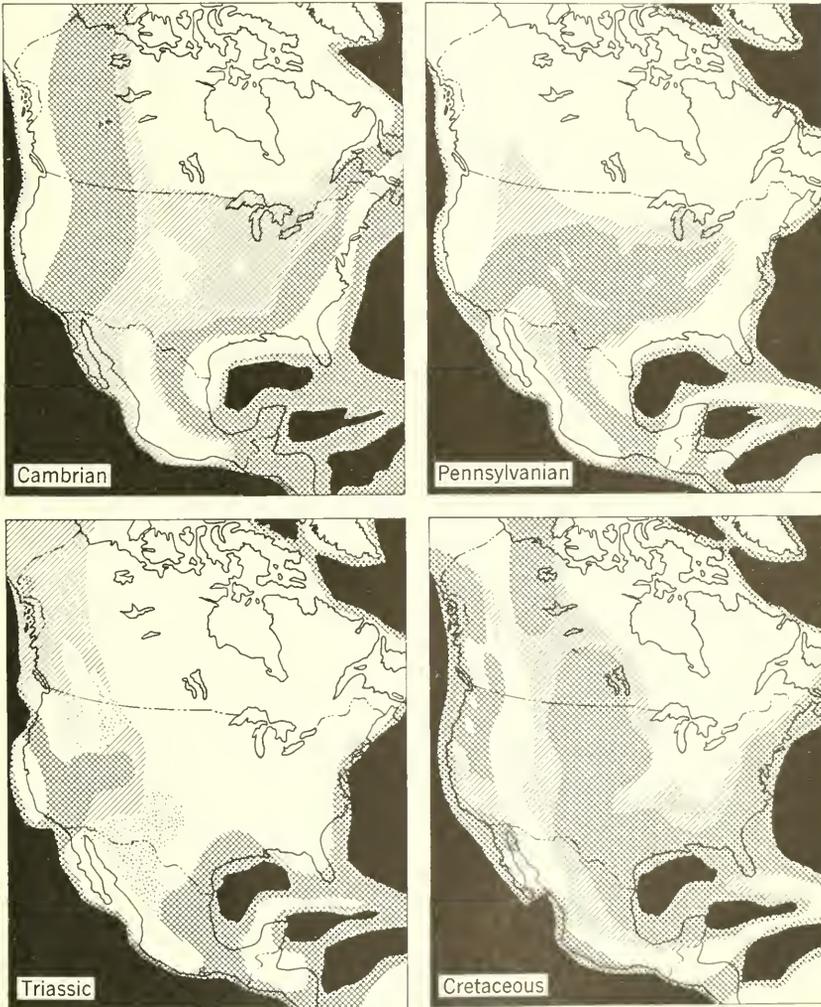
Through the course of time there have occurred innumerable environmental changes that might have brought previously isolated populations back together. The effects of ancient cataclysms have been modified or completely erased from the record. Two relatively recent overlapping events have undoubtedly produced effects which are conspicuous today. The first of these events is the Pleistocene glaciations, which changed climate on a vast scale, causing plants and animals to migrate or perish. The glaciers also scoured the earth, mingling soil types, creating lakes, and rearranging drainage systems.

The advent of man has had similar effects. It is difficult to overestimate the importance of man as a factor in evolution. First with fire and then with domesticated plants and animals, he has modified the environment. Many of the instances of interbreeding of previously separated forms are the result of man's conscious or unconscious intervention. By breaking into the vast stored-energy reserves of climax ecological communities, man has diverted energy for his own purposes and grossly modified what we even yet think of as the "natural" (prehuman) environment.

Fusion of Populations. At one extreme, populations may have been isolated for such a short time or subjected to such similar conditions that divergence has been minimal. When the populations reunite, individuals mate at random and the offspring from matings between parents of different populations are as successful as those from members of the same isolate. The two previously isolated populations then fuse into a single population. This is seen whenever *Drosophila* lines, isolated for a few generations in the laboratory, are combined, or when guppies kept for a few years in one aquarium are dumped in with those that have been kept in another. The situation is certainly very common in nature also; it has not been given very much attention by zoologists.

Meeting with No Gene Exchange. At the other end of the spectrum, populations that have diverged a great deal may come together and all attraction between individuals of the different populations may have been lost, resulting in no interpopulation matings. In most cases this means that gene flow between the evolutionary units has ceased, although, as in *Drosophila paulistorum*, genetic information may still be exchanged by such isolates via a "ring of races." The pattern in *Ensatina* is of great interest, as it is

Fig. 10.13 | Distribution of seas in the northern Western Hemisphere during four geologic periods. Black, oceanic areas; dark gray, most persistent seaways on the continental platform; light gray, areas submerged during part of period only; dotted light gray, areas of temporary flooding; white, persistent land areas. (From Moore, 1949, *Introduction to Historical Geology*, McGraw-Hill.)



not yet known whether the differentiated terminal populations will fuse or whether they will differentiate further to produce a typical ring-of-races pattern. Situations where two or more similar kinds of organisms live in close proximity without apparent hybridizing are numerous, but there seem to be no documented cases where rejoining segregates have shown no interest in each other. This does not indicate that such situations never develop, merely that they have not been observed.

Perhaps the most likely candidate for a situation in which two closely related kinds of animals have become sympatric and have not required selection against hybrids to reinforce isolating mechanisms (as described below) is in the flycatcher genus *Empidonax*. N. K. Johnson has recently studied an area in eastern California in which two forms, *Empidonax wrightii* (gray flycatcher) and *E. oberholseri* (dusky flycatcher), are sympatric. It is possible that this sympatry is of very recent origin, the result of habitat changes brought on by logging operations in the middle of the last century. *Empidonax wrightii* breeds in sagebrush or small trees and tends to forage in open areas, whereas *E. oberholseri* is a forest-chaparral bird. Where they overlap in an area of mixed clearings and broken forest the birds retain their habitat separation but defend their territories *interspecifically*. The two kinds are so similar that they can be distinguished with assurance only by careful wing measurements and wing-tail ratios. Johnson has been able to detect distinct differences in vocalizations, presumably concerned with pairing and pair-bond reinforcement, but the challenge calls and appearance are so similar that *E. oberholseri* territories are defended against *E. wrightii* and vice versa. In spite of this similarity, several dozen mated pairs collected by Johnson all showed positive assortment (no *oberholseri-wrightii* pairings), indicating that the birds have no trouble in properly choosing mates. Perhaps the recognition signs (whatever they may be) were originally weaker and were reinforced by selection, but if this was the case the process must have been completed very rapidly.

Limited Gene Exchange. In a similar case of sympatry, presumably permitted by human disturbance of the environment, two kinds of Mexican towhees, *Pipilo erythrophthalmus* and *P. ocai*, have come into contact and are now hybridizing. In this case previous ecological isolation (*P. erythrophthalmus* mostly in oaks and brushy undergrowth, *P. ocai* mostly in coniferous forest and associated undergrowth) seems to have broken down when lumbering and agriculture produced second-growth situations suitable to both forms. Indeed, hybridization at one level or another is widespread

among birds (e.g., gulls, ducks, grackles, grosbeaks, honeycreepers, birds of paradise) and is usually interpreted as occurring in zones of secondary contact. Whatever its interpretation, it is evident that differentiation of bird populations may be a much more complicated process than one would assume from the neat arrays of "species" and "subspecies" found in bird checklists.

Similarly, it has been shown rather clearly that in many groups of plants considerable genetic interchange is possible after the so-called specific level of differentiation has been reached. This may be entirely at the diploid level, or it may involve polyploidy and apomixis. Examples of the latter have been discussed in Chap. 9. Most instances of such hybridization fall into the category of what has been called introgressive hybridization. The chances of an F_1 hybrid offspring crossing with another such hybrid in the early stages of hybridization are much less than the probability of crossing with one or the other of its parents. The hybrid derivatives are almost always intermediate with respect to their ecological requirements, just as they are intermediate with respect to morphological traits. Backcrosses to one parent or another will thus be more likely to find an appropriate ecological niche than the F_1 or F_2 individuals. The result is that genetic submergence of the two hybridizing entities is unlikely to occur. Rather, portions of the germ plasm of one species will infiltrate the genotype of the other. Variability of the parental types will be increased in the direction of the hybridizing entity, and the species or subspecies may be able to increase its range and to move into habitats previously unoccupied.

An interesting example of this in the sunflower genus (*Helianthus*) in California has been studied by Heiser. *Helianthus annuus* is a common weedy species found in most of the United States; there is considerable evidence that it was introduced into California by Indians in relatively recent times. *Helianthus bolanderi* occurs in California in two races. One is almost completely restricted to serpentine soils, an ecological situation in which relatively few and specialized plants are found. The other subspecies is a weedy form. Heiser has shown that the weedy race of *H. bolanderi* probably originated from the introgression of genetic material of the widespread weedy *H. annuus* into the serpentine race of *H. bolanderi*. The details of how this came about need not concern us here, but by making the appropriate crosses the derived subspecies can be synthesized in the laboratory. It is interesting that the introgression has been reciprocal; in addition to creating a larger, weedier form of *H. bolanderi*, it has resulted in the formation of a smaller form of *H. annuus*, apparently with extended ecological amplitude.

Most species of plants seem to be strongly restricted ecologically. Where the ecological barriers are strong, genetic interchange does not often take place, and the hybrids with their intermediate ecological preferences do not survive. But when the ecological barriers break down, as in habitats subject to erosion or disturbance by man or glaciers, for example, the intermediate types may suddenly find suitable habitats and become common. When crossing between two species does occur, the result usually is not the swamping of the original species but the enrichment of the variation of the parental forms. Indeed, this appears to be very common in many genera of perennial plants studied in the United States.

Selection against Hybrids. It seems likely that, when highly differentiated populations rejoin, selection operating against hybrid individuals usually reinforces factors tending to prevent hybridization. The exchange of genetic information between the isolates often becomes negligible. It is entirely possible that, when more is known about the processes of differentiation, it will be discovered that hybridization between individuals of rejoining segregates is almost universal, in other words, that mechanisms preventing exchange of genetic material between differentiated forms usually arise only through relatively unsuccessful hybridization after sympatry has been reestablished.

An interesting experimental demonstration of this mechanism was obtained by Koopman, who synthesized artificial mixed populations of *Drosophila pseudoobscura* and *D. persimilis* and held them at low temperatures (16°C) at which sexual isolation between the two is at a low ebb (i.e., hybrids are formed more readily at low than at high temperatures). Under the experimental conditions, the hybrids were extremely unsuccessful, but Koopman intervened to produce complete failure of hybridization by removing all hybrid individuals before they could reproduce (hybrids were identified by genetic markers).

Over a period of several generations the proportion of hybrids formed showed a marked decrease, indicating a reinforcement of whatever factors were operating to prevent hybridization. Koopman was able to show that the isolating mechanism was at least in part sexual; i.e., males "preferred" to mate with females of their own kind.

In nature, *D. pseudoobscura* and *D. persimilis*, although occurring in the same geographic areas, presumably do not hybridize for two reasons. First of all, there is considerable ecological isolation, *D. persimilis* usually occurring higher in the mountains and preferring cooler, shadier spots than *D. pseudoobscura*. Sexual isolation must also play a part, for except at low temperatures newly captured

flies show little tendency to hybridize. It is suspected that other undetected factors also help to keep the two entities apart in nature. In the experiments just described, the two known factors were removed by crowding the flies together at low temperatures. In a very short time the action of natural selection established a barrier that was at least partly sexual where one had not existed previously.

Unfortunately, we know very little about which combinations of gene flow and hybrid inviability lead to fusion of reuniting segregates and which lead to total differentiation. This is a wide open field for study.

Patterns of Differentiation

The Galápagos Finches and African Cichlids. The complexity of differentiation patterns must not be underestimated. A great many forces seem to have interacted to produce the complicated pattern observed today in the Galápagos finches. It is likely that the Geospizinae are all descended from a small flock (perhaps a single pair) of fringillid ancestors which accidentally reached the islands from the South American mainland. It is highly unlikely that the immigrants would have represented a large and random sample of the parental population; indeed, they were most likely a small and biased sample, containing only a restricted segregate of the parental gene pool. This sampling error means that the selective forces on the islands, even if they were similar to those of the mainland, would operate differentially on the island birds, because they are operating in a genetic environment quite different from that on the mainland. Remember that, in discussing the operation of evolutionary forces, a single locus cannot be considered in isolation; the effects of pressure on one locus will depend in part on the composition of the entire genotype. Sampling error and the resultant change in genetic environment that commonly occurs when new colonies are established have been described as the *founder principle*. It is, of course, a special case of genetic drift.

Once the finches were established on one island, it was only a matter of time before migrants reached others in the group. Populations on different islands, being subjected to different selection pressures and the effects of the founder principle, probably differentiated rapidly. When migrations and remigrations brought differentiated forms into contact, selection in many cases must have operated against the tendency to hybridize, as described above. Size and shape of the beak of Galápagos finches are related to the kinds of food eaten and also are used by the birds for identifying mates. Abundance of different food sources varies among the

islands, and it is likely that selection caused some differentiation in the beaks and associated structures in isolation. When contact was reestablished, selection probably caused greater differentiation of these structures because they were important in recognition. Such differentiation also seems to have an additional advantage in reducing the types of individuals eating the same kind of food. Such selection for "reduced competition" obviously occurs, but its exact mode of operation is unclear.

The history of the *Haplochromis* swarm must have been similar to that of the Galápagos finches. Migrants from river systems colonized ancient Lake Victoria. Multiple colonizations (separated by appropriate time intervals) could alone account for the observed diversity. New arrivals found old immigrants already partially differentiated; selection against hybridization finished the job. In addition, repeated cycles of drying and inundation may have alternately fragmented and reunited segregates, permitting the mechanisms of differentiation to act. It is also possible that areas of different types of bottom, shoreline, water depth, etc., acted (and act today) as intrinsic barriers to the dispersal of the various forms within the lake.

Sibling Butterfly Species. The *Erebia tyndarus* group is another excellent example of the subtle interactions possible between differentiated forms. For instance, in spite of their different life-cycle adjustment to altitude, *E. cassioides* and *E. nivalis* seem to be strongly influenced by each other's presence or absence, the altitudinal restriction appearing where the two forms occur together. The present distributional picture seems to represent the results of differentiated populations interacting over a varied field. As with Darwin's finches, the exact nature of these interactions is difficult to specify. "Selection to avoid competition" is not an explanation in itself. It is necessary to know exactly how differential reproduction of genotypes came about.

Presumably there was some differentiation before meeting. For instance, when the populations ancestral to today's *E. nivalis* and *E. cassioides* populations came together, the *E. nivalis* may have, on an average, lived more toward the upper limit of the joint range and *E. cassioides*, on an average, nearer the lower limit. Then there must have been some advantage accruing to the *E. nivalis* genotypes that "preferred" the high altitude location and those *E. cassioides* that tended to remain low. Perhaps the relative scarcity of the other form reduced the possibility of wasting gametes through unsuccessful hybridization. Then again, maybe unlike larvae tended to cannibalize each other. Perhaps waste products of the *E. nivalis* larvae tended to inhibit the growth of *E. cassioides*, and/or vice versa.

The food requirements of the various isolates may have been too similar, or the number of available niches too restricted to permit the sort of habitat specialization seen in Darwin's finches.

The result is that each form now occupies the areas to which it is best suited. The historical details will probably never be known. Some forms, perhaps, lacking the genetic variability to differentiate further, became extinct. This could happen when severe conditions in an area greatly reduced the food supply, and larvae of another *Erebia* species proved to be much more efficient at utilizing the restricted food supply. Some forms (e.g., *E. calcarius* and western *E. cassioides*) may never have met. It is interesting to note that, in the *E. tyndarus* group, hybrid sterility exists in crosses between distant relatives such as *E. iranica* ($n = 51$) and *E. calcarius* ($n = 8$) where there is no behavioral isolation. These forms have apparently never been in contact; thus the selective basis for the development of isolating mechanisms has never been present.

Differentiation of Parasites. Patterns of differentiation that involve strains preferring different foods or hosts are poorly understood. It has frequently been observed that, in the laboratory, strains of parasitic organisms may be successfully switched from the usual host organism to another by transfer of large numbers. For instance, the human louse, *Pediculus humanus*, can be converted into a rabbit louse. Large numbers are transferred, and the relatively few able to feed survive and reproduce. This process of selection eventually results in a strain that is happy on rabbits but unenthusiastic about men. (Individuals will feed on men, but a colony will not thrive.) A similar selective process may well be responsible for the transformation of head lice into body lice when the former are subjected to the normal environment of the latter. (It has been suggested that the genetic structure of louse populations encourages a plasticity that makes the transformation in either direction relatively simple.) Needless to say, this structure is itself undoubtedly a result of selection. The *Ascaris* may differ from the *Pediculus* principally in that the *Ascaris* are not so protean genetically.

There can be little doubt about the selective advantage accruing to those cuckoos whose eggs closely match those of the host bird. Rates of desertion of eggs laid in the nests of the usual host are much lower than of those laid in the nests of unusual hosts. However, the exact way in which gentes developed and are maintained is still somewhat of a mystery. It seems unlikely that gentes are genetically isolated from each other. There is no sign of differentiation among them *except* in the egg habitus; such differentiation would be expected if each gens was an isolated evolutionary unit. However, because only superficial characteristics are studied in many

ornithological investigations, such differentiation may be present but undetected. There also seems to be no mechanism that could prevent interchange of genetic information in places where several gentes occur together, especially in view of the rather large territories occupied by the males.

The resemblance between the cuckoo egg mimics and the series of mimetic polymorphs found in females of *Papilio dardanus* is largely superficial. The major difference lies in the necessity for the female cuckoos to lay their eggs in the nest of the proper host species. (The choosing of the proper nests by the female cuckoos may be explained by the phenomenon of imprinting.) It is not sufficient for a population to be genetically structured so that a multiplicity of distinct forms is produced; the structure must be such that the proper egg type is laid by a bird which chooses a particular foster parent. Thus if the female cuckoo raised in the nest of a reed warbler were to be inseminated by a male of the gens parasitizing the white wagtail, her eggs might be better mimics of white wagtail eggs than of reed warbler eggs. She would continue to lay her eggs in the "wrong" nest, and in all probability her young would have a relatively low chance of survival. Unfortunately, nothing is known of the genetics of cuckoo egg color, and so the importance of the male contribution is conjectural.

It seems likely that, in both cuckoo gentes and *Papilio dardanus* mimetic polymorphs, differentiation may have taken place in isolation. When two differentiated isolates of the butterflies came into contact in areas where both models were present, disruptive selection established a polymorphic system (as described in Chap. 7). However, when two cuckoo gentes, each parasitizing a different host, came into contact in an area occupied by both hosts, another factor was probably added. In addition to disruptive selection (lower reproductive success of genotypes producing eggs intermediate between the hosts), there was probably also selection favoring behavioral patterns that encouraged positive assortative mating (pairing of individuals raised by the same foster parents). This seems to have been accomplished most successfully where the host forms have somewhat different ecological requirements, the male cuckoos remaining in the familiar habitat where they were reared and consorting with females of like background.

In places where the habitats of the host forms tend to overlap, intermediate-type eggs are often laid and the mimicry breaks down. The gentes of cuckoos seem to be somewhat intermediate between polymorphic forms and what might be called host races. The degree of perfection of the mimicry apparently is dependent on the degree

of ecological isolation enjoyed by the gens. Where gentes occur together in the same general area, there is no sign that this degree of isolation is sufficient to produce enough genetic differentiation to result in reproductive incompatibility. There is every indication that such gentes are *not* “incipient species” and that divergence at the species level occurs in geographic isolation. Needless to say, the exact status of the cuckoo gentes is deserving of much additional study.

Allopatric Speciation

Differentiation of physically isolated populations, when this differentiation goes to the point that reunion of the populations does not occur if contact is reestablished, is known as *allopatric speciation*. An abundance of evidence suggests that allopatric speciation is the fundamental cause of organic diversity. It is the splitting mechanism, which, coupled with extinction, is necessary to explain the large numbers of relatively distinct kinds of plants, animals, and microorganisms that populate the earth.

Little is known about the time required for populations to differentiate. In any given case, many variables would affect the required time span, including population sizes, magnitude of selection pressures, degree of isolation, and the genetic system of the organism. In most cases speciation seems to be a much more drawn-out process than could be conveniently observed by the evolutionist. However, much recent work (e.g., that on industrial melanic moths and on *Cepaea* and *Natrix*) indicates that selection pressures in nature may be generally higher than once thought; if this is the case, then speciation may also occur more rapidly than has been assumed in the past. At any rate, the evidence on which is based the view that allopatric speciation is the primary splitting mechanism in evolution is not direct observation but the presence of patterns of variation that seemingly represent every conceivable stage in the postulated process. Some of these have been discussed in this chapter; the biological literature is replete with others.

Sympatric Speciation

Can distinct new kinds of organisms arise in the absence of physical isolation of populations? The answer is certainly “yes” in the case of allopolyploidy (discussed in Chap. 9) and for organisms in which sexual processes are absent. Each individual of completely asexual organisms (such as some rotifers) is a genetic isolate, and species are

clusters of clones that owe their similarity to interclone selection.

One of the enduring controversies among evolutionary theorists concerns the possibility of sympatric speciation by sexual organisms. Certainly, as stated above, the vast majority of evidence indicates allopatric speciation to be the rule, and many cases that have been presented as evidence for sympatric speciation are easily explained on other grounds (e.g., the cichlid-species swarms). However, one argument against sympatric speciation is that gene flow will swamp out any differences produced by a disruptive selection pressure. There has recently been some provocative work by Thoday and his coworkers and by Streams and Pimentel which indicates that this is not necessarily so. These workers have shown in laboratory experiments with *Drosophila* that disruptive selection can produce divergence in the absence of isolation. For instance, Thoday and Gibson subjected a wild-type population to disruptive selection for chaeta number, with both high and low selected individuals being placed in a common vial for mating. At the end of 12 generations the original population had split into two populations, which produced few hybrids. Therefore, sympatric speciation may not be theoretically impossible, but its significance in nature is yet to be determined. As Slobodkin has aptly stated:

In one sense, the distinction between theoretician, laboratory worker, and field worker is that the theoretician deals with all conceivable worlds while the laboratory worker deals with all possible worlds and the field worker is confined to the real world. The laboratory ecologist must ask the theoretician if his possible world is an interesting one and must ask the field worker if it is at all related to the real one.

In the sympatric-speciation controversy the ball seems to have been passed to the field worker.

SUMMARY

Available evidence indicates that differentiation in isolation is the primary source of organic diversity. Populations physically separated from each other (so that gene flow is minimized or absent) have different evolutionary "experiences" and thus differentiate genetically. If this process proceeds beyond a certain point, the populations will not reunite if contact is once again established. The investigation of this genetic "point of no reunion" and the development of generalizations concerning it are among the most difficult

problems confronting evolutionists. Populations that have become so distinct as to obviate the possibility of future merger may still exchange genetic information, reciprocally obtaining variation that may stimulate further evolution. It should not be assumed, however, that the "purpose" of evolution is to create diversity nor that occasional genetic interchange between nearly isolated groups is in some sense bad or aberrant.

REFERENCES

- Bowman, R. I. 1961. Morphological differentiation and adaptation in the Galápagos finches. *Univ. Calif. Publ. Zool.* vol. 58. The comprehensive source on the Geospizinae. Includes extensive references to the literature, including Lack's classic 1947 monograph.
- Brown, W. L., and E. O. Wilson. 1956. Character displacement. *Systematic Zool.* 5: 49-65. A good series of examples of the phenomenon.
- Clausen, J. 1951. *Stages in the Evolution of Plant Species*. Cornell Univ. Press, Ithaca, N.Y. A brief survey of the classic studies of Clausen, Keck, and Hiesey on ecotypic differentiation in plants.
- Dobzhansky, T. 1951. *Genetics and the Origin of Species*. Columbia Univ. Press, New York. This is the main source for the genetic aspects of population differentiation.
- Keck, David D. 1957. Trends in systematic botany. In *Survey of Biological Progress*, vol. 3. Academic, New York. Many examples of differentiation of populations of plants are discussed.
- Mayr, E. 1963. *Animal Species and Evolution*. Harvard Univ. Press, Cambridge. This scholarly and exhaustive treatise supersedes the author's earlier classic *Systematics and the Origin of Species* (Columbia Univ. Press, New York, 1942). It will long remain the source book on speciation in animals.
- [ed.]. 1957. The species problem. *Am. Assoc. Advance. Sci.* Symposium 50. A series of articles, many of which are pertinent to this chapter.
- Stebbins, G. L. 1950. *Variation and Evolution in Plants*. Columbia Univ. Press, New York. Contains many examples of differentiation in plants.
- Thoday, J. M., and J. B. Gibson. 1962. Isolation by disruptive selection. *Nature* 193: 1164-1166. This paper and Streams and Pimentel (*Amer. Naturalist* 95: 201-210) are the critical references on sympatric divergence in the laboratory.
- Woodson, Robert E. 1962. Butterflyweed revisited. *Evolution* 16: 168-185. The resampling of a transect made in 1947 across the United States is described and the results evaluated. Many papers on differentiation of populations are published in *Evolution*, and a survey of the back numbers will be of interest to any student of the subject.

11

major patterns of variation

Can the processes that account for the differentiation of populations be the same ones that are responsible for the great diversity of life? The efficacy of mutation, selection, migration (in the genetic sense), and drift in producing different colors of *Linanthus* flowers, geographic variants among butterflies, or species of birds has been described in the preceding chapter. Now the question may be asked: Is the same constellation of factors also responsible for the differences among flowers, butterflies, and birds? Are these factors responsible for the existence of extremely distinct clusters as well as for those separated by relatively small gaps? Because of the primarily taxonomic orientation of early evolutionary studies, this is often considered to be the problem of the origin of higher taxonomic categories. Some paleontologists and geneticists have felt that higher categories, such as genera, families, and orders, may have resulted from evolutionary processes (macroevolution) different from those studied at the species level (microevolution). It seems clear from the evidence from many fields of biology that, because of the immense amount of time during which evolution has been taking place, there is no need to postulate other processes in addition to those previously discussed.

EXTINCTION AND BIOGEOGRAPHIC PROVINCIALISM

The existence of extremely distinct clusters can be accounted for by extinction or by inadequate geographic sampling. Of course, with possible very rare exceptions such as certain fish species whose entire populations seem to occur in single small springs, even the most distinct clusters are made up of smaller subclusters with some degree of variation among them.

Extinction

The sole surviving member of the reptilian order Rhynchocephalia, the tuatara (*Sphenodon punctatus*), is found only on about a dozen islets off the coast of New Zealand. The groups of individuals on different islands certainly belong to different mendelian populations, but the degree of genetic divergence among these populations (and the amount of interchange among them) is unknown. Other animal isolates of this sort are numerous. The strange Peruvian butterfly *Styx infernalis* is a member of the family Lycaenidae (related to

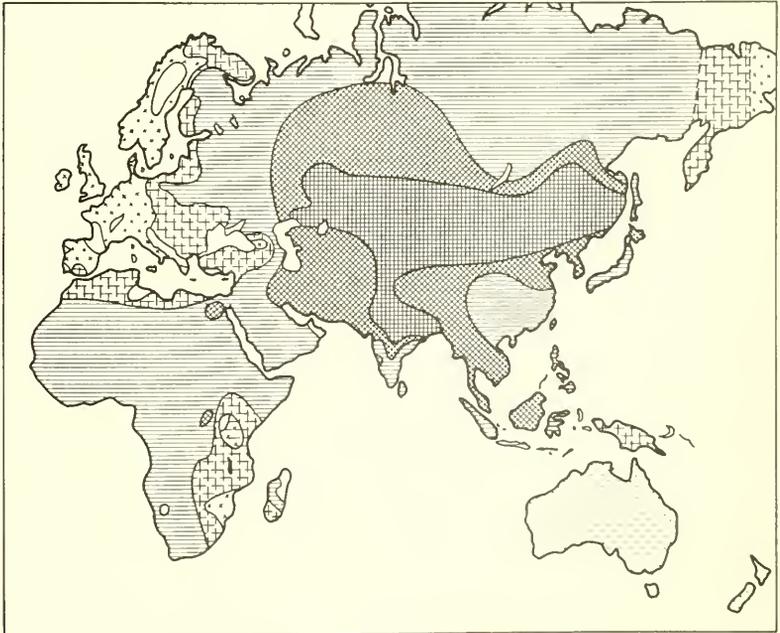
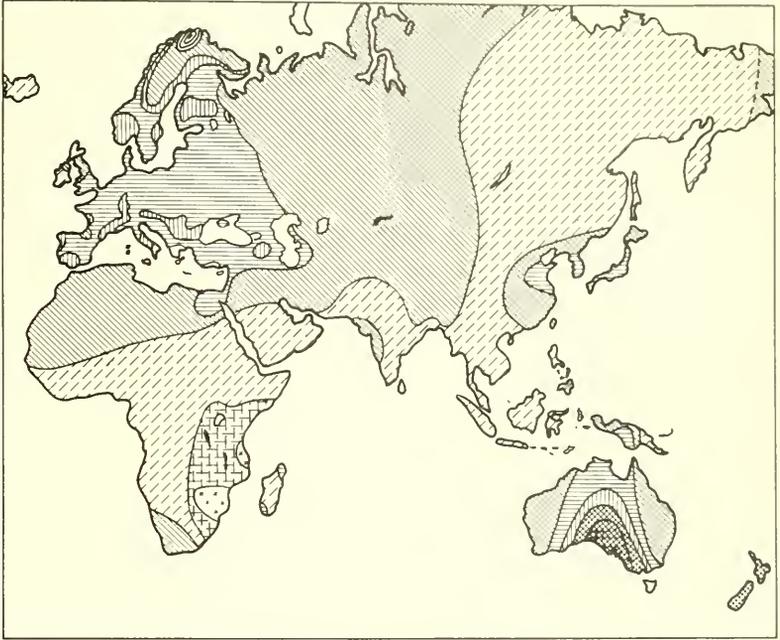
our common blues and hairstreaks), but its many structural peculiarities clearly set it apart from other lycaenids, and it is placed in a separate subfamily. Again, nothing is known of the degree of differentiation that may exist within the cluster.

If one ignores his fossil record, man is a very distinct organism. There is complete reproductive isolation between *Homo sapiens* and his nearest living relatives (the anthropoid apes). As far as is known, differentiation within the human species has not progressed to the point where segregates within the species are infertile upon crossing. However, in contrast to *Sphenodon* and *Styx*, there is a great deal of geographic variation within *Homo sapiens*. Our concepts of "race" are based primarily on variation in a few conspicuous external characters (skin color, hair type, skull shape), but there is also variation in less obvious characters, notably blood type and hemoglobin type (Chap. 7). The *Homo sapiens* cluster therefore does not fragment easily into distinct subclusters. Virtually all subgroups of man exchange genes to some extent, with the result that patterns of variation are exceedingly complex. Indeed, discordant variation in which patterns for the various characters studied are widely different is very common. A good example of this discordant variation can be seen in the comparison of distributions of blood types in human populations (Fig. 11.1). The distributions of blood group genes *A* and *B* show little resemblance.

Examples of very distinct forms are also found commonly in the plant kingdom. *Ginkgo biloba*, the maidenhair tree, is, like *Sphenodon*, the only living member of its group, a very distinct order of gymnosperms. The phyletic line to which it belongs can be traced far back into the fossil record. During the Mesozoic there were many genera and species of Ginkgoales (Fig. 11.2). For some reason unknown to us, the line became extinct in the Tertiary, with the exception of *Ginkgo biloba*. The exact native habitat of the ginkgo is not known, but for centuries the Chinese have cultivated the species for its edible seeds. In China most of the plants are grown in temple gardens. Since the plant has virtually no insect or fungal pests and since its leaves turn a striking gold color in autumn, ginkgo has become a common and popular street tree in most temperate parts of the world. It seems to survive in areas where the worst environmental pollutions which man can produce are abundant. *Ginkgo*, like many other isolated gymnosperms, is very diverse genetically, having many horticultural variants.

The dawn redwood, *Metasequoia glyptostroboides*, also apparently is the last survivor of a genus of gymnosperms related to *Sequoia* and *Sequoiadendron*. Unlike *Ginkgo*, *Metasequoia* was first

Fig. 11.1 | Maps showing discordant variation in the distribution of blood group genes (above, gene A; below, gene B) in aboriginal human populations. Degree of shading indicates areas occupied by populations with approximately the same frequency for the gene in question. (From Mourant, 1954, *The Distribution of Human Blood Groups*, Blackwell Scientific Publications, Oxford; F. A. Davis Company, Philadelphia.)



described as a fossil. It was not until some 5 years after its description from leaf impressions in Pliocene deposits in Japan that living plants were found growing in China. Again, this tree apparently has been preserved from extinction at least in part through cultivation by the Chinese.

In addition to such instances of completely isolated species, there are also cases of two or only a few closely related forms which, as a group, are clearly separated from their nearest living relatives. In the butterfly genus *Neophasia* (Pieridae) are found what are considered by all lepidopterists to be two distinct species with no intermediates and little intraspecific variation. One species, *N. menapia*, is widespread in western North America, where it feeds on various coniferous trees. Both sexes are white, with black markings restricted largely to the leading edge and apex of the forewings. *Neophasia terlooti* is found in northern Mexico and Arizona; it also feeds on conifers. Males are similar to those of *N. menapia*, but the dark markings on the forewings are more extensive. The females resemble the males, except that the white ground color has been replaced by orange-red. No red females of *N. menapia* are known, and no white females of *N. terlooti* are found.

Living elephants are an interesting example of two very distinct species as the only survivors of a diversified group. Thus the African elephant (*Loxodonta africana*) clearly is the closest living relative of the Indian elephant (*Elephas maximus*) and vice versa. Both, however, have closer relatives among known extinct forms not directly ancestral to them.

Detailed studies of the closed-cone pines of western North America have revealed a similar situation among these plants. *Pinus masoni* is known only from the Pliocene. From study of the abundant fossils, it has been suggested that *P. masoni* became extinct in the Pleistocene after giving rise to two separate lines of development. One of these produced *P. linguiformis*, which also became extinct in the Pleistocene. From *P. linguiformis* arose *P. attenuata*, which has a fossil record extending well back into the Pleistocene and which is today the commonest species of closed-cone pine in California. The second phyletic line deriving from *P. masoni* gave rise to *P. muricata*. This species survives today and is abundant along the Pacific Coast, together with its derivatives *P. radiata* and *P. remorata*. If only modern pines are considered, *P. attenuata* and *P. muricata* are obviously closely related morphologically. Both, however, have close relatives in the fossil forms that preceded and overlapped them in time, only to become extinct during the Pleistocene. These two pines appear to be vigorous expanding species with

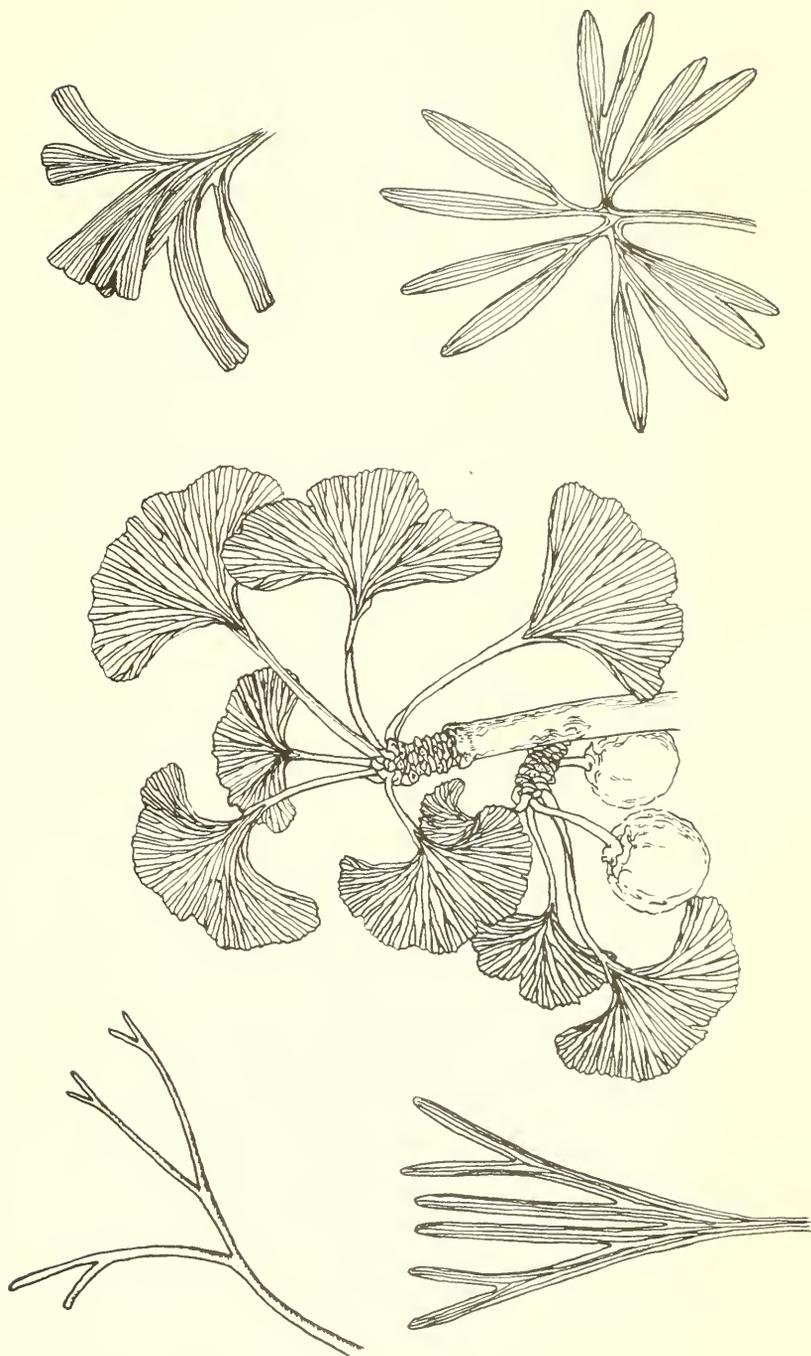


Fig. 11.2 | *Ginkgo biloba* and extinct relatives. Center, *Ginkgo biloba*; upper left, *Sphenobaiera furcata*, Late Triassic; upper right, *Ginkgoites lunzensis*, Triassic; lower left, *Baiera longifolia*, Jurassic; lower right, *Ginkgo lepida*, Jurassic. (Adapted from Andrews, 1947, *Studies in Paleobotany*, Comstock Publishing Company, and after Kräusel, 1943, *Paleontographica* 87B, and after Heer.)

considerable genetic variability. *Pinus radiata* has suffered range reduction in recent times and perhaps would be on the road to extinction were it not for the fact that the tree is much cultivated and has been introduced into many parts of the world where it is grown for paper pulp manufacture.

The situations just described, where a species or small group of species appears to be very distinct from other such groups, all involve extinction. The group is distinct because closely related forms have not survived. When the fossil record is considered (if such is available), the distinctness of the species disappears. Similar misconceptions result when forms living in a rather broad geographic area are studied in only a part of their range. Distinct clusters seem to be present when a limited geographic area is considered, but when the world picture is studied, this conclusion no longer obtains. As with the previous examples, the problem is one of sampling, in this instance insufficient sampling in space rather than insufficient sampling in time.

Biogeographic Provincialism

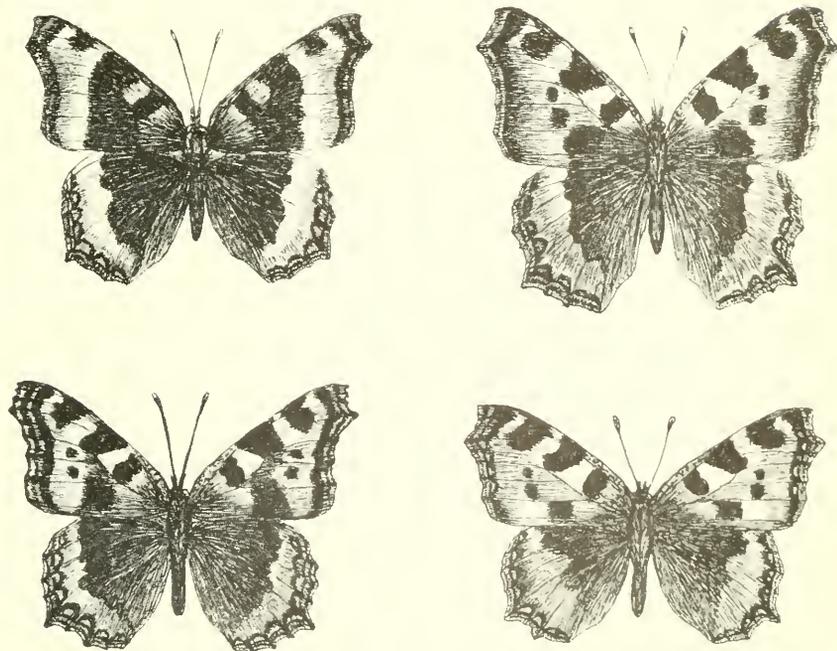
In North America, there are four distinct kinds of animals included in the butterfly genus *Nymphalis* (*N. antiopa*, *N. milberti*, *N. californica*, and *N. vau-album*). Individuals may be assigned to one of the four forms with certainty, no intermediates having been discovered. When *Nymphalis* of the Palearctic region are considered as well, the impression of neat packages disappears. The relationship of the cluster that we call *N. vau-album* to the Eurasian form of the same name is open to some question. In the few characters studied (size, color pattern, genitalia) in samples from North America and Eurasia there is considerable overlap in variation. As in most other cases, an estimate of the actual degree of differentiation must await thorough studies of large samples of characters. Similarly, the amount of differentiation between *N. milberti* and the Palearctic members of the *N. urticae* complex (Fig. 11.3) and among *N. californica* and the Old World *N. polychloros* and *N. xanthomelas* needs further investigation. There are myriad similar situations.

In Yellowstone National Park there are two kinds of bears: black bears (*Ursus americanus*) and grizzly bears (*U. horribilis*). If the Park were the entire range of the grizzly, then grizzly bears would form a distinct apparently uniform cluster of the same sort as was described for the tuatara (*Sphenodon*). However, the grizzly ranges northward to Alaska, where populations are made up of very large

individuals (Alaska brown bears, *U. middendorffi*) and thence into Eurasia (*U. arctos*). It seems likely that these bears form an intergrading series of clusters. The polar bear (*U. maritimus*) is a very closely related cluster adjusted primarily to marine life in the Arctic. The brown and polar bears are largely allopatric, although occasional individuals meet along the Arctic coast. To our knowledge, intermediate individuals have not been reported in nature (although zoo hybrids are well known). Thus, although bear taxonomy might seem simple to the inhabitant of Yellowstone Park, consideration of the world picture introduces problems. Are the European bears really the “same species” as the Yellowstone bears? Are the polar bears really a “different species”? Are these questions biologically important?

This problem is also common in plants. As with animals, it is particularly evident in those forms that have a circumpolar or circum-

Fig. 11.3 | Closely related butterflies of the genus *Nymphalis*. Upper left, *N. milberti*, Wyoming; upper right, *N. caschmirensis*, Nepal; lower left, *N. urticae*, Sakhalin; lower right, *N. urticae*, Hungary.



boreal distribution. Often the same species may masquerade under different names in Canada, Europe, and Russia until monographic study, bringing together specimens from all areas for the first time, shows the true distribution. It may seem unnecessary to belabor the point in such detail here. However, it is surprising that biogeographers often accept the results of local floristic and faunistic studies without considering this particular source of bias.

Reticulate Variation

A rather different situation, and one not well understood, occurs in various groups of organisms. Here a species is well-marked and easily distinguished. There appears to be little or no morphological intergradation so that each cluster is clear-cut. In the milkweed family (Asclepiadaceae), for example, once the rather complicated floral morphology is understood, a series of nonoverlapping taxa (species) are recognized easily. It is interesting that in this family of flowering plants it is very difficult to delimit clusters of these primary taxa. The pattern of variation is such that genera are virtually impossible to define. The condition in which characters considered important by the taxonomist appear in different combinations in many species is known as reticulate variation. Perhaps this is a result of the complex obligate insect-pollination mechanisms found in these plants, but it seems to be common at the species level in various groups of plants and animals.

Reticulate variation must be distinguished from reticulate evolution. Reticulate evolution is the joining of phyletic lines (through crossing) and has been demonstrated clearly in many plants where it usually involves doubling of the chromosome number of the hybrid. Instances of this sort in both plants and animals are discussed in Chap. 9. In the Asclepiadaceae, there is no reason to suspect that union of formerly separate phyletic lines has taken place, and there is no indication that polyploidy has played a role in species formation.

THE FOSSIL RECORD

In several senses, time is the crux of the problem of "macroevolution" as opposed to "microevolution." The past history of life can be studied only by examination of fossils and comparison with extant forms. Opportunities for checking these observations and the conclusions drawn from them are few indeed. The discovery of "living fossils" such as *Latimeria* and *Metasequoia* provides such a check.

Latimeria is a living representative of the coelacanth fishes, a group once thought to have become extinct in the Cretaceous. *Metasequoia*, the dawn redwood, was first described as a fossil from the Pliocene, only to be found extant in China some years later. Another check of our inferences drawn from comparing recent and fossil forms is the discovery of previously postulated “missing links.” The most famous such find was perhaps Dubois’s discovery of the remains of *Homo erectus* (*Pithecanthropus*), a fossil man with “ape-like” characteristics (see Chap. 12).

Fossils must be viewed as a very biased sample of the remains of past life. Disturbances in the earth’s crust have all but wiped out critical parts of the fossil record, and the most interesting and vital earlier portion is the most distorted. Parts of some organisms, such as vertebrate bones, shells of mollusks and Foraminifera, woody portions of plants, and cuticles of leaves, are more readily fossilized than others. Organisms less well endowed with hard or resistant parts (e.g., worms, larval insects, most algae and fungi) are less often preserved. The habitat of the organism also has a large effect on the probability of its becoming a fossil. A steppe-dwelling animal or plant stood a much smaller chance of being preserved than one from a swamp. Factors favorable for the preservation of plant remains often are not suitable for animal preservation. (For example, acid conditions that might preserve leaves would dissolve shells and bones.) Finally, certain specialized habitats, such as tar pits, mineral water bogs, and volcanic slopes, may be preserved almost *in toto* at times with whatever assortment of organisms might happen to be present or attracted to them.

Nevertheless, the fossil record is sufficiently ample and diverse that paleontologists have recognized many patterns and described processes thought to have been responsible for their development. Many analytical problems are peculiar to paleontology. For example, in addition to the taxonomic difficulties resulting from diversification across a heterogeneous environment (*horizontal speciation*), one must contend at the same time with differentiation through time (*vertical speciation*).

Modes of Evolution

Simpson and others have summarized what is known of the major patterns of evolutionary change, particularly with respect to animals. Simpson divides these patterns into three modes. Many instances of the first mode—the splitting of phylogenetic lineages—may be traced in the fossil record. These range from the division of the archosaurian

reptiles into terrestrial and aerial lines (represented now by the crocodiles and birds) to the formation of species of mammals. On the other hand, some lineages apparently did not split for long periods of time but underwent such gradual morphological change that taxonomic distinction anywhere along the continuum is virtually impossible, except at the beginning and the end. This evolutionary mode is called phyletic evolution. Simpson recognized also a third mode, quantum evolution, which is rapid change involving the acquisition of characteristics for a completely different way of life. The partial or complete joining of phylogenetic lineages is difficult to recognize in the fossil record, although presumably it played the important role in the past that it does today.

One of the most interesting problems that can be studied with the fossil record is the rate at which evolution has occurred. There are many different ways of measuring rate of evolution. At present none of them is entirely satisfactory, but nonetheless they are of great interest. In many of the well-worked-out lineages of vertebrates and mollusks, rate of change in particular characters can be studied with time as a dimension. It is also possible to measure the rate of "formation" of taxonomic categories, assuming that these are proportional to some stage of morphological distinctness or some degree of genetic isolation. The rate of extinction of taxonomic groupings, as expressed in survivorship curves, also may be of use. It must be remembered, of course, that comparisons based upon taxonomic distinctions between groups must be interpreted with great caution. There is ample evidence from the study of living and fossil forms that what is called a genus, say, in one group may not be equivalent biologically to what is so designated in another.

The multivariate-correlation analyses now being employed in numerical taxonomy (Chap. 13) seem to offer real possibilities for the development of more satisfactory methods of measuring evolutionary rates. By studying changes through time in a large sample of characters, objective estimates of the total amount of structural divergence may be obtained. The smaller the degree of correlation between successive samples, the greater the amount of evolution. In such an analysis, arbitrary taxonomic judgments can be avoided.

The measurement of time also is beset with difficulties. While there are modern methods of dating which presumably give reliable results, there is not general agreement concerning the beginning or the duration of the major geologic periods. Age determinations have the same sampling problems as studies of fossils and must be correlated with the occurrence of known fossils. Experimental error may be relatively large. In general, establishment of an absolute time

scale is most useful for rather long periods of time. For shorter spans of geologic time, it is often necessary to use a relative scale, placing organisms earlier or later in time, according to their relative positions in layers of sediment, the level of their pollen in varves, etc. For the most part, the evolutionist must be content with an approximate age for fossils, even though he may be almost certain of the sequence of appearance of a given series of forms.

Rates of Evolution

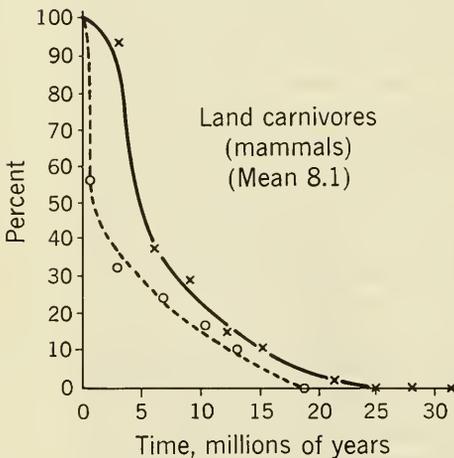
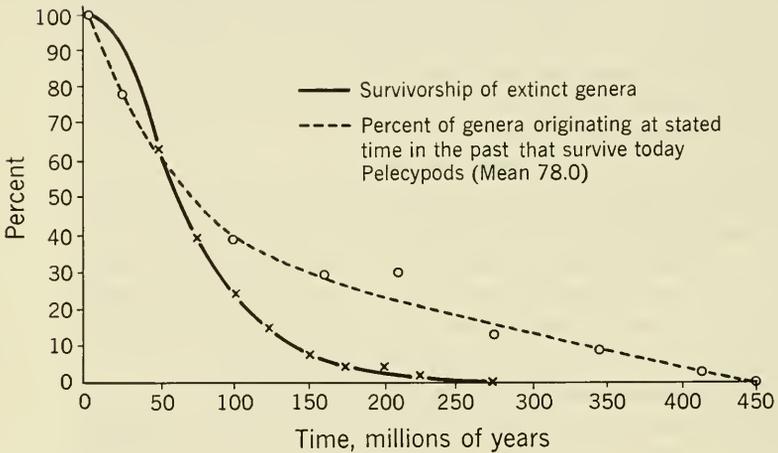
Rates of phyletic evolution and of splitting vary greatly. Evolutionary rates are complex functions of many factors in the environment and in the organism and of interactions among these factors. Changes in genetic systems, the disappearance or appearance of predators or parasites, changes in temperature, increasing salinity of the sea, rise in sea level, mountain building, and change in intensity of solar radiation are a random sample of the factors that may act and interact to affect the rate of evolution.

If the rates of evolution for the various members of a major taxonomic grouping are plotted as a frequency diagram, they form an asymmetrical distribution with the modal rate nearer the maximum rate. Simpson has called this distribution horotelic, and the rates falling within it are horotelic rates. In most groups it will be found that some organisms apparently evolved at rates either slower or faster than those making up the horotelic distribution. These have been termed bradytelic and tachytelic rates, respectively.

The land carnivores and the pelecypod mollusks may be compared to illustrate horotelic rates. Simpson has calculated survivorship curves for these groups (Fig. 11.4). The fact that the mean survivorship for genera of the mollusks is 78 million years in comparison with 8 million years for a genus of mammals strongly suggests that the carnivores have evolved perhaps ten times faster than pelecypods (in terms of duration of arbitrarily established genera). If it is postulated that correlation of survivorship and rate of evolution is perfect and positive, then a frequency distribution of rates can be plotted (Fig. 11.5). These distributions are quite similar, even though the absolute rates differ markedly, and form the horotelic distributions for the Pelecypoda and the Carnivora.

If the pelecypods are now examined in greater detail, with survivorship of exclusively fossil genera compared with genera arising in the past and still existing, the phenomenon of bradytely is revealed. Again using Simpson's calculations and graph (Fig. 11.4), it can be seen that actual survival is greater than expected survival.

Fig. 11.4 | Survivorship curves for genera of pelecypod mollusks and land carnivores. Continuous lines, survival of genera now extinct; broken lines, survival of genera known as fossils that are still living. Ordinate, percent of genera surviving; abscissa (continuous lines), duration of extinct genera in the fossil record; abscissa (broken lines), time elapsed since appearance in fossil record of genera now living. (From Simpson, 1953, *The Major Features of Evolution*, Columbia University Press.)



Some living genera have had distinctly longer spans than genera that have become extinct. The longest-lived extinct genera lasted 275 million years, but extant genera that have survived for 400 million years are also known. According to Simpson, then, any living pelecypod genus older than about 250 million years represents a bradytelic genus. Its rate of evolution, measured in this fashion, is outside the horotelic distribution, toward the slow end of the scale.

One can easily think of many groups of plants and animals in which the rate of evolution appears to be very slow. It must be remembered, however, that bradytely is a statistical effect, detected by special means of analysis. So to label contemporary organisms that have changed little for long periods of time is thus not strictly correct. Organisms of many different kinds, such as opossums, giant sequoias, crocodiles, and club mosses, appear to have evolved very slowly. Whether they can be classified as bradytelic is another matter. Nor is it possible, with the present state of our knowledge of these or of groups such as the pelecypods, to determine why evolution appears to have been at least partly arrested. There is no reason to believe that such organisms are more "primitive," have a low mutation rate, or are depauperate genetically and less variable.

The method of study using survivorship curves, which makes bradytely apparent, cannot show the presence of rates faster than those of the horotelic distribution. Organisms with the very rapid rates of evolution referred to as tachytely exhibit this phenomenon presumably for relatively short periods of time and then slow to horotelic or bradytelic rates if they do not become extinct. Rapid evolution or tachytely often is associated with a new mode of existence, what Simpson has called a new adaptive zone, and is characteristic of quantum evolution. By adaptive zone is meant here not simply the place where the organisms live but the mode of life in such a place as well. It has been suggested that tachytely is one of the various possible reasons for the gaps in the fossil record which often occur at the apparent origination of a new phyletic line. If evolution took place at an unusually rapid rate and particularly if the ancestors of the new line were distributed in partially isolated, small populations, the chances of their becoming fossilized would be very small. Simpson's view of a possible relationship between horotely, bradytely, and tachytely is shown in Fig. 11.6. Here a bradytelic line produces a tachytelic branch which becomes horotelic.

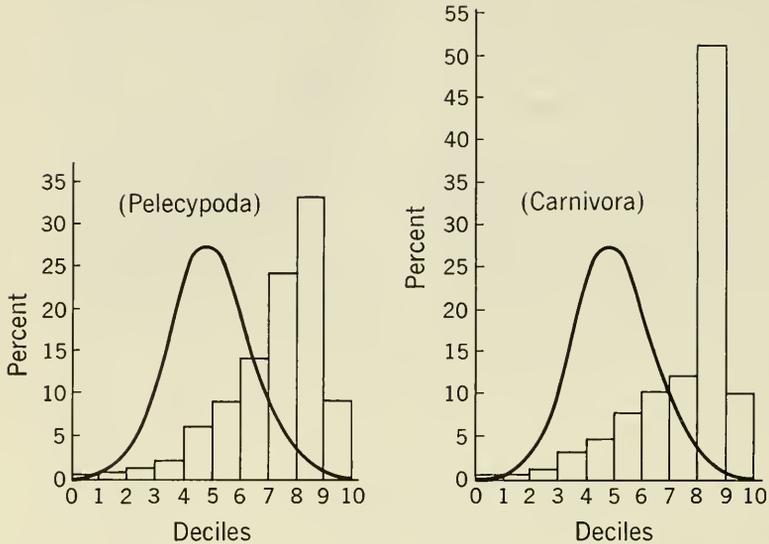


Fig. 11.5 | Frequency distributions of evolutionary rates in genera of pelecypod mollusks and land carnivores. Histograms are based on survivorship of extinct genera (see Fig. 11.4) and on the assumption of perfect negative correlation of survivorship and rates of evolution. Ordinate, percent of genera in each class; abscissa, rate of evolution expressed in deciles so that histograms may be compared despite differing absolute rates. Normal curves equal in area to the histograms are drawn for comparison. (From Simpson, 1953, *The Major Features of Evolution*, Columbia University Press.)

MAJOR EVOLUTIONARY PATTERNS

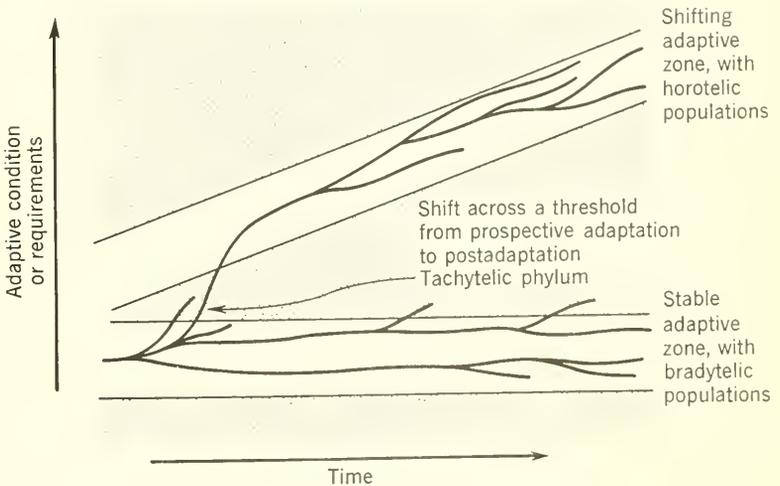
Adaptive Radiation

The birds perhaps represent a group that experienced an initial period of rapid evolution. They split rapidly from the archosaurian reptiles in the Mesozoic, apparently perfecting flight through selection for increased flight range and agility in a group of climbing-gliding reptiles. Once true flight was attained, its advantages (for escape, dispersal, food seeking, etc.) led to rapid proliferation of the group. Such proliferation is sometimes called *adaptive radiation*. Apparently there was sufficient overlap between the flying and gliding adaptive zones that the more successful birds replaced the group

from which they arose. It is interesting to note that the "gliding zone" still remains largely unoccupied (except for a few fish, lizards, snakes, and mammals), although the mammals have successfully entered the aerial zone (or a specialized part thereof), in part at least, by specializing in night flying and sonar hunting.

An outstanding example of adaptive radiation in animals is the tremendous diversity of the marsupials in Australia. In the absence of placental mammals, marsupials developed grazing forms (some kangaroos), burrowing forms (marsupial moles), forms resembling tree and flying squirrels (phalangers), rabbit-like forms (hare wallabies), wolf-like carnivores (Tasmanian wolves), badger-like carnivores (Tasmanian devil), ant-eating carnivores (banded anteater), and arboreal forms with no obvious placental equivalent (koalas, tree kangaroos). Unfortunately for the fields of comparative psychology, linguistics, and sociology, no marsupial equivalents of the primates appeared. The poisonous snakes of the family Elapidae (cobras and their relatives) similarly show adaptive radiation in Australia. They have produced, among other types, forms superficially resembling the vipers or pit vipers (Viperidae or Crotalidae). There are, of course, many other examples of adaptive radiation. The Galápagos finches and African lake cichlids are good examples

Fig. 11.6 | Diagram to show a representation of horotelic, bradytely, and tachytely. See text. (From Simpson, 1953, *The Major Features of Evolution*, Columbia University Press.)



of such radiation on a scale less spectacular than that of the Australian mammals and reptiles.

There are also instances of adaptive radiation by plants. Within most of the large plant families there has been radiation into trees, shrubs, lianas, and various types of herbs, including aquatics. A number of families have also independently produced saprophytic and insectivorous derivatives. Specialized types of adaptive radiation are concerned with particular mechanisms in plants. Grant has shown that a remarkable series of pollination systems exists within the phlox family (Polemoniaceae); these are diagrammed in Fig. 11.7. The basic floral type with five corolla lobes, five stamens, and a superior ovary (usually with three stigma lobes) has become modified so that bee flowers, hummingbird flowers, butterfly flowers, hawk moth flowers, bee fly flowers, beetle flowers, and even bat flowers occur. There are also flowers that are regularly self-pollinated (autogamous) and flowers that are self-pollinated in the bud (cleistogamous). It seems likely that selective forces leading to developmental modifications have resulted in this diversification which takes advantage of most types of available pollinators. Specialization in the Polemoniaceae has taken place at the generic and subgeneric taxonomic levels. In other angiosperms, very nearly an entire family may be specialized for one pollinating agent, usually wind, as in the grasses (Gramineae). In the almost exclusively wind-pollinated sedge family (Cyperaceae), there are one or more insect-pollinated forms (e.g., *Dichromena*) whose clusters of reduced flowers and associated leaves simulate flowers.

These examples indicate that the concept of adaptive radiation has been applied to changes involving both relatively long and short periods of time. It may refer to diversification at what taxonomists would call the specific level, as well as to proliferation of phyla within very broad adaptive zones. It may even be used to describe the evolution of special relationships such as those between flowering plants and their pollinators. It is clear that the meaning of the term adaptive radiation must, in large part, be determined from the context in which it is employed.

Differing Rates of Evolution and Adaptive Zones

It is unwise to speculate too specifically about the causes of differing rates of evolution. Possibly organisms in ecological situations that change only slowly in the course of geologic time show bradytely. It has been suggested that the world's oceans represent such a situation, but we really know relatively much less about marine habitats

than land ones. Other organisms in the same general habitat may not be bradytelic. Similarly, the "cause" of an instance of tachytely is usually impossible to determine. Entry into a new adaptive zone clearly is involved. It is almost impossible to avoid visualizing adaptive zones and thinking of discontinuities (nonadaptive zones) between them even though they represent an abstract space whose many dimensions are all the factors of the environment, including other organisms. In the past, as today, the situation must be exceedingly intricate, involving complexly (and often cyclically) shifting gradients.

In some way, it would appear that certain lineages gain "access" to a new adaptive zone that is constantly changing. This new zone must be "contiguous" in a multidimensional sense. The organisms must be physically near it, happen to be provided (by the mechanisms of population genetics) with genotypes that will survive and function in it, and be able to exist with the organisms already present or possibly to replace them. Having successfully "entered" an adaptive zone, the group may then diversify to occupy subzones of the original zone or spread further into contiguous zones. The amount of proliferation of adaptive subtypes seems to be primarily a function of the extent (diversity) of the adaptive zone. The Strepsiptera, curious, highly modified insects which are endoparasitic in bees, wasps, and other insects, seem to have entered a rather narrow adaptive zone. The birds apparently have found a relatively wide one. It is important also to remember that what today appears to be a relatively unstable (and relatively unoccupied) intermediate zone may at one time have been quite stable. The successful entry of reptiles into the completely aerial zone quite possibly "unstabilized" the gliding zone.

As has been emphasized in Chap. 5, there is a strong tendency for biologists to fragment the environment to serve their own analytical purposes. While the concept adaptive zone refers to a way of life rather than a physical area, it nevertheless represents an artificial fragment of the space-time continuum in which the organisms are found. In the final analysis, it is the total situation that evolves, even though we may choose to separate organic evolution from environmental change. The results of our study depend to a very large extent on the choice of artificial distinctions. Science progresses by comparing the results of study of similar situations from different points of view until a relatively unvarying answer is obtained. It seems clear that the study of the evolution of organisms together with changes in "their habitat" has not reached the point where answers are unvarying.

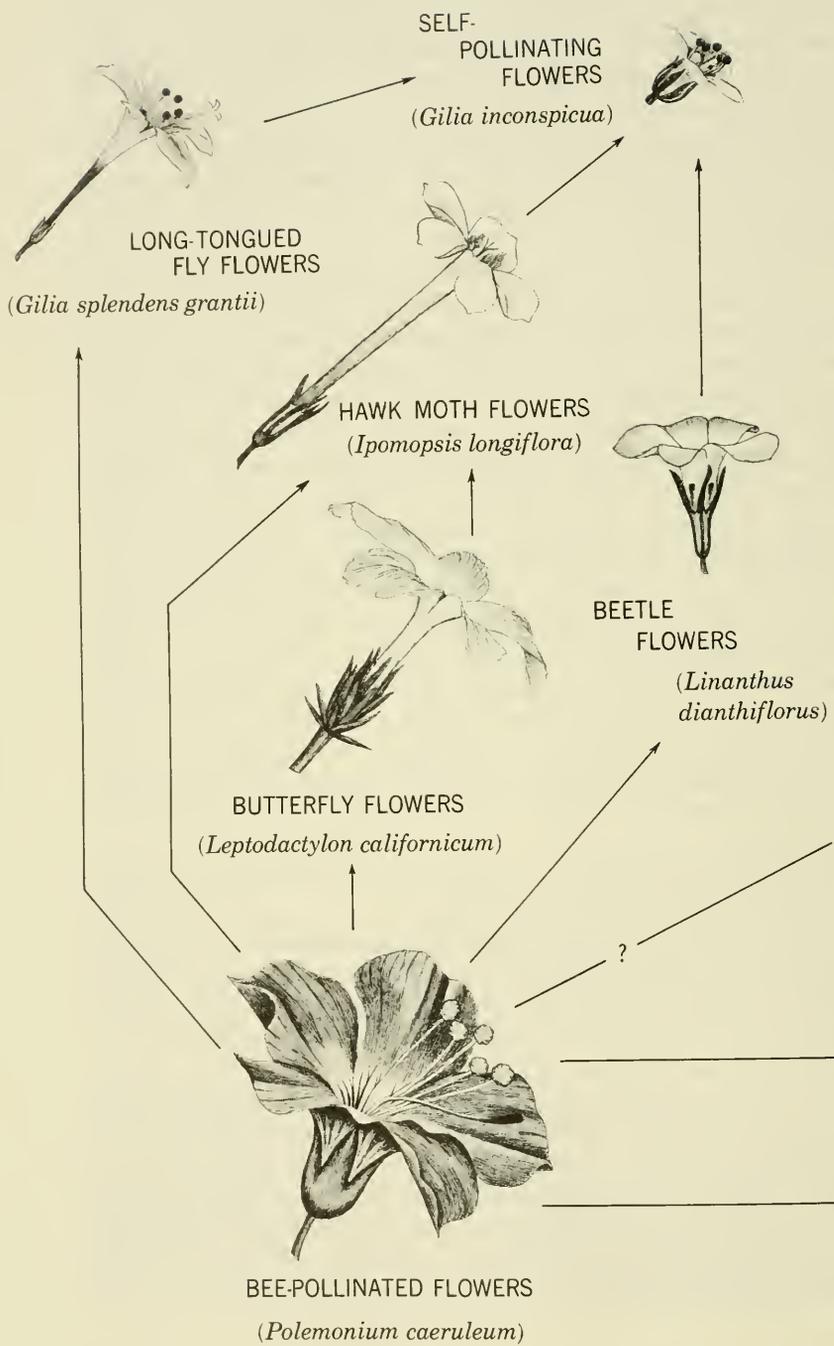
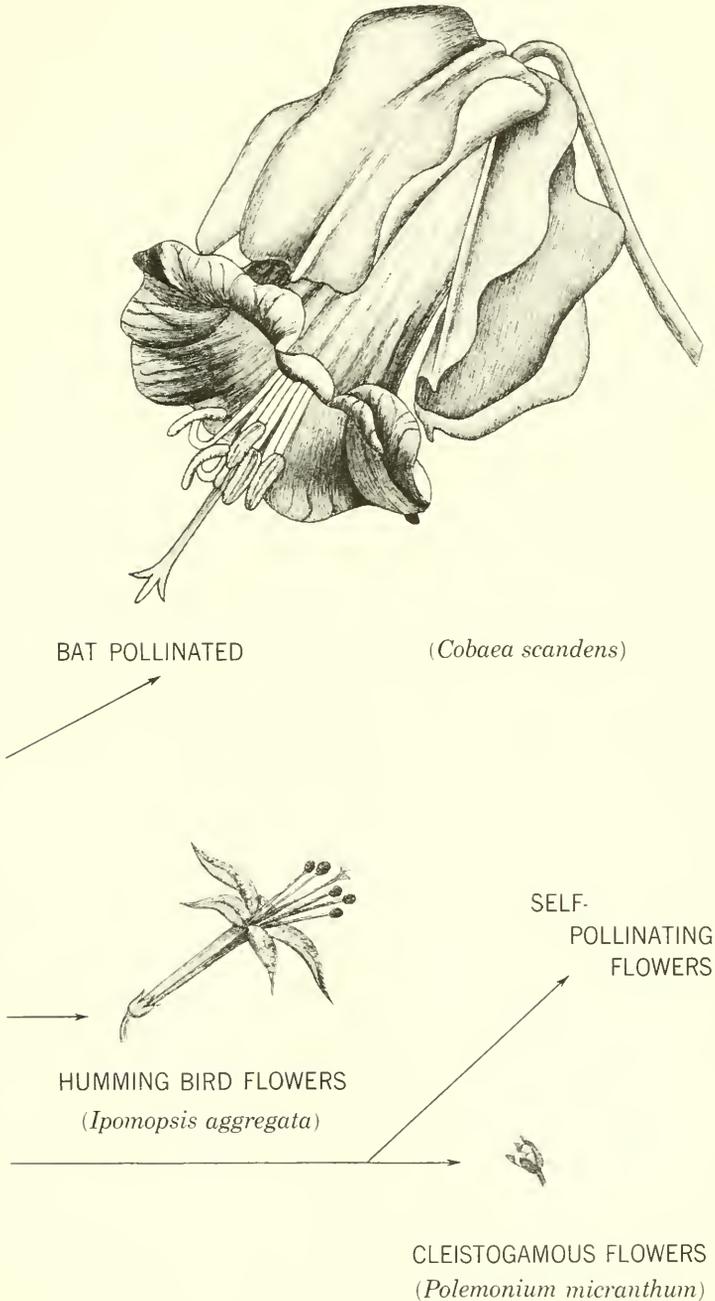


Fig. 11.7 | Diagram to illustrate diversity of pollination types in the Polemoniaceae. Flowers exemplify structural types associated with the various systems of pollination; arrows indicate possible directions of evolution of pollination systems. (After Grant, unpublished.)



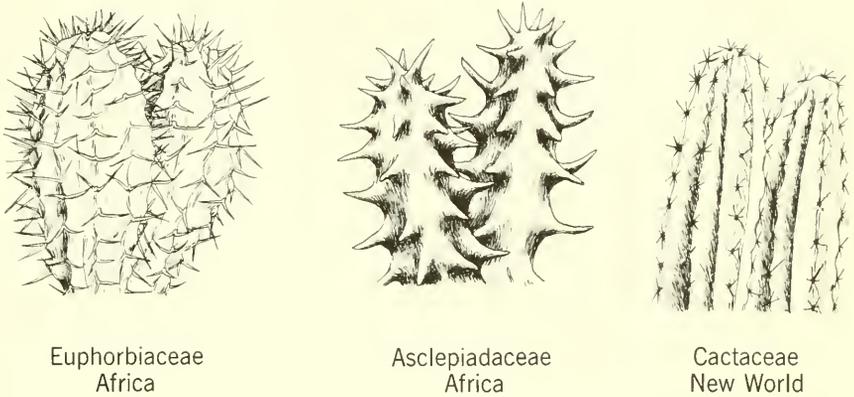
Competition

The same problems arise with respect to the consequences of two organisms meeting in the same adaptive zone. It is usually thought, or at least stated, that the inevitable result is some sort of "competition." The term competition has been used in so many different ways that its general unqualified use conceals rather than reveals information (see Chap. 13). Furthermore, with respect to plants, the term usually must have a meaning rather different from its possible meanings when applied to animals. By extension, the word competition has been used to refer to situations where major groupings of organisms have replaced others in adaptive zones of great breadth. Thus it is often said that placental mammals have eliminated, through competition, the marsupials and monotremes over much of the earth's surface or that mammals as a group have completely exterminated the mammal-like reptiles. The angiosperms appear to have replaced the gymnosperms in most parts of the world also; this too is described as the result of competition somehow extended to the level of higher taxonomic categories. In retrospect, one can look at any one of these situations and say that, by definition, the surviving organisms were "better adapted" than those which became extinct. Extinction of one group, however, is not the only possible outcome of "competitive occupation" of the same adaptive zone. One or both of the occupants may become more specialized, thus restricting or eliminating the interaction between the types. Cockroaches, at one time the dominant group of insects, have changed from what was once probably a generalized herbivorous or omnivorous zone and now make their living mainly as scavengers. Their former zone seems to have been highly "fragmented" among a great many insect specialists, particularly of the orders Hemiptera, Homoptera, Orthoptera, Coleoptera, Lepidoptera, Diptera, and Hymenoptera—mostly relative newcomers on the evolutionary scene.

Convergence

Sometimes organisms that are not closely related enter similar adaptive zones and, as a result of selection, come to bear a superficial resemblance to each other. Classic examples are those of whales and fish and desert succulent plants of various families. In the aquatic environment, the selective advantage of genotypes producing phenotypes with a certain type of streamlining is obvious. Desert plants (Fig. 11.8) often resemble each other in having a thick cuticle and

low surface-volume ratio, both of which reduce water loss, and are often armed with spines which tend to discourage desert animals from eating them. The three plants of Fig. 11.8 belong to three separate families, Euphorbiaceae, Asclepiadaceae (Old World), and Cactaceae (New World). The spines in all three kinds are derived from different structures.



Euphorbiaceae
Africa

Asclepiadaceae
Africa

Cactaceae
New World

Fig. 11.8 | Convergence in desert plants. Left, *Euphorbia*, Euphorbiaceae, Africa; center, *Huernia*, Asclepiadaceae, Africa; right, *Cereus*, Cactaceae, Latin America.

More complex are the various patterns of mimicry in which selection favors genotypes that are least likely to be destroyed by predators. An example of mimetic convergence is shown in Fig. 11.9. In this case *Alcidis agathysus* (moth) and *Ideopsis daos* (butterfly) are presumably distasteful to predators, whereas *Papilio laglaizei* (butterfly) and *Cyclosia hestinioides* (moth) are thought to be palatable. Selection has apparently favored any genotypes within populations of the latter two that produced phenotypes resembling in any degree the protected forms.

Convergence among relatively closely related forms is sometimes called *parallelism*. For example, several lines of mammal-like reptiles probably independently acquired characteristics by which we define mammals. There is a continuum between convergence in the strict sense and parallelism, and the difference between the two is unimportant.

HIGHER CATEGORIES

Much attention is given in the literature to the subject loosely described as the "origin of higher categories." In the strictest sense, this is a problem for the psychologist, for higher categories (Reptilia, Lepidoptera, Rosaceae, Basidiomycetes) are, like species, concepts, not things. Their origin is shaped by many often unsuspected factors, such as preconceived systems of analysis, language structure and usage, and others. (See Chap. 13 for a discussion of this problem.) Nevertheless, the concepts stand for something, and it is pertinent to inquire into the causes of the patterns commonly observed in nature.

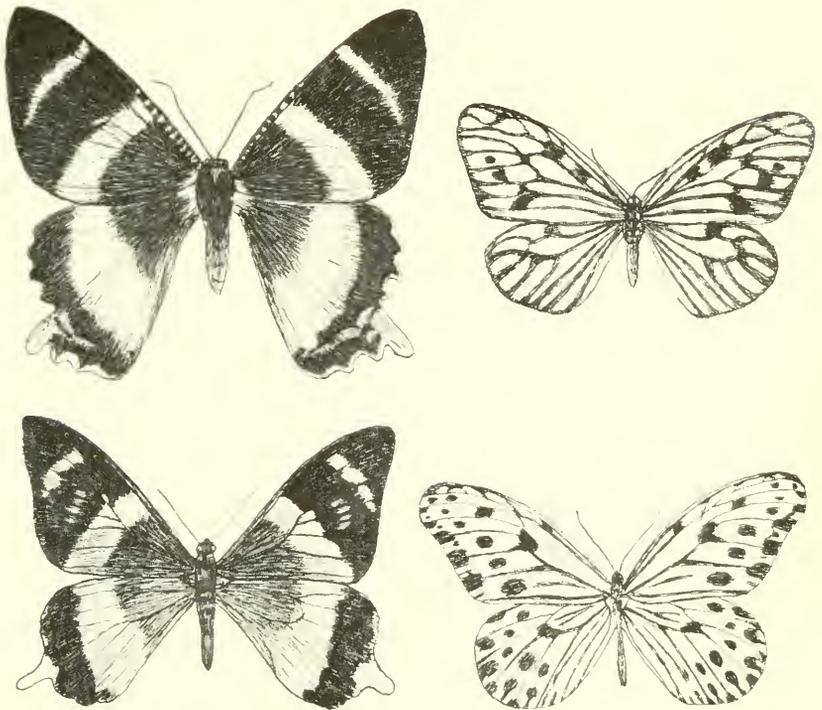
It seems likely that major discontinuities of the fossil record are a result of accidents of sampling. If a group enters a new adaptive zone during a period of tachytely, the chance of fossilization during the brief transition period is reduced simply because of its brevity. There may be gaps in the foliage of a tree, but even a phylogenetic tree has continuous branches. The category system of Linnaean taxonomy has somewhat magnified the size of apparent discontinuities. Rare organisms, more or less intermediate in characteristics between major clusters, are generally arbitrarily assigned to one or the other large cluster for the sake of convenience. Thus monotremes are lumped with mammals, micropterygids with moths, and fungi with plants. At relatively low taxonomic levels, reticulate evolution leads to complications. If a new species of plant is the amphidiploid hybrid derivative of two other species in different subgenera, it is often described as a member of an existing subgenus rather than as the sole member of a third one.

As noted earlier, taxonomic higher categories are in part the result of extinction which produces morphological discontinuities. This is a subject with which it is difficult to come to grips, and it has received only superficial attention from biologists. It is related to the matter of competition previously discussed. Specialized groups, when interacting with primitive groups, have often proved more successful, with the eventual disappearance of the more primitive types. The comparison of primitive and specialized here implies no judgment of quality; two groups are compared as to the amount that they presumably have changed from the base line of their most recent common ancestor. Thus crocodiles are more primitive than birds. Situations are also known where primitive types have persisted and specialized forms disappeared. That these can be "explained" as the persistence of less specialized groups against the

competition of overspecialized types only serves to illustrate the difficulties in dealing with ecological situations of this sort.

Many major discontinuities observable today seem to have had their origin before the start of a satisfactory fossil record. Even where a good fossil record of intermediate types exists, however, one cannot be sure of the exact causes of the present gaps. The commonly stated hypothesis that bird competition accounts for the absence of *Archaeopteryx*-like organisms in the recent fauna may be entirely incorrect. Perhaps these early types specialized in feeding on an organism that became extinct for climatic reasons. One might, of course, construct a large number of hypotheses, most of which have about equal probability of being incorrect.

Fig. 11.9 | Convergence presumably due to mimicry. Upper row: left, the moth *Alcidis agathysus*; right, the moth *Cyclosia hestinioides*. Lower row: left, the swallowtail butterfly *Papilio laglaizei*; right, the danaine butterfly *Ideopsis daos*. All from New Guinea. (After Punnett, 1915, *Mimicry in Butterflies*, Cambridge University Press.)



EVOLUTIONARY TRENDS

In retrospect one can observe evolutionary trends of virtually any desired degree of generality, ranging from a trend toward increased melanism in a British moth to a trend toward increasing complexity in the biosphere. Unfortunately such trends observed a posteriori have all too often been interpreted as if the evolutionary process was a means to a predetermined end. The fallacy of this view may be exposed with a very crude analogy. A driver leaving New York City might, at each intersection he encountered, take the fork that seemed to promise the easiest going (based upon what he could observe at the intersection about the amount of traffic and condition of the road). At the end of a week of this whimsical travel he might be found on the Indiana toll road. A teleologically oriented observer would doubtless claim that someone had planned a trip to Chicago for him. Readers interested in the sorts of trends that have been observed in the fossil record are referred to the works of Rensch and Simpson. These writers are highly successful in interpreting these trends in the light of the basic mechanisms of mutation, recombination, selection, and drift.

Increase in Size

Two very general trends are considered briefly here and in the following section. In many phyletic lines of animals, there is a tendency toward increase in size. (This has been called Cope's rule.) The validity of this generality, in the broadest terms, can be questioned only if one is willing to assume that the earliest living organisms were above or near the middle of the present size spectrum. From the discussion of the origin of life (Chap. 1) it will be seen that this was hardly likely. Possible selective advantages of being large can be found in virtually every physiological function of organisms: maximum exposure of leaves to photosynthesis (trees), heat conservation (whales), room for complex brains (pigs), or resistance to desiccation by a low surface-volume relation (barrel cacti).

The fossil record shows many trends toward larger size. A well-documented instance is that of the phylogeny of horses, with dog-sized Eocene horses giving rise to, among others, the contemporary work horses. The mammal record is replete with similar stories, although exceptions are known (e.g., modern marsupials and sloths are smaller than their Pleistocene counterparts). It is necessary, but sometimes difficult, to differentiate between reversal of a size-change

trend and the extinction of large organisms, leaving only smaller related forms to represent a group.

Large size seems to have been selected for in some animals because of concomitant benefits derived through allometry. Allometry refers to differential growth of body parts. The horns and antlers of ruminants, for example, often show a strong positive allometry. As body size increases, they grow proportionately much larger. (The head of a postnatal human being grows less, proportionately, than the rest of the organism as a whole; it shows negative allometry.) Horns and antlers are important both in defense and in battles between males for access to females. It does not seem unreasonable, therefore, to assume that the large size of many ruminants is accounted for in part by selection for larger weapons. This is an example where selection for proportionately larger appendages may have produced, through positive allometry, a correlated increase in body size.

It is also possible that, in some cases, selection for large body size on the basis of increased efficiency of arrangement of internal organs, say, could have produced appendages overlarge for their supposed function. Such might be the case with the evolution of *Megaceros*, the Pleistocene Irish elk which had the largest antlers of any known deer. As long as the disadvantage in large antlers did not counterbalance the advantage of large overall size, the trend would continue. The discussion is perhaps overly speculative, but it shows that there is no reason to view the great size of these antlers (or the giant mandibles of stag beetles, or many other such instances) as the result of some sort of "momentum" that carried once-adaptive trends to nonadaptive extremes. As should be obvious from a consideration of population genetics (see Chap. 6), this is a meaningless analogy. Selection against extremes would bring a trend to an abrupt halt as soon as the adverse effects counterbalanced the beneficial effects of the trend. As Simpson has pointed out, organisms that have extreme characteristics may seem bizarre to human eyes, but this is no reason to infer that they are inadapative. Indeed, the thriving possessors of many bizarre features (male peacocks, bottle-brush weevils, narwhals, plants with intricate flowers or such complicated modes of pollination as pseudocopulation) are hardly support for the idea that these characteristics are liabilities.

Increase in Complexity

Perhaps the broadest and most general trend that has been postulated is that toward increased complexity. Difficult as it is to specify

level of organization within groups of organisms, few biologists would deny that an aardvark is more complex or highly organized than a coacervate droplet. A monarch butterfly is clearly a more complicated apparatus than an amoeba or even a fern. Although relatively simple organisms still are present in some adaptive zones (more conspicuously perhaps in aquatic ones), the superiority of more highly organized types in many situations apparently is attested by their seeming dominance. However, dominance in an ecological situation is an exceedingly difficult thing to measure. Do the pine trees in a coniferous forest "dominate" the fungus that inhabits their roots and without which they could not survive? Do mammals "dominate" the bacteria and other organisms in their intestinal flora that elaborate vitamins necessary for their life? Indeed, careful study of any ecological situation reveals interactions among organisms that make comparisons of "superiority" and "dominance" exceedingly difficult.

Nevertheless an aardvark cannot be produced by amassing coacervate droplets. Many complex problems of structure and function had to be solved before DNA could use aardvarks or man to make more DNA. These problems apparently were solved slowly, one or a few at a time, over long periods of time. The solutions may well have spelled the doom of less efficient types, and the visible record of life becomes one of increasing complexity or organization. Some more simple organisms also have survived, presumably to become integrated with highly complex ones into complex ecosystems. The basic question remains unanswered: Why should DNA have evolved aardvarks and men for making more DNA when bacteria and other simpler organisms apparently can serve just as well? Perhaps the answer lies in the complexity of ecosystems whose cybernetic mechanisms result in great stability. But this is a difficult problem to study in the fossil record. A major evolutionary trend intimately associated with increase in complexity is the trend toward increased homeostasis in the individual, population, and ecosystem.

SUMMARY

There is no evidence to justify the assumption of an essential difference between the mechanisms that produce gene-frequency changes within populations and those which account for the differences between men and microbes. In view of the time available for the evolutionary process, mutation, recombination, selection, and drift quite adequately account for the diversity of life. The discontinuities in variation patterns appear to be the result largely of ex-

inction. The discontinuities in the taxonomic description of variation patterns reflect extinction plus generous sampling errors. Examination of the fossil record has resulted in a classification of the major patterns of phylogenetic change as splitting of lineages, phyletic evolution, and quantum evolution. Rates of evolution appear to have fluctuated widely in the course of time. In addition to the standard rates for a group, there often have been unusually slow and unusually rapid rates. The so-called problem of the origin of higher taxonomic categories is seen to be a composite of linguistic, analytic, and evolutionary problems.

REFERENCES

- Rensch, B. 1960. *Evolution Above the Species Level*. Columbia Univ. Press, New York. An interesting analysis of evolutionary patterns, primarily in animals, with detailed consideration of trends in evolution and of the evolution of the nervous system.
- Simpson, G. G. 1953. *The Major Features of Evolution*. Columbia Univ. Press, New York. The most thorough and general account for zoology of the patterns of phyletic change and their explanation in modern biological terms. Simpson's more recent chapter in Sol Tax [ed.], *Evolution After Darwin*, Univ. Chicago Press, Chicago, 1960, vol. 1, pp. 117-180, is an excellent brief consideration of the problems.
- Stebbins, G. L. 1950. *Variation and Evolution in Plants*. Columbia Univ. Press, New York. The best source for an overall view with genetical orientation of the record of past plant life. The chapter The evolution of flowering plants, by D. I. Axelrod in *Evolution After Darwin*, *op. cit.*, pp. 227-305, contains more recent work on the Angiospermae.

4

human evolution: physical and cultural

The phenomenon of man has been explained in many ways by man. Our view is that the theory explaining the evolution of other organisms is necessary and sufficient for man as well. Cultural evolution is an inevitable consequence of man's biological evolution.

In this section the evolution of man and of his culture is considered from various aspects. Chapter 12 places in biological perspective a very brief description of what is known of the evolutionary history of Homo sapiens. No special processes appear to be responsible for the origin of man, but with the development of culture and the extragenetic transmission of information, a complication appears: evolution within culture itself. The evolution of man now seems to be a resultant of the interactions between biological evolution, in the usual sense, and this psychosocial evolution.

One aspect of man's culture is his attempt to deal with the physical universe he perceives around him. His techniques for handling reality determine what reality he sees. Man's understanding of the process responsible for his coming into existence is an aspect of this more general problem and is discussed in the last chapter.

12

the evolution of man

From the point of view of processes, the evolution of *Homo sapiens* is unique. The evolutionary forces described thus far have played and still play an extremely important part in human evolution. However, in addition to these forces, an entirely new kind of evolution, that of culture, has entered the picture. This nongenetic body of information is, like genetic information, transmitted from generation to generation. The evolution of all organisms except man depends, with very minor exceptions, upon the information stored in the nucleotide code and upon its expansion and rearrangement through mutation and recombination. In man there is superimposed upon this a large body of extrinsic information which, at least in theory, is potentially available to all members of the species. Through the utilization and manipulation of this body of information, man has evolved prosthetic devices (both mental and physical) that have given him a unique ability to modify his environment and, indeed, to influence the evolution of all organisms on the face of the earth.

MAN'S EVOLUTIONARY HISTORY

Man shares a vast inheritance with all mammals. Those interested in the long story of the attainment of mammalhood are urged to consult textbooks on vertebrate paleontology. The conquest of land by vertebrates and the eventual appearance during the age of the dinosaur of our inconspicuous warm-blooded ancestors with differentiated teeth and highly developed devices for fetal nourishment make a fascinating story. However, it is a story which sheds little additional light on the processes of evolution. The genotypes that, through recombination, provided more efficient tetrapodal locomotion, eggs resistant to desiccation, metabolic control of body temperature, faster conducting neurons, and all the other "inventions" on the road to the status of mammal contributed their information differentially to the gene pool of subsequent generations. At some point early in mammalian history, quite likely in the Paleocene (70 million years ago), came the first evolutionary step that was to lead eventually to the differentiation of man from the rest of the mammals through the possession of culture.

We can only guess at the reason or reasons for this step; perhaps it was the presence of efficient terrestrial predators, perhaps an abundance of fruit. But, for whatever reason, in one group of mammals, individuals living in the branches of trees and shrubs started

to leave more offspring than their cohorts who preferred a strictly terrestrial life. Ascent into the trees meant the penetration of an entirely new environment, an environment in which the requirements for survival were strikingly different from those met by terrestrial animals. Many of the trends caused by selection operating on an arboreal creature need little explanation. Flexible grasping organs at the ends of the limbs are useful devices for remaining in trees. When leaping from branch to branch it obviously is necessary to be able to judge distances, and genotypes that tended toward good binocular vision were likely to reproduce themselves better than their less fortunate relatives. Genotypes with the eyes rotated toward the front of the head tended to have binocular vision only if a large long snout did not interfere. Both binocular vision and grasping hands and feet lessened the need for a long snout for investigation and manipulation. Shortening of the snout and the resultant reduction of olfactory membranes would be a handicap for a ground-dwelling animal, and genotypes having it would probably be selected against. However, in the treetops the loss of sense of smell was less serious and was more than compensated for by improved vision.

Stereoscopic vision in itself would be of little use without the neural mechanism necessary to evaluate the sensory input and translate it into highly coordinated voluntary movements. Thus, in the arboreal primates, selection resulted in a trend toward high development of the cerebral cortex as a center for evaluation of sensory input and the formulation and initiation of responses to the environmental stimuli received. Because of the arboreal habitat, sight and touch came to override smell and hearing as sources of information.

Living in trees presents some serious problems in the care of offspring. In primates this gave a selective advantage to individuals that had smaller litters but gave them a high level of care. In many mammals sexual activity is confined to a single season of the year, and the young are born at a time when a suitable food supply is available. In the tropical-forest environment of our distant ancestors the food supply of fruits and insects was presumably relatively more constant than in temperate zones. Thus there was probably little selection in favor of a single period of sexual activity. In the absence of this factor, selection favored year-round sexuality leading to the continuing presence of males, the establishment of the family group, and increased protection for the smaller litter of helpless young.

Man is not the only descendant of the shrew-like animals that originally invaded the trees. Like man, baboons have returned to a wholly terrestrial life, while chimpanzees and gorillas spend most,

but not all, of their time on the ground. Remaining in the arboreal habitat is an array of forms including such diverse primates as orangutans and gibbons, as well as monkeys, marmosets, tarsiers, and tree shrews.

It is important that our early ancestors lived in the trees, but it is also very important that they left them. It is difficult to see how a culture even vaguely resembling ours could have been developed by tree-dwelling organisms, if for no other reason than that there was an almost complete lack of raw materials for even primitive technology in the arboreal habitat. Although the reasons why our ancestors left the trees are obscure, perhaps one was that some of the larger primates found competition from smaller more agile ones too severe. Because of their increased size and intelligence, they were better able than their ancestors to cope with the problems of terrestrial living. Almost certainly the return was gradual, and at one time our ancestors must have lived much as do modern-day chimpanzees, foraging on the ground in the daytime but retreating to the trees at night. It seems likely that the efficient bipedal posture so characteristic of man was achieved after early prehomnids left the shelter of the trees and began to forage in bands out on grassy savannahs. Fossil evidence indicates that an abundance of food was available in the game animals that roamed the open spaces, and selection probably favored any protohuman genotypes permitting, by whatever means, utilization of this food resource. An upright posture, providing reasonably rapid locomotion while at the same time freeing the hands to grip stones or staves, would have been at a premium. Intelligence and social organization would also have had their reward in food.

It is important to remember, when one is casually discussing our family tree in this manner, that the evolutionary processes discussed are no different in principle from those accounting for bandless water snakes or banded snails. To say that our ancestors moved out of the trees to escape the competition of more agile foragers is merely a shorthand for the following: At one point in our evolutionary history any recombinant that had the slightest behavioral tendency to descend from the trees and forage on the ground had a better chance of contributing to the gene pool of the following generations than other genotypes lacking this tendency. The frequency of the kind of genetic information producing this sort of behavior therefore increased in the populations concerned and the behavioral norm was slowly shifted. A great many generations after the first pioneer individuals foraged briefly on the ground, the behavior of all individuals in the populations concerned became terrestrial.

The details of the human fossil record are not particularly pertinent to our theme. A brief review of the salient features of the record (as we interpret it) is given here for the convenience of those not familiar with them. The earliest fossil organisms generally conceded to be "men" are the Australopithecines (members of the genus *Australopithecus*). These men, who may have made their appearance in the upper Pliocene (1.75 million years ago) and who disappeared some 500,000 to 600,000 years ago, were fully erect and bipedal, and made and used stone tools. The time of emergence of *Australopithecus* is doubtful because of uncertainties in the dating of recent finds, especially the so-called "*Zinjanthropus*." The primate fossil record prior to *Australopithecus* sheds little light on the line leading to man, although one fossil from the lower Pliocene (some 10 million years ago) known as *Oreopithecus* seems to be more related to our distant ancestors than to those of monkeys or apes.

Direct descendants of one group of the Australopithecines probably are the Java and Peking men and their relatives, *Homo erectus*. The first fossil *H. erectus* has an estimated age of 600,000 years, indicating a possible overlapping in time with some of the Australopithecines. Most *Homo erectus* probably disappeared around the time of the Riss glaciation, some 200,000 to 250,000 years ago. The last remnants of this species may well have persisted in geographic isolation after selection had transformed other groups of *H. erectus* into what we now call *Homo sapiens*. Other less well-documented remains indicate that *H. erectus* was widespread and quite variable and had achieved a culture involving the use of fire and tools.

It seems likely that much of the confusion regarding the emergence of *Homo sapiens* has been caused by reticulate evolution. About the time of the last interglacial (100,000 to 200,000 years ago), various populations of the geographically variable *H. erectus* probably gave rise to numerous populations of *H. sapiens*. These populations had varying fates; some died out, others met and fused through interbreeding, and some may have persisted and evolved in relative isolation until after the last glaciation. The famous Neanderthal man seems to have been a geographic variant of *H. sapiens*, one which disappeared, in all probability, from different combinations of causes in different areas (interbreeding with more modern *H. sapiens*, competition from more modern *H. sapiens*, starvation due to disappearance of game, etc.).

Once our predecessors became upright, there remained only one major physical change to convert them into modern men. This change was a great increase in brain size and skull volume. *Austra-*

lopithecus, one of our earliest upright ancestors, had a brain volume of 450 to 600 cc (about that of a large ape). The cranial capacity of *H. erectus* bridges the gap between the largest great apes and modern man, the smallest skull on record having a capacity of 775 cc, and the largest, 1,200 cc, well within the range of present *H. sapiens*. The Java men tended to have a slightly smaller brain than Peking men. Modern men (*Homo sapiens*) average about 1,450 cc. Because of the physical limitations on pelvic expansion in anthropoid females, most of the growth resulting in large brain size is postnatal. This great postnatal growth in skull capacity results in a very long period of helplessness in the infants of the larger-skulled forms, creating a mother-offspring relationship that has left a considerable mark upon our present-day culture.

In summary, then, man owes many of his most characteristic features to an ancestral sojourn in the trees. It is responsible for the well-developed association centers of his brain and the skillful manipulating devices on his forelimbs. It also gave him his family association with its year-round sexuality and mother-offspring relationship. All these were instrumental in the development of culture, which will be considered next.

CULTURE

At one time it was commonly thought that man's large brain made it possible for him to invent culture. It now seems that possibly the reverse was true. The earliest presumed ancestors (or near ancestors) of modern man, the Australopithecines, were erect, tool-making creatures with brains not differing appreciably in size from those of modern-day anthropoid apes. The evidence indicates that the Australopithecines were animals of the plains and that they were primarily vegetarian. There is also evidence that their diet was supplemented somewhat with the meat of small animals. Little is known about the tools used by these protohumans, but it seems unlikely that they could have left the shelter of the forests before they acquired a reasonable security by employing rocks and clubs in their own defense. A variety of stone tools found in association with the latest Australopithecine discovery (*Zinjanthropus*) removes any reasonable doubt that Australopithecines made and used tools. This association is *prima facie* evidence that Australopithecines had at least a rudimentary culture.

There can be little doubt that an ape-brained anthropoid, quite possibly our own direct ancestor, was the possessor of a complex

body of information that passed from generation to generation non-genetically. It also seems highly likely that these protohumans utilized a reasonably complex system of verbal communication. The making of stone implements is not as simple as the twentieth-century armchair observer might believe. While it is conceivable that young Australopithecines learned to do this merely by careful observation and mimicry, it seems more likely that a certain amount of spoken instruction went along with the demonstration. The possession of culture, and perhaps of speech, by these long-extinct, very small-brained anthropoids clearly outlines the probable solution of one of the most vexing problems in human evolution, the "cause" of the roughly threefold increase in brain size between that of earliest fossil man and modern man.

As culture became important in prehuman society, genotypes with the mental characteristics permitting optimal utilization of this extragenetic information were more successful reproductively than their less-well-endowed cohorts. Genotypes were favored that produced brains with the highest ability to associate, integrate, and store incoming sensory data and to utilize these data in a manner that enhanced the survivability of the genotype. This selection pressure resulted in a trend toward great expansion of the cerebral cortex and an increase in the number and complexity of the neuronal systems necessary for "thinking and speech." It is not unreasonable to assume that much of this increased volume is the result of a premium being placed on storage capacity. Man's tremendous neopallium is relatively more free from commitment to special sensory and motor functions than that of other mammals. These "uncommitted" areas may be presumed to be concerned with association and memory. This presumption is supported by results obtained from electrical stimulation of the brain in conscious patients undergoing brain surgery. For example, stimulation of the temporal lobe may lead to the patient rehearsing a complete symphony or reliving an event of the distant past. When a human being is subjected to a frontal lobotomy, his sensory and motor functions are relatively unimpaired, but he becomes "irresponsible."

There is a considerable body of literature on the reasoning power of chimpanzees. On certain types of tests designed primarily to evaluate human reasoning power, some "chimps" score higher than many human adults. Indeed, as Harlow succinctly puts it, if man is defined as the possessor of mental abilities that occur in other animals only in the most rudimentary forms, if at all, we "must of necessity disenfranchise many millions . . . from the society of *Homo sapiens*." Chimpanzees may lack culture not because of any

great lack of reasoning power but because of some other factor that inhibited the development of speech or the regular utilization of tools, or the reduction of inter-male aggressiveness. The "invention" of rudimentary culture started a selective trend that led eventually to man's large brain; the large brain did not just mysteriously develop and then discover culture.

Cultural and biological evolution cannot proceed independently. Indeed, from the very beginning of culture, man's evolution has been characterized by the interactions of biological and cultural evolution. The existence of culture put a selective premium on certain types of brains; the evolution of the brain permitted an expansion and enrichment of the culture. Such interactions were certainly very important during the transition period from the Australopithecines to *Homo sapiens*, but they are still very much with us. Before going further into such interactions, however, we shall consider some characteristics of culture and some features of cultural evolution.

One of the outstanding characteristics of human cultures is their tremendous diversity. Human beings speak some 2,800 different languages, describe their genetic relationships with each other with myriad complex kinship systems, believe in a great diversity of gods and spirits, are organized into groups which practice every degree and kind of governmental control, and fill their everyday lives with galaxies of taboos concerning everything from forms of salutation to shapes of wine glasses. This cultural diversity is by no means superficial; indeed, people of different cultures often have very basically different world views. This difference is frequently reflected in the language of a culture, and in a very real sense, as discussed in Chap. 13, the language creates the world view.

Language differences are among the most important of all cultural isolating mechanisms. Communication of information about complex phenomena may be exceedingly difficult within a culture (as almost any teacher will gladly testify), but between cultures with widely different languages the problems are immense. The reader is invited to contemplate the difficulties of explaining even a simple word such as "also" to an Eskimo if there are no dictionaries, a shared third language, or even the certain knowledge that an equivalent concept exists in his mind. The intricate and highly developed language of the Eskimos does not have a structure congruent with that of our language.

In spite of their great diversity, however, many similarities may be observed among cultures. Some form of religious belief is virtually universal. It has been suggested that these beliefs are based on

observed differences between living and dead human beings, the assumption being that the absence of breathing and lowering of the body temperature result from the desertion of the body by a spirit. This seemingly logical assumption combined with, among other things, dreams and ignorance of the forces of the physical world, is thought to be the basis of all religions. The elaboration of these or other simple ideas into the complex pattern of religions that we have today was a long and complicated process. It seems eminently fair to say that, even with the flourishing of science in the last few centuries, man's creation of spirits, gods, and the related paraphernalia of religion has had the most far-reaching effects of any cultural phenomenon. In most societies of the past and in the majority of societies today, organized systems of religion provide the principal means for the individual to orient intellectually to his physical and cultural surroundings. Among other things, such systems of orientation make it very difficult for the individual to appreciate the outlook of members of other societies.

Most people in every culture believe that their own way of doing things is, in some absolute sense, *right*. They are unaware, or at most only dimly aware, of their own biological and cultural history. They do not understand why they love their children, why the sun comes up in the morning, or why they must hate their country's enemies. They accept the dicta of their culture without question. The acceptance of these dicta at one point in time and space may well have added to the viability of the culture. At another point the same set of values may be suicidal.

Many of the important rules for living in our culture are believed by some to have been handed down from heaven a mere few thousand years ago. Most of them probably trace to the time when human beings gave up a nomadic hunting and food-gathering way of life and, with the invention of agriculture, began to settle down in rather large organized groups. There were numerous advantages to living in such groups, among them cooperative defense, the ability to carry out projects requiring a great deal of manpower, and the opportunity for specialization into various trades and professions. For groups of any size, from family on up, to enjoy the fruits of cooperation, internal strife must be kept at a minimum. Thus, for instance, intergroup selection favored those groups that suppressed killing within the group. One logical way to do this was for the elders to tell the young that killing a member of the in-group would offend the spirits, and indeed that is essentially the way it is done today in our own society. It should be noted carefully that, in spite of constant reiteration of "Thou shalt not kill," our society allows

certain kinds of killing of socially sanctioned types. Thus society can kill its internal enemies (assorted "criminals"), and killing its external enemies is encouraged. The social approval of killing outsiders at one time doubtless had considerable selective advantage for the society as a whole, but improved weapons make this no longer true. Certain types of murders within our society, although technically illegal, are approved socially. This is particularly true in situations where members of minority groups are the victims.

To recapitulate, cultures are extremely diverse and are separated by, among other things, language barriers. In spite of this, there are common threads running through most, if not all, cultures that make it rather obvious that major features of human culture have proliferated from a common source. People are generally unaware of their biological and cultural history, and most assume that they were, miraculously, born into the culture which has "The True Word."

A major interaction between cultural and biological evolution has been in the change of selection pressures. The development of modern medical techniques; the elimination of many large predators; the increase of the food supply through improved agricultural methods; control and evaluation of the environment with furnaces, air conditioners, dams, radar weather-warning systems, and the like have permitted many otherwise nonviable genotypes to persist. The diabetic controls his disease with insulin and reproduces; there is time to lead the congenitally blind man to the storm cellar because of the tornado warning over the radio. Thus some differentials in reproduction have been ironed out by cultural factors in *some* societies. However, some recently introduced cultural factors have imposed other selective pressures by favoring genotypes that are relatively immune to insecticides in their food, air pollution, nervous tension, heart disease, and cancer. In the last two cases differential reproduction is increased because, with increasing life spans, reproduction is carried into the years when these diseases are prevalent.

The patterns of gene flow in human populations have also been tremendously changed by cultural developments. Systems of transportation have steadily improved, moving the entire human population more and more in a direction of panmixia. However, this trend has been countered to some degree by immigration quotas and other cultural barriers to random mating.

Other interactions between cultural and biological evolution are obvious. Incest taboos tend to lower the coefficient of inbreeding. Social disapproval of interracial, interreligious, and interclass mar-

riages tend to keep the population in many parts of the world divided into relatively small partially interbreeding groups (somewhat analogous to Wright's model for a population with a structure favorable for evolutionary progress).

In recent years in western countries groups with the highest intellectual attainments have voluntarily limited their family size to a greater degree than other segments of the population. Since intelligence has a genetic component, this differential is selection against intelligence. There are, however, many complications that make it impossible to predict the consequences of this recent ominous trend.

The influence of our primate background on our culture has been profound. The loss of a sharply defined oestrus period in the female and the general helplessness of the primate infant, with the concomitant establishment of a family group stable throughout the year, has led to systems of interpersonal relationships that have been vastly elaborated in cultural evolution. On top of the relatively simple male-female and female-offspring relationships of prehuman family groups, cultural evolution has produced the monstrously complex set of phenomena usually included under such topics as love, sex, and kinship. That these phenomena have become deeply and basically interwoven into the entire fabric of our behavior has been amply demonstrated by anthropologists and psychologists. These phenomena enter into choices of political systems and political leaders, legal systems, the characteristics of the deities that men have devised, and even into choices of designs for automobiles.

Unfortunately, very little is known about the ways in which culture evolves. Some similarities with biological evolution are obvious, but the value of the following analogies is open to considerable doubt. They are given here more as food for thought than as established fact.

Many apparent parallelisms may be detected. Virgin births are found in the mythologies of many different cultures. Complex puberty rites are also widespread, ranging from severe tests of manhood involving torture and genital mutilation to ceremonies such as Christian confirmation and Jewish Bar Mitzvah. Ceremonial appeals to spirits are nearly ubiquitous—*vide* Navajo dancers and San Francisco ministers appealing to their gods for rain. Some examples seem closer to the biological phenomenon of convergence: the appearance of functionally similar structures in very dissimilar entities. An example of this might be the military dictatorships which sprang up in both Germany and Japan between World Wars I and II. The histories of the two cultures in which these phenomena appeared were widely divergent, and yet in many superficial aspects the

dictatorships were similar. The stories of virgin births in different mythologies may be a better example of convergence than parallelism. (The line is difficult to draw in any case.) Similarly, the idea that one may achieve a desired condition by eating a portion of a cadaver is widely and spottily distributed through human cultures. The bodies of victims put to death in Aztec religious ceremonies were devoured so that the eater could establish close contact with his god. As Linton has said, "It was a religious concept not unlike that of the Christian communion except that the Aztecs were painfully literal about it."

An obvious cultural analogue of natural selection can be found in the differential reproduction of entire cultures. The body of information making up some cultures has become more and more widespread (that is, has been possessed by more and more individuals) while others have decreased or become extinct. The cultures of some small groups have doubtless disappeared without a trace. However, cultural evolution is obviously more reticulate than biological evolution, and large cultures virtually never disappear without transferring some of their information to other cultures. Although American Indian cultures have been badly swamped and in some cases completely destroyed by the spread of western Europeans, some of their elements have been transferred into western European culture. The use of tobacco is a good example.

The ascendance of individuals with novel ideas may be a random phenomenon in human society. Thus one could consider the advent of Aristotle, Darwin, Hitler, Buddha, Tecumseh, etc., to be a sort of cultural analogue of mutation. Men with their proclivities are doubtless present from time to time in all cultures but, as with gene mutations, the proper environment is necessary for them to gain prominence.

An interesting analogy can be drawn between genetic homeostasis and cultural integration. As will be remembered from Chap. 7, when strong selection is applied to a single character, only a certain amount of progress can be made before the effects of unbalancing a well-organized genotype counterbalance the selective pressure on the character. In other words, natural selection works to preserve a well-balanced genotype. It is possible that overdevelopment of some feature of a society may lead to the destruction of the integrated properties of the society. One might view the development of an extreme military dictatorship in Japan in this light. Another example was the promulgation of a fantastic taboo system by the Hawaiian priesthood, which eventually led to the destruction of the entire religious system.

Today this imbalance can be seen in the overdevelopment of the physical and biological sciences relative to our other disciplines. For many centuries our systems of ethics (the tested rules under which a society operates) have been taught and maintained by church and state. It is either too much trouble or impossible to orient most people to the real basis for ethics, and so these institutions control human behavior through a combination of force, social pressure, and promised supernatural punishment. As scientific knowledge has increased over the past few centuries, governments and churches have slowly changed their ideas so that they do not conflict directly with the findings of science. In the past few decades, however, the progress in science has far outstripped the ability of our extremely conservative religious and governmental systems to adjust to the changes. Medical advances and public health programs have permitted an unprecedented surge in population size, a surge which the ill-informed portion of our cultural structure will not permit us to counteract. Increased population pressures increase the danger of war, but our most enlightened political and religious leaders and, indeed, many of our scientists seem to have only the vaguest grasp of the possible consequences of another world conflict. The natural sciences have helped to initiate and support the population explosion and have produced thermonuclear weapons, nerve gases, and agents of biological warfare. In a sense they are in the same position as parents who permit their children to play with loaded guns. One of the possible consequences of applying too strong a selection pressure against a single character in a *Drosophila* experiment is that the line will become extinct. Perhaps in permitting this tremendous gap to develop between the scientists and the laymen, we have doomed our line to the same fate. Extinction may well be the ultimate interaction between cultural and biological evolution.

SUMMARY

Homo sapiens is the product of biological and cultural evolution. The processes of his biological evolution do not differ in kind from those of other diploid, outcrossing organisms. Cultural evolution, change in the mass of nongenetic information shared by human beings, is easily recognized but poorly understood. The two kinds of evolution are inextricably bound in a complex of interactions. *Homo sapiens* is the only organism to have become aware of its origins and of the possible evolutionary consequences of its actions. It remains to be seen what the consequences of this knowledge will be.

REFERENCES

- Dobzhansky, T. 1962. *Mankind Evolving*. Yale Univ. Press, New Haven, Conn. Introduction to the entire literature on human evolution may be gained from the extensive bibliography of this scholarly and interesting book.
- Linton, R. 1955. *The Tree of Culture*. Knopf, New York. A very readable account of the diversity of cultures.
- Montagu, Ashley [ed.]. 1962. *Culture and the Evolution of Man*. Oxford Univ. Press, New York. A series of stimulating essays on the interaction of organic and psychosocial evolution.

13

the theory of evolution

Man is the product of biological and cultural evolution, and man has developed the explanation of evolutionary processes put forth in this book. It is therefore inevitable that our view of evolution has been colored by the biological and cultural history of *Homo sapiens* in general and by that of western science in particular. To ask What is the true (or objective) explanation of organic diversity? is to fall into the error of assuming the existence of absolutes. It is not possible temporarily to renounce our membership in the human race and view the available data with Jovian detachment. It is possible, however, to point out some of the obvious sources of bias, some of the weak points in the story, some current points of controversy, and some possible ways of increasing our understanding. Complete objectivity may be unattainable, but perhaps we can hope to approach it asymptotically.

ANTHROPOCENTRISM

Perhaps the most obvious effect of being human observers is the nearly ubiquitous tendency to use *Homo sapiens* as a standard. This species chauvinism is manifest in many ways. It is easily recognized in its most naïve form when the assumption is made that evolution has always worked toward man as its ultimate goal. Thus Lecompte du Noüy states, "Evolution begins with amorphous living matter or beings such as the Coenocytes, still without cell structure, and ends in thinking Man, endowed with a conscience. It is concerned *only* with the principal lines thus defined. It represents *only* those living beings which constitute this unique line zigzagging intelligently through the colossal number of living forms." (Du Noüy, p. 66; emphasis his.)

In more subtle forms, such ideas persist in diverse ways in modern evolutionary literature. Often the term "higher animals" is used to refer to those more like *Homo sapiens* than "lower animals"; the implications of the "higher" and "lower" are quite clear. When standards of "success" in evolution are selected, by some odd coincidence the winning characteristic usually seems to be one in which man excels: ability to control the environment, intelligence, possession of culture, retention of "generalized" characteristics, etc. Some other rather obvious standards are often glossed over, for example, persistence through time (cockroaches excel here), total numbers of individuals (the forte of microorganisms), and reproductive potential (many candidates, such as the house fly and beef tapeworm).

People just assume that man *must* be the most successful organism and define success accordingly. (Since man invented the language, he most certainly has a right to do so.) However, the threat of thermonuclear extinction hangs more heavily over our heads than over the cockroaches, and we may yet envy them their ability to crawl under rocks and their relative immunity to radiation.

Since most scientific work is done by individuals who are reproductive (or, more rarely, postreproductive) members of *Homo sapiens*, the "adult" stage of the life cycle has acquired a certain prestige relative to other stages. For instance, illustrations of phylogenetic trees almost invariably depict series of adult organisms, and the taxonomy of almost all groups is based primarily on this stage of the developmental sequence. How different would be our view of evolution if we were intelligent May flies, with a long nymphal life in which to ruminate over nature, followed by a few frantic, flapping days as reproductives? Similarly, mosses might have a rather different view of the relative importance of the haplophase and the diplophase; if dandelions were authors, one might find sexual reproduction discussed in the literature as a rare and imprudent luxury.

Needless to say, there is not a shred of evidence to suggest that man is the ultimate goal of evolution; indeed, there is none to indicate that he is even the terminus of his own lineage. If there were purposive forces guiding evolution, we would expect to find traces of them in the process; in the absence of such evidence, it must be assumed that such forces do not exist.

CULTURAL BIAS

Evolutionary theory has been almost exclusively the product of Western minds—minds that think in terms of the Indo-European languages. The structure of these languages has acted to mold our view of nature into a form easily handled by the language. Ideas such as that an effect implies a cause, or a creation a creator, have, since Aristotle, been considered to be immutable laws of logic. It is interesting that Oriental religions have emphasized the artificiality of the subject-object dichotomy. Their philosophies aim to eliminate this division, the supposed result being similar in many ways to the professed goals of psychotherapy in Western cultures. A linguistic need for a doer and the done, for objects and relationships among them, may have deeper and more damaging effects than are presently realized. Our language requires us to put things into various relationships even when it is patent nonsense to do so. For instance,

we are compelled to say "It is snowing," although the "it" is a meaningless word which soothes our sense of syntactic aesthetics only. Similarly we tend to think of natural selection as *something* that somehow changes a population.

People of other cultures order natural phenomena in ways quite different from those we consider natural and proper. For instance, Eskimos have no generic term for water, but they have a detailed and useful terminology describing the various kinds of frozen and liquid water. Gauchos have some 200 terms for horse colors, but they divide the vegetable world into four species: *pasta*, fodder; *paja*, bedding; *cardo*, woody materials; and *yuyos*, all other plants. As a language system develops, the effects of its structure seem to be invasive and widespread. All aspects of the culture eventually are involved, and a network develops that is difficult to escape. It has been suggested that the person most nearly free to describe nature impartially would be a linguist familiar with many widely different linguistic systems.

Some impression of the relation of language to behavior and to the description of nature can be gained by comparing even superficially the basic aspects of Indo-European languages with a very different language. The language of the Hopi Indians has been studied in considerable detail by Whorf and offers revealing comparisons. It is difficult to describe the differences in English, for the languages are scarcely congruent. For example, our concept of plurality causes us to use cardinal numbers in referring both to real and imaginary pluralities. We count 10 objects and regard them as a group. (However, we say that there are "10 at a time," introducing the concept of time into group perception.) When we refer to 10 hours or to any other cyclic sequence, actually only one item is experienced at a time; the others are remembered or predicted. We think of time in such a way as to "know" that there was a day yesterday and that there will be a day tomorrow. We can actually quantify "tomorrow" quite "precisely" in minutes, hours, days, months, and years. The Hopi Indian, on the other hand, would not think of using numbers for entities that do not form an objective group. He recognizes a group of 10 Indians. But, if they stay for a visit, he reports that they "left *after* the tenth day," not that "they stayed 10 days."

It is interesting and important to realize that similar differences between the languages are manifest when physical quantity, phases of cycles, and other aspects of time such as duration are investigated. Our mass nouns, which we use to refer to unbounded homogeneous phenomena, imply, besides indefiniteness, lack of outline or size.

When we particularize, we often must say “body of water,” “dish of food,” or “bag of oats.” The relator “of” denotes or suggests *contents*; we must have a “container” for the “portion” of matter described. In Hopi, mass nouns also imply indefiniteness but not lack of outline and size. “Water” always means a specific mass or quantity of water. No “container” is implied. One could give examples almost without end. In Hopi, there is no basis for a formless item such as our “time”; our structuring of time with three verb tenses does not occur. Metaphors involving an imaginary “space” (“this discussion is *over* my head”) are lacking.

It seems clear that such concepts as Newtonian time, space, and matter are inherent in the language of the Newtonian physicist. A scientist working in a language with very different structure conceivably might have been compelled to describe nature in, say, relativistic terms. It also seems clear that much of what we think of as “real,” “commonsense,” and “beyond doubt” in biology are receipts from our language and culture. Biologists have much to learn from the study of the ways other cultures with different languages view nature. Biologists may also benefit from using what is perhaps the only less-biased language presently available to them for describing nature. This language is mathematics.

SCIENTIFIC BIAS

Good examples of the effects of language on the biologist’s view of nature are not difficult to discover. Biologists have long believed that sexually reproducing organisms occur in distinct clusters or kinds, commonly called *species*. In the 20-year period between 1937 and 1957 outstanding evolutionists such as Theodosius Dobzhansky and Ernst Mayr, taking cognizance of the evolutionary importance of isolation, attempted to develop definitions of the concept *species*, using genetic criteria. Mayr’s short definition, as given in his classic *Systematics and the Origin of Species*, is the one still employed in essence by the majority of modern evolutionists:

Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups.

This definition is a description of what is known as the *biological-species concept*. Its acceptance was responsible for a strong shift of emphasis toward studies of evolving entities in nature rather than the application of static concepts to dried insects and stuffed birds. It was recognized that all other taxonomic categories, such as genera and families, could be adjusted arbitrarily in size. If a worker thought that *Homo sapiens* and *Homo erectus* were too different to

be placed in the same genus, he could place the Java Man in the genus *Pithecanthropus*. Others might disagree with him but could not demonstrate that he was wrong. Such disagreements rested only on opinion. With the biological concept at the species level, things were different; one had only to find out if two populations were actually interbreeding, or, in the absence of the physical contact necessary to permit this gene exchange, were at least *potentially* able to interbreed. Partially differentiated segregates within a species were called subspecies and were considered, with considerable justification, to represent the early stages of species formation. In borderline cases, such as the *Drosophila paulistorum* example discussed in Chap. 10, where information derived from laboratory crosses did not permit a clear "species or subspecies" decision, the description "species *in statu nascendi*" has been used.

In recent years a group of biologists has questioned the continuing utility of the biological-species concept. They regard the apparent distinctness of species (as a sweeping generality) as an artifact of the procedures of taxonomy. These procedures decree a hierarchic structure in which every entity to be recognized formally with a "scientific" name must be assigned to some level in the hierarchy. In other words, taxonomists were required to find distinct entities, whether or not any existed. Soon after the idea of biological species was promulgated, it became obvious that the great multiplicity of genetic systems found in plants, as discussed earlier, resulted in a very limited applicability of the concept in botany. The concept was never intended to apply to asexual organisms, but it has also proved difficult to apply in the many groups of plants where sexual reproduction makes up only one part of the genetic system, where allopolyploidy has produced a reticulate phylogeny, or where the "organism" is multiple (as in lichens). As more knowledge of the invertebrates is uncovered, the inadequacy of the biological-species definition has also been apparent.

The last stronghold of the utility of the concept was in the insects and vertebrates. However, there seems to be only one entity, a vertebrate, about which we have sufficient information to be reasonably safe in assuming that it is a "biological species." This vertebrate is *Homo sapiens*. We have sufficient information about interbreeding within the group to be relatively sure that all subdivisions can exchange genes with all others (the sort of information that is usually lacking). In addition, man's nearest living relatives are so different from him that the possibility of gene flow is discounted. Recent investigations of insects, *which did not start from the premise that organisms must (in most instances) occur in distinct clusters*, have indicated that the ease with which various groups

of insects may be fragmented into distinct biological species has indeed been overestimated. A study of North American butterflies showed that less than one-half of the genera could be divided neatly into groups of entities that might correspond to biological species.

In retrospect, these conclusions are not very surprising. The very nature of the biological-species definition makes its use in practice impossible. The accepted test of conspecificity (or lack of it) is what happens (or would happen) when two forms occur together in nature. Even when, conveniently, two forms are sympatric, studies may reveal some level of partial interbreeding and make a firm decision impossible. In such a situation, the question revolves around whether or not swamping will overcome any tendency toward isolation caused by a selective disadvantage of the hybrids. This problem has been discussed in the chapter on differentiation of populations; since the environmental conditions are certain to change, the only way to answer the question of what will happen is to wait and see.

In allopatric entities the problem is complicated by the idea of "potential interbreeding." One must predict the courses of populations if they approach each other and the events at their hypothetical meeting under assumed conditions. Then, if the formation of hybrids is postulated, the fitness or viability of the hybrid population must be estimated. Unfortunately, fitness and viability are very difficult to estimate for a population of *Drosophila* in a bottle, let alone for a hypothetical population resulting from presumed hybridization of populations that have traveled unknown routes to an assumed locality where postulated conditions prevail.

Laboratory tests of interbreeding potential, while yielding valuable information, are not considered definitive. Two kinds of mice, *Peromyscus leucopus* and *P. gossypianus*, will hybridize in the laboratory, but where they occur together naturally in the Great Dismal Swamp of Virginia they remain distinct. Laboratory hybrids between northern and southern populations of *Rana pipiens* do not develop properly. As discussed in Chap. 10, these northern and southern frogs are connected by a long chain of intermediate populations. Should these intermediate populations suddenly become extinct, would the two terminal groups represent two "good" biological species? The question cannot be answered because the biological-species concept has no operational definition. There is no set of operations by which a value can be assigned to each entity: in this case, either "good species" or "not good species." It is conceivable that, if the two terminal populations approached one another naturally, selection might alter them so that they would interbreed freely on meeting; then again it might not.

The biological-species concept might be redefined in a way that would make laboratory tests conclusive; the problem of cutting the continuum of possible degrees of success in hybridization would remain. In addition, the amount of work involved in delimiting a single species would be staggering, and one would still be faced with the omnipresent problem of the experimental biologist: deciding what the experimental results tell him about situations in nature.

Considering the patent difficulties of dealing with the concept of species, how can one account for its great tenure in the biological literature? The idea seems to have had its origins in western European parochialism. As in the bear example in Chap. 11, the apparent distinctness of clusters is much enhanced when only a small geographic area is known. Equally, inadequate sampling over a large geographic area will increase the impression of distinctness. If an expedition from Mars collected samples of man by shooting a few inhabitants of Norway and one or two African pygmies, the Martians might easily come to the conclusion that there were two distinct species of man.

The appearance of Darwin's *Origin of Species* signaled the end of the idea that species were eternal and unchanging but did relatively little to dispel the notion of prevalence of distinct clusters. However, the idea that scientists, in expecting to find discrete species, were imposing their own prejudices on nature was not entirely lost on biologists of the last century. J. Victor Carus (*Geschichte der Zoologie*, 1872) stated:

It is of interest to note that in Aristotle the difference between plants and animals is already touched upon. . . . Regarding the nature of some marine growths one may be in doubt whether they are plants or animals. . . . Even the ascidians, says Aristotle, properly may be called plants since they give off no excrement. . . . One sees that Aristotle fell into the same error as almost all moderns. The term "plant," which came to us as part of our language, was interpreted as a term that must correspond to a class of naturally occurring entities. The same thing has happened to later workers with respect to the term "species." Instead of investigating whether there exists in nature anything that is unchangeable and circumscribed and that corresponds to this term, and then, in the absence of such, to allow nature her liberty and only artificially to assign a meaning to it that corresponds to the current state of knowledge, one simply assumed that one was compelled to consider the words as a symbol for one of nature's secrets, a secret that one might still hope to unveil.¹

¹We are indebted to Prof. R. G. Schmieder for translating this passage and bringing it to our attention.

In the 90 years following the writing of this passage biologists have been rather well disabused of the idea that species are unchangeable, but the idea that they are "things" lying in wait to be discovered in nature lingers on.

There may be an additional cultural factor tending to prevent recognition of anything but neatly segregated animal entities in nature. There is a revulsion against so-called "miscegenation" in many parts of Western culture. It has been suggested that, although it is considered permissible for plants to engage in illicit activities (hybridization), such behavior could not be recognized in animals. The validity of this interesting speculation is, to say the least, difficult to evaluate. There can be little doubt, however, that cultural factors strongly influence the biologist's view of the structure of nature.

If the generalization that organisms exist as distinct species is largely invalid, does this mean that there is no practical way of investigating the diversity of nature? At first glance, it might seem that the current nomenclatural structure would be an insuperable obstacle to reasonably objective description of the patterns of variation found in the earth's biota. However, as long as names are viewed merely as convenient landmarks in the continuum of life, rather than as possessing some deep (if obscure) meaning in themselves, the problems are not too serious.

In recent years taxonomists have been investigating multivariate methods of assaying similarities among organisms. These techniques rely on high-speed, automatic, data-processing equipment to compare simultaneously many features of organisms or groups of organisms and to express numerically the degree of similarity of each entity in the study with every other entity. For instance, it is easily within the capabilities of modern digital computers to compare 200 different butterflies with each other, each of the 19,900 individual comparisons being based on 100 or more attributes of the individuals compared. Such computing systems obviously have a capacity that transcends that of the human mind for making relatively objective multiple comparisons. The details of the techniques are beyond the scope of this book, but an introduction to the field of numerical taxonomy is provided through a single brief example and in the references at the end of this chapter.

Development of these techniques for comparing organisms should be of considerable aid in solving some of the more vexing questions about the evolutionary process. Methods have been developed that mathematically and pictorially express the patterns of relationship found in numerical taxonomic studies. In this way, a portion of the

cultural bias may be removed; at least the computer presumably does not have a deep fear of miscegenation.

A short example follows to show how numerical methods may reduce the number of subjective decisions the investigator must make in describing organic diversity. It must be emphasized that the pilot study described below is not given in support of any sweeping generality about the structure of nature. It is merely a very brief example of one method that may be profitably used to investigate that structure. The specimens studied are not treated as a sample from a larger population; they are the entities to be compared. It will be obvious to the reader that many more individuals from many populations would have to be compared before the general structure of even the *Euphydryas editha-chalcedona* complex could be elucidated.

Thirteen male individuals of checkerspot butterflies (*Euphydryas*) were compared on the basis of 75 characters of their skeletal morphology and color patterns. By the standard methods of butterfly taxonomy, eight of these individuals had been identified as belonging to the species *Euphydryas editha* and three of them to the species *E. chalcedona*. Two of the specimens came from a population (Kings Canyon) which, on the basis of classic procedures, could not be assigned with certainty to one species or the other. Therefore, since the techniques of taxonomy did not permit such intermediacy, these two individuals had been assigned by the taxonomists to what seemed the most similar species, *E. editha*. The specimens and their coded designations are listed in Table 13.1.

In some areas of California *E. editha* and *E. chalcedona* are found together, and no intermediate individuals have been observed. In others, such as the Kings Canyon area, "problem" populations are found, and the apparent distinctness blurs. At this point, note that the taxonomist has, in essence, done the following: recognized that the *editha* individuals are more similar to each other than to the *chalcedona* specimens (and vice versa). Although recognizing that the two Kings Canyon specimens are different from the *editha*, he has decided that they are more like the *editha* than the *chalcedona*.

The first step in the numerical analysis involved the determination of the states of the various characters used in the comparisons. The dimensions of markings on the wings, distances between the tips of certain wing veins, sizes of structural features, etc., were measured under a microscope. Other characters which did not lend themselves to direct measurement were quantified by coding into states.

When all the characters had been evaluated for each specimen, a digital computer was employed to calculate product-moment corre-

lation coefficients as a measure of the similarity of each individual to every other individual.¹ These coefficients are conveniently displayed in an array called a *Q* matrix (Table 13.1). *Q* matrices show the estimates of similarities among individuals. One may wish to know the patterns in which characters are associated, for instance, whether or not individuals with long forewings also tend to have a wide spot in the discal cell of the forewing. In this case, coefficients may be calculated that show the relationships of the characters with each other; these may be arrayed in what is known as an *R* matrix. In our example, each of the 13 individual butterflies is compared with all 12 others, giving 78 ($13 \times 12/2$) comparisons. The coefficients comparing each of the 75 characters with all 74 others were computed, but the *R* matrix containing the 2,775 ($75 \times 74/2$) coefficients is too large to reproduce conveniently. The *R* matrix is especially useful in providing clues as to whether two characters are actually measurements of the same thing. (For instance, in a human being one would not ordinarily consider the color of the left eye and the color of the right eye as two separate characters, since in most samples they would be perfectly positively correlated.)

It is helpful in visualizing patterns of relationship to express the structure in a *Q* matrix in the form of a dendrogram (treelike diagram). One way is to form the nucleus of clusters with pairs of highly correlated entities and to add individuals to the clusters according to a specified procedure. The relationships of the 13 *Euphydryas* specimens as obtained by one method [weighted variable group (WVG)] of expressing structure in a matrix are shown in Fig. 13.1. The only significant feature of this diagram of relationships is the level at which stems join. The level at which two individual stems join may be read at the ordinate as the correlation coefficient of the two entities. When stems of groups join, the level is an average correlation of the two groups. Note that, while the dendrogram makes it much easier to grasp the basic patterns of relationship in the *Q* matrix, considerable information is lost in the process of expressing the structure. Thus, although the relationships of the Kings

¹ The product-moment correlation coefficient may take values from -1 to $+1$. Perfect positive correlation (maximum similarity—the correlation of an individual with itself) is $+1$, perfect negative correlation (maximum dissimilarity in every character) is -1 . A correlation coefficient of zero indicates no correlation; the individuals are neither more nor less similar than one would expect if the character values for each were assigned at random. In the matrix of coefficients given, those with a value larger than .25 are significantly different from zero ($P < .01$). The product-moment correlation coefficient is only one of several coefficients which may be used to assay similarity or difference.

Canyon specimens to the *editha* cluster are shown, the information that KING579 is much more similar to WOOD613 than KING8461 is to WOOD613 is not in the dendrogram.

At first it may seem that all the complicated manipulations of the numerical taxonomic procedure have only confirmed the semi-intuitive conclusions of the original taxonomists. This is, however, not the case. First of all, it is now possible to replace vague statements about relationships with more precise information. With the preface “based on the evaluation of the 75 characters coded as above, the calculation of product-moment correlation coefficients, and a weighted-variable-group search for structure in the *Q* matrix,” it can be stated, for instance, that the two Kings Canyon specimens are correlated at the .543 level and that the average correlation of these

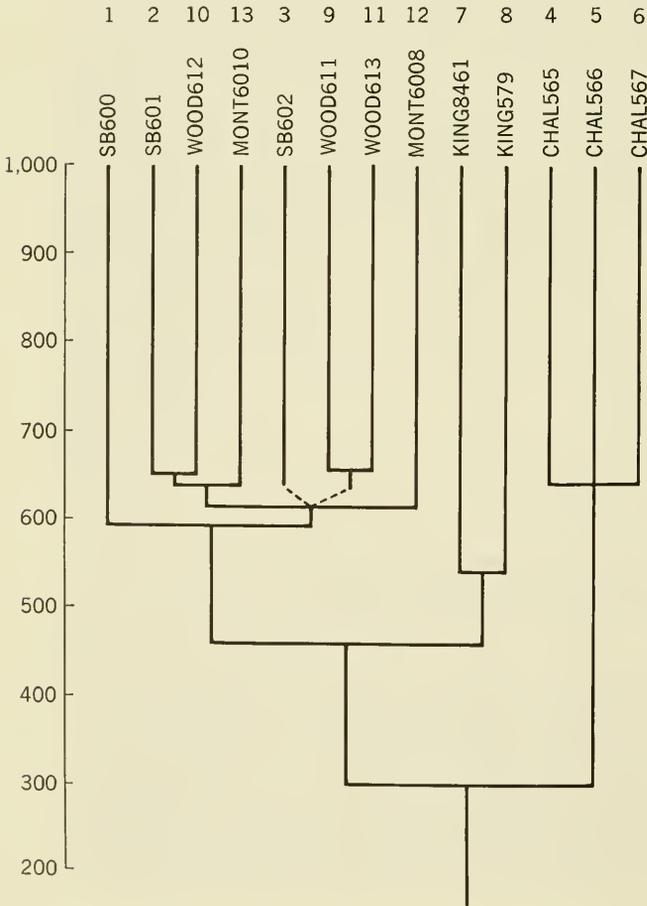
Table 13.1 | *Q* Correlation Matrix—Specimen × Specimen

	2	3	4	5	6	7	8	9	10	11	12	13
1	.530	.540	.000	-.123	-.090	.311	.101	.499	.472	.423	.423	.376
2	xxxx	.571	-.050	.077	.031	.496	.424	.594	.649	.305	.536	.572
3		xxxx	.392	.190	.416	.443	.365	.640	.549	.479	.606	.498
4			xxxx	.603	.642	.229	.378	.220	.103	.248	.160	-.072
5				xxxx	.594	.298	.275	.069	.119	-.022	.067	-.115
6					xxxx	.219	.468	.369	.172	.400	.245	.171
7						xxxx	.543	.313	.425	.103	.520	.330
8							xxxx	.470	.471	.471	.396	.470
9								xxxx	.537	.655	.564	.499
10									xxxx	.431	.580	.588
11										xxxx	.363	.472
12											xxxx	.501
13												xxxx

Specimen Code

- 1-3 *E. editha* (SB600, SB601, SB602): San Bruno Hills, San Mateo County, California, elevation 600 feet, April 3, 1960.
- 4-6 *E. chalcedona* (CHAL565, CHAL566, CHAL567): Pinnacles National Monument, San Benito County, California, elevation 1,300 feet, April 26, 1959.
- 7-8 *E. editha* (KING8461, KING579): Kings Canyon National Park, California, elevation 9,000 to 10,000 feet, July 20-21, 1958.
- 9-11 *E. editha* (WOOD611, WOOD612, WOOD613): Woodside Experimental Population, San Mateo County, California, elevation 540 feet, March 22, 1961.
- 12-13 *E. editha* (MONT6008, MONT6010): Route 198, 20 road miles east of Route 101, Monterey County, California, elevation 2,500 feet, April 20, 1960.

Fig. 13.1 | Diagram of relationships of specimens of *Euphydryas editha* obtained from Q matrix by the weighted variable group method. Ordinate is the correlation coefficient multiplied by one thousand. (From Ehrlich, 1961, *Syst. Zool.* 10.)



specimens with the specimens in the *editha* cluster is .462. The Q matrix and WVG diagram are answers in themselves, expressions of the similarities of the individuals studied. There is no need for complicated guesswork about interbreeding potentials to establish which (if any) of the clusters should be named and considered "good" species. Names (or numbers) may be given to clusters wherever convenient. In general, they may be considered analogous to floats thrown into the ocean to be used in charting currents. Too many floats would confuse the picture; too few would lose detail.

Needless to say, an accurate description of patterns of variation is of extreme importance in the study of evolutionary processes. Evolutionary theory is an explanation of the origin of organic diversity, both neontological and paleontological. Therefore, agreement on the nature of this diversity and unambiguous methods of describing it are obvious prerequisites to achieving maximum coherence in our theory. Otherwise we shall always be somewhat in the position of the blind men formulating a theory of elephant morphology.

It is not being suggested here that human and cultural biases and subjective taxonomy have conspired to give an entirely fallacious picture of the structure of the biotic world. It is being suggested that in several areas distorted ideas may be impeding progress toward a more thorough understanding of evolutionary processes. For instance, it seems very likely that the required taxonomic structure (as well as the cultural factors discussed) may have resulted in serious misapprehensions about the transfer of genetic information among groups of animals. Unfortunately, most taxonomic studies do not provide the kinds of data that are helpful in establishing just what patterns are present; all too often the results merely present nature tied up in neat packages. This became especially obvious during the writing of the chapter of this book dealing with differentiation of populations. North American butterflies are considered by most taxonomists to consist of an array of some 400 "species" and many more "subspecies." Unfortunately many (probably most) of these entities exist only in the cabinets of collectors, not in nature. The appalling complexity of some of our butterfly interrelationships is now slowly being elucidated; that of many others can only be guessed. The inadequacy of current taxonomic systems for describing the observed situations is very striking. It is in the area of description that numerical taxonomy is superior to classical taxonomy. Phylogenetic or other interpretation of the results is done by the taxonomist rather than the computer.

It would, of course, be folly to assume that the situation in butterflies (or birds, or any other group) can be considered representative

of that in all animals. We greatly need studies of patterns of differentiation in all groups. These studies must be made with sampling and analyses designed to describe the patterns present regardless of their configurations, not to apportion the variation into prepared compartments. The protestations of taxonomists, especially those working with vertebrates, that they almost always find "good" species must be discounted. Their methods and attitudes tend to exclude all other possibilities. For instance, as D. A. West pointed out in his interesting paper on grosbeak hybridization, "[hybrid] specimens are often labeled as one or the other species and are thus buried unreported in collections."

When more objective analyses have been completed, it may be discovered that the process of differentiation of populations is more complex than commonly supposed. If this is the case, the splitting part of the evolutionary process can be given much closer scrutiny.

More objective and quantitative methods of describing relationships will also be of aid in the study of the evolution of developmental systems. Can the larvae and adults of holometabolous insects evolve semi-independently? Can the gametophytic and sporophytic generations of the same plant follow different evolutionary pathways? If so, one could expect two separate numerical taxonomic studies, one based on adult characters and the other based on larval characters, to give systems of relationship that were not entirely congruent. At least one recent study comparing adult and larval mosquitoes has shown some discordance. It is all too common to think of evolution as operating on adult forms only, whereas actually the entire course of development is under selective control. The study of interactions of evolutionary pressures at various stages of development has barely been started.

In this section, the so-called species problem has been used as representative of a whole class of problems because it has held great interest (often mainly practical) for most evolutionists. Ideas such as niche, community, and climax, which are ecological concepts having much in common with the biological species, could be similarly treated. Further discussion of these may be found in references listed in Ehrlich and Holm (1962).

EVOLUTIONARY BIOLOGY

In the past two centuries, few, if any, scientific ideas have been subjected to as many vicissitudes as the idea of evolution through natural selection. The theory was violently opposed by many clergymen when it was first proposed by Darwin and is still anathema to

many religious groups. Many clerics today may have serious reservations, particularly in regard to man's place in the evolutionary scheme. Evolution has the distinction of having been legislated against by some of our states; indeed, the teaching of evolution is still technically illegal in the state of Tennessee. More than one hundred years after the idea was first put forth, few laymen have any real idea of what it is all about. In most high school biology classes (and textbooks) the subject is not touched on at all or is dealt with only in euphemisms. A high school teacher was recently quoted in the *Palo Alto Times* (California) to the effect that he had been experiencing little difficulty in teaching evolution in a local school system, although in Arizona he had met with less success because many students and other teachers had refused to accept his statements on the subject. There followed a flurry of letters to the editor, condemning the teacher for daring to express such dangerous and heretical ideas.

Evolutionists have not met with smooth sailing within biology either. Many outstanding scientists of Darwin's day vigorously opposed the idea, and until the science of genetics began to mature in the 1920s and 1930s the theory of natural selection led a tenuous existence. Today the vast majority of biologists accept the theory of evolution, although a great many of them have only a passing acquaintance with recent thinking on the process itself. In addition, there has always persisted a small but determined group of scientists and pseudoscientists who use distorted versions of evolutionary ideas to support their own social theories. Those interested in this aspect of evolution should consult Dobzhansky's excellent *Mankind Evolving*. It is perhaps only natural that the massive (and often ignorant) opposition presented to evolutionary theory should have left its mark on the theory itself. There can be little question that it has.

The most obvious aspect of evolutionary theory that may be at least partially explained as reaction to the Bishop Wilberforce approach has been the development of a rather stringent orthodoxy. This orthodoxy is easily detected in the compulsion of biologists to affirm *belief* in evolution (rather than to accept it as a highly satisfactory theory) and to list *proofs* that evolution has occurred. It is, of course, a matter of debate as to where healthy conservatism leaves off and dogma begins. Suffice it to say that the discipline is at least close enough to the danger area to call for some critical reexamination of basic tenets.

By the standards of science, the idea that all modern organisms are the modified descendants of organisms that lived in the very distant past is almost, but not quite, a "fact." Scientific facts are

percepts that people easily agree on: the height of a column of mercury, the number of rats in a litter, the length of a femur, etc. Perhaps the best description of this idea of descent with modification is that it is a theory that seems to be overwhelmingly supported by the available evidence. To a lesser degree, the same statement can be made for the broad outlines of the evolutionary process as currently understood.

The strong urge to believe in present evolutionary theory, which is so evident among workers in the field, seems to stem partly from a very common human error, the idea that one of a number of current explanations *must* be correct. One usually finds the theory of evolution being contrasted with that of special creation, a one-sided contest, to say the least. The demonstration that the idea of special creation is scientifically meaningless does not, however, “prove” that the theory of evolution is correct. Current faith in the theory is reminiscent of many other ideas which at one time were thought to be self-evidently true and supported by all available data—the flat earth, the geocentric universe, the sum of the angles of a triangle equaling 180 degrees. It is conceivable, even likely, that what might facetiously be called a non-Euclidean theory of evolution will be developed. Perpetuation of today’s theory as dogma will not encourage progress toward more satisfactory explanations of observed phenomena. As Hardin puts it: “There is always a considerable lag in teaching. Many years ago it was remarked that the Military Academy of St. Cyr in France trained its students splendidly to fight the battles of the *last war*. So it is in science teaching; we too often train our students to fight battles already won, or equip them with weapons that no longer fire.”

Is our current explanation of evolutionary processes without flaws? Hardly; even the most sanguine evolutionist would admit that there is much to learn. The fine theoretical structure of population genetics has not been thoroughly tested in natural populations. Indeed, it is only recently that biologists have begun to realize that very large selection coefficients may be the rule rather than the exception in nature. (One of the triumphs of theoretical population genetics was to show that, in view of the long periods of time available, very small selection coefficients could account for the observed diversity of life.) Although the broad outlines of the splitting processes in evolution seem to be understood adequately, no general mathematical treatment has been possible, and many of the details are obscure.

For instance, the kinds of interactions that lead to patterns of differentiation such as are shown by the Galápagos finches (Chap. 10) have not been satisfactorily analyzed. To say that “competition be-

tween *Geospiza magirostris*, *G. fortis*, and *G. fuliginosa* on Indefatigable Island caused them to adapt to more specialized feeding niches” sounds very impressive and scientific but is almost meaningless. The word “competition,” for instance, has many meanings and very unfortunate connotations. In this case, it might imply that at first all three kinds of birds utilized the same limited food supply. Competition is not between kinds but between individuals. If we assume that there was at least a slight differentiation in food preference in isolation, individuals of the same species would “compete” with each other more strongly than with the individuals of other species. Presumably, for food specialization to be enhanced, some selective advantage would have to accrue to variants that tended to restrict their diets to particular types of food. It is very difficult to see the selective advantage of such restriction, but it must be tied in with the presence of several different species because, where a species occurs alone, its members tend to be more general feeders. The problem may involve complex interactions among such factors as feeding efficiency, recognition characteristics, psychological reactions to individuals of other species, changes of the food supply in lean years, the general structure of the ecosystem, and so forth. Whatever the factors, more study is needed.

There are many other points of disagreement among evolutionists, some more important than others. Some biologists still think that under certain circumstances populations of diploid outcrossing organisms may differentiate without the intervention of physical isolation (through disruptive selection or positive assortative mating). Others cite cogent reasons why this so-called sympatric speciation is unlikely. As mentioned in Chap. 7, there is still considerable disagreement on the role of drift in evolution, and the disagreement will doubtless persist until more is known about natural populations.

Much work needs to be done to clarify, and make operational (if possible) concepts such as population fitness and adaptation. The former concept is involved in such questions as Which is more fit, a population showing a high degree of polymorphism or one that is homozygous for superior alleles at most loci? This may be like asking: Which are better, apples or oranges? Certainly the question cannot be answered until and unless a satisfactory definition of population fitness can be formulated.

Adaptation is one of the most overused terms in biology. Natural selection has become recognized as an a posteriori description of events, but adaptation, the result of selection, has been relatively tenacious of its status as a *thing*. It is difficult to see much merit in the term, as all known organisms are the result of more than a billion

years of selection and are therefore “adapted.” Often adaptation is used in vague comparisons of an organism’s way of life with the extent of usable habitat (parasites are more “narrowly adapted” than omnivores). At worst, it is used for inciting wonder at the diversity of vertebrate forelimbs, bird beaks, or pollination mechanisms. (One is reminded of Lincoln’s remark that his legs were, miraculously, just long enough to reach the ground.) In the former instance, once the relationships are described (preferably quantified), the comment on adaptation seems extraneous. Under present conditions, elephants cannot survive in as many places as human beings. Does it really help to add that elephants are more narrowly adapted than people? The continuing idea that adaptation is some phlogiston-like beneficial substance that a population may possess in varying quantities has been at least partly responsible for the difficulties that theorists have had in coming to grips with the problems attendant to the question of population fitness.

Because of the extremely loose application of the term adaptation in the biological literature, it might be wise to drop it completely. The many fine studies of microevolution discussed earlier (e.g., those of Dobzhansky on *Drosophila*, Kettlewell on *Biston*, Clausen et al. on *Achillea*, etc.) are best viewed as investigations of natural selection, not as studies of progressive adaptation. The populations concerned are always “adapted”; at different points in time they are “adapted” to different conditions. More examples of problems could be given, but these should suffice to convince the reader that there are still some questions left to be investigated.

EPILOGUE

Many scientists like to feel that they approach the world in a completely objective manner. For instance, a biologist may scoff at the religious, saying that they accept on faith a system of beliefs that cannot be put to a rational test. The scientist all too often overlooks the articles of his own faith, a faith that almost always includes a belief in a real world in which a sort of statistical order exists. He believes that internal consistency of a theoretical construct is “good,” that quantification is “good,” that curiosity is “good,” and that certain kinds of logic are pertinent to his real world. He may even resort to appeal to authority.¹ Virtually all scientists dogmatically ac-

¹ An outstanding recent example is: “The number of people who accept the philosophy of the numerical taxonomists seems to grow despite rather severe qualifications made by some of the most authoritative biologists.” (S. G. Kiriakoff, *Systematic Zool.* 11: 180, 1962.)

cept as fact that there has been a past and there will be a future, although neither concept is readily amenable to operational analysis. Finally (although not exhaustively), subjective aesthetic standards such as “beauty” are part of the criteria used in judging many scientific theories.

In this book, we have accepted most of these standards and have clung to other dogmata, *faute de mieux*. Our reasons are manifold and subjective; in brief, they are that, by accepting these standards, we gain insight which we find pleasing. (It is important for the student of science to remember, however, that other methods of gaining insight may be equally or even more satisfying to others.) We have, for instance, assumed that events in long time stretches can be induced from knowledge of short time stretches. It is, of course, conceivable that we are doomed to the sort of disappointment that awaited the physicists who thought that the “laws” which applied to baseball could be applied to subatomic particles.

Being scientists does not, however, absolve us of all responsibility as human beings. One must stand ready to make value judgments, and if necessary to implement these judgments, when scientific decisions in the usual sense are not possible. An ardent believer may state that the human population can never be large enough, since for him each soul reflects the glory of a god; a politician may claim that the destruction of a continent is preferable to a change in political or economic philosophy. We could not contend that either is wrong in an absolute sense, but we can easily evaluate both views as inimical to goals that we cherish. The scientist may abdicate political or moral responsibility because the problems involved cannot at present (or may never) be analyzed by his rules. In our opinion, he is as culpable as the preacher or senator who does not attempt to appreciate what men can gain from science. Science is a human activity; where it becomes divorced from man, it loses meaning.

The biologist, and in particular the evolutionist, seems to be in an enviable position to help integrate science with other human thought patterns and activities. Physicists and mathematicians have contributed so much of the literature on the philosophy of science that an important fact often has been ignored. Unless our sense data have completely misled us, physicists and mathematicians are themselves products of evolution.

Man is a curious animal, and his curiosity has led to such questions as whether or not there is a reality divorced from the human mind. Indeed, the most important philosophical questions still hover, as they have for centuries, in the area of the mind-matter duality and the nature of percepts. It may be that a thorough understanding of

the processes that led to man and his curious mind will help us to decide whether such questions have any meaning. It is our guess that they will be found meaningless and that when this is widely recognized both science and man will have reached a new level of maturity.

REFERENCES

- Dobzhansky, T. 1962. *Mankind Evolving*. Yale Univ. Press, New Haven, Conn. See the discussion of Social Darwinism and Racism, pp. 10–15.
- Du Noüy, Lecompte. 1947. *Human Destiny*. Longmans, New York. Very little in this volume would be acceptable to a biologist acquainted with evolutionary processes.
- Ehrlich, P. R., and R. W. Holm. 1962. Patterns and populations. *Science* 137: 652–657. This paper expounds the prejudices of the authors of this book and cites other authors with similar views.
- Frank, Philipp. 1957. *Philosophy of Science*. Prentice-Hall, Englewood Cliffs, N.J. A good discussion of the link between science and philosophy as seen by a physicist.
- Hennig, W. 1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. Deutscher Zentralverl., Berlin. This is by far the best account of the concepts and views of the phylogenetic school of taxonomists.
- Sneath, P. H. A., and R. R. Sokal. 1962. Numerical taxonomy. *Nature* 193: 855–858. A fine brief summary of the philosophy, methodology, and literature of this field.
- Sokal, R. R., and P. H. A. Sneath. 1963. *Principles of Numerical Taxonomy*. Freeman & Co., San Francisco. A rigorous and scholarly treatment of the scientific aspects of modern taxonomy.
- West, D. A. 1962. Hybridization in grosbeaks (*Pheucticus*) of the Great Plains. *The Auk* 79: 399–424. The bibliography of this paper is a guide to the literature on hybridization in birds.
- Whorf, B. L. 1956. *Language, Thought and Reality*. Wiley, New York. An excellent source of Whorf's ideas on the relationship of language to behavior and *Weltanschauung*.

glossary

- Abiogenesis** the origin of life from nonliving systems.
- Acentric fragment** a fragment of a chromosome lacking a centromere.
- Acrocentric chromosome** a chromosome with a terminal or nearly terminal centromere.
- Adaptive radiation** evolutionary diversification, often over a relatively short period of time, of a group of organisms, presumably following their entry into a new adaptive zone; also used with reference to structures.
- Adaptive value** the survival value and reproductive capability of a given genotype relative to other genotypes in the population.
- Adaptive zone** the “way of life” of a taxonomic group of organisms, in a broad sense; may be subdivided into adaptive subzones.
- Adenine** one of the two purines (β -aminopurine) involved in the structure of DNA and RNA.
- Adenosine diphosphate (ADP)** a compound made up of adenine, the five-carbon sugar ribose, and two phosphate groups, which is involved in the mobilization of energy in cellular metabolism.
- Adenosine triphosphate (ATP)** ADP with an additional phosphate group attached by a high-energy bond; decomposition of ATP to ADP makes energy available for other reactions.
- Adventitious embryony** production of an embryonic sporophyte by mitotic divisions from tissues of another sporophyte without an intervening gametophytic generation.
- Agamic** without gametes; used with reference to complexes of organisms in which all individuals reproduce asexually.
- Agamospermy** formation of seeds without fertilization, with male gametes, if present, serving only to stimulate division of the zygote.
- Aggregate** any grouping of more than one object.
- Allele** one of the several alternative states of a functional gene unit.
- Allometry** different growth rates in different parts of the same organism.
- Allopatric** with nonoverlapping geographic ranges.
- Allopatric speciation** differentiation of populations in geographic isolation to the point where taxonomists recognize them as separate species.
- Allopolyploid** a polyploid formed by increase of chromosome number in an individual with more than one type of genome.
- Allotetraploid** a polyploid formed by doubling of chromosome number in a diploid hybrid between two organisms with different genomes or by the fusion of diploid gametes of such organisms.
- Amino acids** the chemical building blocks of proteins; on hydrolysis, proteins yield amino acids.
- Amphidiploid** a tetraploid organism that is diploid for two genomes, usually from different species.
- Aneuploidy** increase or decrease of chromosome number by values less than whole genomes.

- Apogamety** agamospermy in which cells other than the egg form the new embryonic sporophyte.
- Apomixis** all forms of reproduction in which meiosis and syngamy are partially or completely circumvented.
- Apospory** agamospermy in which somatic cells of the sporophyte produce a diploid gametophyte through mitotic divisions.
- Arrhenotoky** parthenogenesis resulting in the formation of haploid male offspring, the females being diploid.
- Articular** a bone found in the jaw of many vertebrates which presumably has been modified into the malleus of the mammalian ear.
- Artificial selection** the choosing by man, as far as possible, of the genotypes contributing to the gene pool of succeeding generations.
- Asexual reproduction** apomixis, q.v.; often used to refer to vegetative propagation.
- Autocatalysis** promotion of a reaction by its end products.
- Autopolyploid** a polyploid formed by increase in the number of identical genomes in the same organism or by the fusion of diploid or polyploid gametes from organisms with essentially identical genomes.
- Autosome** a usually euchromatic chromosome that is not a sex chromosome.
- Autotetraploid** an autopolyploid with four similar genomes.
- Autotriploid** an autopolyploid with three similar genomes.
- B chromosome** a supernumerary heterochromatic chromosome found in varying quantities in some plants (not necessarily in all cells).
- Backcross** the mating of an offspring to one of its parents or to a parental type.
- Bacteriophage** virus attacking bacterial cells, often resulting in their lysis.
- Balanced polymorphism** polymorphism maintained in a population usually by the heterozygotes, at the locus under consideration, having a higher adaptive value than either homozygote.
- Barrier** a physical or psychological condition that hinders or prevents the movement of individuals (and thus of genetic information).
- Basal granules** cytoplasmic organelles of characteristic fine structure to which cilia and flagella are attached.
- Bimodal population** a population with measurements of a given character clustered around two values.
- Bivalent** the synapsed pair of chromosomes in the meiotic prophase.
- Blastopore** an invagination in the surface of an embryo in the gastrula stage.
- Blastula** an early stage in embryonic development in which the cells are often arranged in a hollow sphere.
- Bradytelic evolution** evolution at a much slower rate than orthotelic evolution.
- Breeding size** the number of individuals in a population that are actually involved in reproduction in a given generation.
- Buffering** protection of a system from change by outside forces.

- Canalization** a description of developmental pathways, usually thought of as resulting from buffering.
- Carotenoids** fat soluble pigments ranging in color from yellow to red; most are tetraterpenes.
- Centric fragment** a portion of a chromosome that contains a centromere.
- Centriole** a cytoplasmic organelle of characteristic fine structure with which the spindle and astral fibers are associated during cytokinesis and karyokinesis.
- Centromere** the portion of a chromosome, usually greatly restricted in length, to which spindle fibers are attached in cell division. Syn.: kinetochore.
- Centrosome** the area surrounding the centriole in many cells, presumably associated with the organization of protein fibers.
- Character** any feature that varies within the group of items under study.
- Character displacement** condition in which sympatric populations of two species are more dissimilar than allopatric populations of the same two species.
- Chemosynthetic** able to elaborate carbohydrate substances of relatively high complexity with only inorganic substances (e.g., sulfur, iron) as a source of energy.
- Chiasma, chiasmata** a cross-shaped configuration of the chromosomes in a bivalent in the first meiotic prophase, usually the visible result of prior cytological crossing-over.
- Chlorophyll** magnesium complexes of porphyrins found as green pigments in the cells of photosynthetic organisms where they absorb light energy.
- Chromatid** a visible subdivision of a chromosome having but one centromere (or behaving as if the centromere were undivided); a half chromosome.
- Chromatograph** the result of treating a substance or mixture with one or more solvents to dissolve differentially and separate one or more constituents of the substance.
- Chromonema** the finest visible longitudinal morphological subdivision of a chromosome.
- Chromosome** the cell organelle with which most of the nuclear genetic information is associated and which contains the centromere or spindle attachment point.
- Chromosome complement** the set of chromosomes included in a nucleus which may include one or more genomes, depending upon the cell and its state.
- Cilium, -ia** a short protoplasmic extension with characteristic fine structure, projecting from a cell and moving with a characteristic pattern and beat; usually present in large numbers.
- Cisternae** apparent spaces within the endoplasmic reticulum whose profiles in electron micrographs suggest they are flattened vesicles.
- Cis state** two mutational alterations in the same cistron or on the same chromosome; as opposed to the trans state, q.v.

- Cistron** an operational unit, equivalent to or smaller than a genetic region, controlling a specific protein.
- Cleavage division** one of the early divisions of the zygote that leads to the formation of an embryo in animals.
- Cleistogamous** producing inconspicuous flowers that never open and are thus self-pollinated.
- Climax community** the relatively stable community following a successional series; usually thought of as characteristic of a particular climatic zone.
- Cline** a gradient of variation in the measurement of a character of a population or in a complex of characters of a population, the gradient often varying in steepness along its length or being stepped.
- Clone** a population derived by asexual reproduction of a single individual.
- Coacervates** aggregates of varying degrees of complexity, resulting from the interaction of two or more colloids.
- Coenzymes** substances which combine with specific proteins to form complexes that are catalytically active.
- Colloid** a dispersion of one substance within another, having properties of both a solution and a suspension.
- Community** the group of organisms found in a particular place.
- Competition** use of the same limited resources by two or more organisms.
- Conjugation** union of cells or organisms during which all or part of the genetic information of one individual is transferred to another.
- Conspecific** considered by taxonomists to belong to the same species.
- Convergence** superficial resemblance resulting from occupancy of similar adaptive zones.
- Cretaceous** the last period of the Mesozoic; beginning about 130 million years ago.
- Crossing-over** the exchange of usually corresponding segments between chromatids of homologous chromosomes; results in chiasmata and gene recombination.
- Culture** a body of nongenetic information transmitted from generation to generation.
- Cybernetic** involving a control or governing mechanism operated by feedback from the process.
- Cytoplasmic inheritance** inheritance of traits whose determinants are not located on the chromosomes.
- Cytosine** the pyrimidine (2-hydroxy-4-aminopyrimidine) involved in the structure of both DNA and RNA.
- Decay of variability** the reduction of heterozygosity because of genetic drift leading to loss and fixation of alleles at various loci.
- Deletion** the loss of a segment of a chromosome.
- Denatured protein** a structurally modified protein showing decrease in solubility and change in biological activity.
- Deoxyribonucleic acid (DNA)** giant molecules which in most organisms are the nuclear repository for the genetic information and which are

replicated and transmitted equationally to daughter nuclei; see nucleic acid.

Dicentric having two centromeres.

Differential segments portions of chromosomes that do not pair in meiosis.

Differentiation the changes observed in development as a zygote becomes a multicellular entity in which many diverse kinds of cells, tissues, and organs are found.

Dikaryosis the condition of possessing two nuclei in each cell.

Diploid having the zygotic number of chromosomes, or having two genomes, in reproductive cells other than gametes.

Diplophase that part of the life cycle in which the zygotic chromosome number is found in reproductive cells other than gametes.

Diplois establishment of the zygotic chromosome number, usually by syngamy and karyogamy.

Diplospory a mode of apomixis in plants in which a diploid gametophyte is formed after mitotic or partly meiotic divisions of the spore-forming cells.

Directional selection selection resulting in a shift in the population mean for the character considered.

Directed alternate disjunction regular movement of alternate centromeres to the same pole of the spindle in nuclei heterozygous for one or more reciprocal translocations.

Disjunction movement of the centromeres of a bivalent to opposite poles of the spindle during the first meiotic anaphase.

Disruptive selection selection in which two or more different genotypes are at an advantage and intermediate types are at a disadvantage.

Disulfide linkage a covalent bonding of cysteine residues (S-S) in or between protein molecules; thought to be responsible for spindle formation.

DNA see deoxyribonucleic acid.

Dominance the effect of the phenotype of a heterozygote for a given locus being more similar to one homozygote than it is to another; the allele involved in the proximate homozygote is referred to as the dominant allele; in complete dominance the heterozygote phenotype is identical to that of the dominant homozygote.

Duplication the presence of a section of chromosome more than once in a genome.

Ecosystem the thermodynamically interrelated set of organisms in a particular environment.

Effective breeding size the breeding size mathematically adjusted so that populations with varying sex ratios, degrees of inbreeding, etc., may be compared.

Effectors small molecules (metabolites) that combine with repressor molecules, activating or inactivating them with respect to their ability to combine with an operator.

Endoplasmic reticulum the system of tubes and vesicles in the cytoplasm of plant and animal cells, the membranes bounding which are usually associated on the outside with ribosomes and are continuous with the plasma membrane and the outer membrane of the nuclear envelope.

Endopolyploidy division of the chromosomes without division of the nucleus, resulting in higher than zygotic chromosome number.

Environmental variance that portion of the phenotypic variance caused by differences in the environments to which the individuals in a population have been exposed.

Enzymes proteinaceous catalysts of cellular reactions.

Epigenotype the series of interrelated developmental pathways through which the adult form is realized.

Epistasis interaction of nonallelic genes.

Erythrocyte the type of hemoglobin-containing cell found in the blood of vertebrates.

Euchromatic describing those portions of the chromosomes that manifest the usual prophase-telophase transformations and contain those genes with major phenotypic effect.

Eupolyploidy increase in chromosome number by whole genomes.

Expressivity a measure of the uniformity of the phenotypic expression of a gene in a particular environment.

Feedback the influence of the result of a process upon the functioning of the process.

Fitness the survival value and reproductive capability of a given genotype relative to other genotypes in a population.

Founder principle the principle which states that, when a new population is established in isolation, its gene pool is not identical with that of the parent population because of sampling error; these differences are enhanced as different evolutionary pressures in the areas occupied by the two populations will then also be operating in different population genetic environments; and the result is increased divergence.

Gametocyte a cell which, through division, will form gametes.

Gametophyte that phase of the life cycle in many plants in which the gametes are produced, usually by mitosis.

Gap a discontinuity in variation.

Gastrula the stage in development following the blastula in which the cells at the surface move to form an invagination (the archenteron), which has an opening to the outside known as a blastopore.

Gene the segment of a chromosome between two closest points of crossing-over; a hereditary unit having more than one state and whose different states produce differences in the phenotype; a segment of genetic material that bears the information specifying the structure of a single protein or polypeptide chain. See cistron, recon.

Gene flow the movement of genetic information within and among populations.

- Gene frequency** the number of loci at which a given allele is found within a population, divided by the total number of loci at which it could occur.
- Gene pool** the total genetic information possessed by a population.
- Genetic assimilation** the incorporation into the genotype, by a selective process, of characteristics appearing in ontogeny as a response to the environment.
- Genetic drift** random fluctuation of gene frequency (usually due to sampling error inherent in the genetic mechanism); present in all populations, its effects are most evident in very small populations.
- Genetic homeostasis** the tendency of populations under selection to regress toward the original mean.
- Genetic load** in a population, the average number of potential deaths per individual due to genetic causes (lethals, semilethals, etc.).
- Genetic system** all the factors, internal and external, that affect recombination in an organism.
- Genetic variance** that portion of the phenotypic variance caused by variation in the genetic environment of the individuals in a population.
- Genome** the minimum set of nonhomologous chromosomes all of which must be present to ensure the proper functioning of a cell.
- Genotype** the totality of the genetic material of a cell (usually restricted to nuclear genetic material); the total genetic endowment of an individual; the genetic endowment of an individual at a given locus.
- Gens** a subset of cuckoos tending to parasitize one kind of bird but not necessarily geographically isolated from other such subsets.
- Golgi complex** a cell organelle of unknown function found in most plant and animal cells, often in proximity to the nucleus, and comprising a series of concentrically arranged cisternae without ribosomes, as seen in electron micrographs.
- Grana** pigment-containing structures within a plastid, usually appearing as many disks stacked in series.
- Guanine** one of the two purines (2-amino-6-hydroxypurine) involved in the structure of DNA and RNA.
- Gynogenesis** reproduction by parthenogenesis in which stimulation by a spermatozoan is necessary for the development of the egg.
- Haplodiploidy** a genetic system found in some animals in which males develop from unfertilized eggs and are haploid, the females being diploid.
- Haploid** having the gametic number of chromosomes, or having a single genome, in reproductive cells other than the gametes.
- Haplophase** that part of the life cycle in which the gametic chromosome number is found in reproductive cells.
- Haploisis** establishment of the gametic chromosome number, usually by meiosis.
- Hardy-Weinberg law** the law stating that, in a panmictic population, in the absence of systematic pressures and genetic drift, the frequency of autosomal genes at a given locus remains constant and that, after one generation, the frequency of genotypes at the locus reaches equilibrium.

- Heritability** the genetic variance divided by the phenotypic variance; an estimator of the degree of resemblance between offspring and parent.
- Hermaphroditic** possessing the phenotype of both sexes in organisms with male-female sex differentiation.
- Heterochromatic** describing entire chromosomes or portions of the chromosomes that do not manifest the usual prophase-telophase transformations and appear to lack genes with major phenotypic effect.
- Heterogametic** producing gametes with differing chromosome complements.
- Heterokaryotic** containing within one cell or coenocyte nuclei of different genotype.
- Heterotrophic** requiring organic carbon for nutrition.
- Higher categories** taxonomic categories above the level of genus in the established hierarchy.
- Holometabolous** having a pattern of development that includes distinctly different egg, larval, pupal, and adult stages.
- Homologue** one of the set of two or more chromosomes which are identical with respect to their constituent loci.
- Horotelic evolution** rates of evolution falling within the distribution (asymmetrical with a mode nearer the upper than the lower end) most commonly found when evolutionary rates are plotted in a frequency distribution.
- Hybridization** gene flow between populations; usually restricted to populations recognized as distinct by taxonomists.
- Hydrated protein** a protein molecule about which water molecules are held.
- Imprinting** the imposition of a stable behavior pattern by exposure, during a particular period in development, to one of a restricted set of stimuli.
- Induction** determination of the developmental fate of one cell mass by another.
- Interstitial segment** that portion of a chromosome between a translocated segment and the centromere.
- Introgression** incorporation of genetic material from one population into that of another by repeated backcrossings; usually restricted to populations regarded as distinct by taxonomists.
- Inversion** reversal of the sequence of a portion of a chromosome.
- Kappa particles** particles of DNA within the cytoplasm of certain individuals of some species of *Paramecium* that result in the death of other individuals with certain genotypes.
- Karyotype** the characteristic phenotype of the chromosomes of an organism; usually used with respect to the chromosomes at mitotic metaphase.
- L chromosomes** see limited chromosomes.
- Limited chromosomes** heterochromatic chromosomes restricted to the germ line in some species of the fungus gnat *Sciara*.

- Linkage** the association of genes as a result of their occurrence in the same chromosome.
- Locus** the position of a gene on a chromosome; the location of equivalent genes (alleles) on chromosomes of homologous sets.
- Lysogenic** referring to those bacteria that carry temperate phages.
- Macroevolution** evolutionary events usually viewed through the perspective of geologic time, such as the evolution of the horse from a dog-sized mammal to *Equus caballus*.
- Megaspores** those spores which, in vascular plants, divide to produce the female gametophytic generation.
- Meiocyte** a cell, the nucleus of which divides by meiosis.
- Meiotic drive** a higher probability of one allele at a locus being included in the gametes than that of the others.
- Melanic** black, dark brown, dark-colored.
- Mendelian population** a reproductive group sharing a common gene pool.
- Mesozoic** the age of reptiles; beginning about 200 million years ago and ending about 70 million years ago.
- Metacentric chromosome** a chromosome in which the centromere is about midway in its length, the arms therefore equal.
- Metalloenzyme** a protein associated with a metal atom or complexes of metal atoms and functioning as an enzyme.
- Microevolution** evolutionary events usually viewed over a short period of time, such as changes in gene frequency within a population over a few generations.
- Microsome** a cytoplasmic constituent, obtained upon centrifugation of homogenized cells, thought to consist of ribosomes and portions of the endoplasmic reticulum (now largely replaced by the latter terms).
- Migration** the transfer of genetic information among populations; or the dispersal and establishment of organisms beyond their place of origin; or a periodic movement of individuals.
- Mimicry** the superficial resemblance of one organism by another, presumably affecting the actions of predators.
- Mitochondria** cytoplasmic organelles, filamentous or spherical, composed of two membranes, the innermost of which is convoluted, that are the site of many reactions of cellular respiration.
- Miocene** a middle epoch of the Tertiary period, beginning about 26 million years ago and ending about 11 million years ago.
- Modifier genes** genes whose major obvious phenotypic effect is to modify the expression of other genes.
- Morphogenesis** the process leading to the development of the characteristic mature form of an organism.
- Multiple allelomorph** an allele occurring at a locus at which at least two other alleles are known to occur.
- Multivalent** an association of more than two chromosomes whose homologous regions are synapsed by pairs.

- Mutagenic agent** an agent leading to an increase in mutation rate above the spontaneous level at a locus.
- Muton** a mutational site within a gene.
- Natural selection** nonrandom (differential) reproduction of genotypes without the conscious intervention of man.
- Neurula** the stage in a vertebrate embryo following the gastrula, characterized by rapid differentiation.
- Niche** the status (way of life) of an organism in a community; its position in the food chain, relationships with the physical substrate, etc.; related to the concept of adaptive zone.
- Nondisjunction** failure of the chromosomes in a bivalent or multivalent to separate at the first meiotic anaphase.
- Nuclear envelope** the outer boundary of the nucleus, composed of two perforate unit membranes, the outer of which is continuous with the endoplasmic reticulum.
- Nucleic acids** complex acids composed of nucleotides.
- Nucleotide** a phosphate ester of the *N*-glycoside of a nitrogenous base; chemical building block of a nucleic acid.
- Oligogenes** those genes with major obvious phenotypic effect; switch genes.
- Ontogeny** the development of an individual.
- Operator** a postulated genetic element that acts as a receiver of specific cytoplasmic signals in the form of repressor-substance molecules and that controls an operon.
- Operon** a unit of linked cistrons, the expression of which is controlled by an operator; a genetic unit of transcription of the DNA code.
- Organelle** a structure of characteristic morphology and function within the cytoplasm; the unicel analogue of an organ in a multicellular organism.
- Organizer** a portion of an embryo that determines the developmental fate of the cell masses with which it comes into contact.
- Oriented meiotic divisions** meiotic divisions with the spindle oriented so that a particular group of chromosomes always enter a polar body rather than the egg.
- Overdominance** the result of the heterozygote being more extreme than either homozygote.
- Oxidation** a reaction in which oxygen is acquired or hydrogen is lost by a compound or in which the valence of the metallic element is raised.
- Pairing segments** the euchromatic regions of chromosomes that synapse with a homologue in the first meiotic prophase.
- Panmixis** random mating.
- Paracentric** applied to inversions that do not include the centromere.
- Parallelism** convergence among closely related forms.
- Parthenogenesis** the development of an individual from an unfertilized gamete.
- Pectate** a compound of pectic substances (acid polysaccharide amorphous carbohydrates).

- Penetrance** a measure of the proportion of individuals homozygous for a gene that show its phenotypic effect.
- Pericentric** applied to inversions that include the centromere.
- Phenocopy** a phenotypic change that simulates a genotypic change.
- Phenotype** the resultant of the interaction of the genetic information with the environment; loosely, the characteristics of an organism exclusive of its genetic endowment.
- Phenotypic variance** the total variance observed in a character.
- Phosphate bond (high energy)** usually the anhydride linkage between phosphate ions which may be an important source of energy.
- Phosphorylation** the addition of a phosphate to an organic compound.
- Photolysis** splitting of water with light as the energy source.
- Photophosphorylation** the addition of phosphate to organic compounds with light as the source of energy.
- Photosynthesis** the processes involved in the elaboration of organic compounds from inorganic compounds with light as the energy source.
- Phyletic evolution** any change occurring sequentially in a single line of descent.
- Phylogenetic** pertaining to phylogeny, the evolutionary history of an organism.
- Plankton** the population of floating organisms in a body of water.
- Plasma membrane** the outer boundary of the cytoplasm, continuous with the endoplasmic reticulum and surrounded by a cell pellicle or wall.
- Plastids** organelles of plant cells, usually containing pigments and usually synthesizing soluble or insoluble carbohydrates.
- Pleiotropy** the influence upon two or more characters, not obviously related, by one or more alleles.
- Pleistocene** the major epoch of the Quaternary period, beginning about 1 million years ago and ending about 10,000 years ago.
- Pliocene** the last epoch of the Tertiary period, beginning about 11 million years ago and ending about 1 million years ago.
- Ploidy** the number of genomes of an organism.
- Polar bodies** the two or three meiotic products that do not develop into eggs in oögenesis in animals.
- Polygenes** those genes without obvious major phenotypic effect; numerous factors affecting a characteristic.
- Polymorphism** the presence in the same population and at the same stage of development of two or more conspicuously different forms of an organism in such proportions that the rarest of them could not be accounted for by recurrent mutation alone.
- Polyp** the sedentary form of a coelenterate.
- Polypeptide** the substance resulting from the formation of long amino acid chains, the acid group of one molecule combining with the base of another molecule with the loss of a molecule of water.
- Polyplloid** containing more than two haploid chromosome complements in the reproductive cells other than gametes, or presumed to contain more than two genomes in such cells.

- Polysaccharide** large carbohydrate molecules resulting from the combination of many smaller carbohydrate and possibly other molecules.
- Polytene chromosome** a giant chromosome consisting of many chromosome strands closely associated along their lengths.
- Population** a set of items in which one is interested; the individuals in a given area at a given time; in many biological discussions, a synonym of mendelian population, although this is often unstated.
- Population biology** the study of the pattern in which organisms are related in space and time and including such disciplines as ecology, taxonomy, behavior, population genetics, and others that deal primarily with the interactions of entire organisms.
- Population structure** the sum of all the factors that govern the pattern in which gametes from various individuals unite with each other.
- Porphyrins** a class of compounds derived from pyrrole nuclei which, in metal chelate complexes, form pigments important in many biological processes.
- Primitive** an organism or character judged to be less changed from a presumed common ancestral state than another with which it is compared.
- Probability density function** a function that describes how probability is distributed among the possible events, that is, the expected relative frequencies of the events.
- Protein** a class of compounds of high molecular weight formed by the combination of amino acids with or without other molecules.
- Proteinoid** a synthetic polypeptide.
- Protist** a unicellular organism.
- Pseudocopulation** a mode of pollination in some orchids in which structures of the flower resemble a female insect and male insects attempting copulation transfer pollen from one flower to another.
- Pseudogamy** parthenogenetic development of an ovum after stimulation (but not fertilization) by a male gamete or gametophyte.
- Purine** an organic base made up of two condensed heterocyclic rings, a pyrimidine ring and an imidazole ring.
- Pyrimidine** an organic base consisting of a six-membered ring system with nitrogen atoms at the 1,3 positions.
- Quadrate** a bone found in the jaw of many vertebrates which presumably has been modified into the incus of the mammalian ear.
- Quantum evolution** rapid evolutionary change resulting in what a taxonomist would regard as a new higher taxon.
- Random sample** a subset of a population selected so that all items in the population are equally likely to be included in the sample.
- Recapitulation** the idea that in the course of development an individual passes through stages similar in form to adults of its presumptive ancestors; often stated as "ontogeny recapitulates phylogeny."
- Recessiveness** the converse of dominance; a completely recessive allele is expressed only in the homozygous state.

- Reciprocal translocation** transposition of two segments between non-homologous chromosomes.
- Recombination** the formation of gene combinations not present in the parental types.
- Recombination index** a measure of the number of new gene combinations that can be produced in a given time; of Darlington: the average number of chiasmata plus the gametic chromosome number.
- Recon** the smallest unit whose interchange between chromosomes may be detected by the techniques of the fine-structure geneticist.
- Reduction** a reaction in which hydrogen is acquired or oxygen is lost by a compound or in which the valence of the metallic element is lowered.
- Regulator gene** the DNA transmitter of specific cytoplasmic signals in the form of repressor-substance molecules.
- Replicate** to duplicate repeatedly.
- Repressors** molecules with the property of combining with a particular metabolite (which may either activate or inhibit it) and a particular operator whose action is then blocked.
- Reproductive cells** the gametes and their immediate predecessors from which they are produced by division.
- Reticulate evolution** evolution in which lines combine as well as split.
- Ribonucleic acid (RNA)** giant molecules of various types, of which, in most organisms, some copy the genetic code from the DNA and carry it to the sites of protein synthesis (messenger RNA) and some aid in the organization of the synthesis (transfer RNA); see nucleic acid.
- Ribosomes** granules associated with the boundary of the endoplasmic reticulum; the presumptive sites of protein synthesis; see microsome.
- RNA** see ribonucleic acid.
- Sample** a subset of a population; a group of items drawn by some procedure from a population and from which one hopes to learn certain things about the population.
- Sampling error** variation due to random elements in the sampling process.
- Segmental allopolyploid** an allopolyploid in which the combined genomes are homologous in many small segments throughout the complement; crossing-over may recombine material from different genomes.
- Selection** differential reproduction of genotypes.
- Selection coefficient** the measure of the disadvantage of a given genotype relative to other genotypes in the population.
- Sex chromosome** usually a largely heterochromatic chromosome functioning at least in part in sex determination.
- Sexual reproduction** reproduction involving the fusion of gametes produced by a prior meiotic process.
- Specialized** applying to an organism or character judged to be more changed from a presumed common ancestral state than another with which it is compared.

- Speciation* the splitting process of evolution, responsible for the existence of different kinds of organisms that are classified as species by taxonomists.
- Species* a group of organisms judged by taxonomists (by diverse criteria) to be worthy of formal recognition as a distinct kind.
- Spindle* the ellipsoidal mass of protein fibers visible during cell division and thought to play a role in chromosome movement and division of the cytoplasm.
- Spontaneous generation* see abiogenesis.
- Stabilizing selection* selection in which genotypes closer to the mean for a character have an advantage over those at the extremes.
- Stationary frequency distribution* the representation of a probability density function showing the way the probability in a given situation is distributed over the possible events.
- Structural gene* the DNA code unit whose primary product is messenger RNA and which thus controls synthesis of a particular protein or polypeptide.
- Structural hybridity* heterozygosity for a chromosomal rearrangement.
- Subspecies* a geographic subdivision of a species deemed worthy of formal recognition by a taxonomist.
- Succession* the sequence of transient communities occurring in an area before the climax (q.v.) community.
- Supergene* a group of genes inherited as a unit.
- Supernumerary chromosomes* chromosomes present, often in varying numbers, in addition to the characteristic relatively invariable complement.
- Switch gene* see oligogene.
- Sympatric* occurring in the same geographic area.
- Sympatric speciation* speciation without geographic isolation.
- Synapsis* the association of homologous chromosomes in the meiotic prophase.
- Syngamy* union of gametes to form a zygote.
- Systematic pressure* one of the nonrandom evolutionary pressures: selection, mutation, or migration.
- Tachytelic evolution* evolution at a much faster rate than horotelic evolution.
- Terminalization* the movement of chiasmata to the ends of the chromosomes during the later stages of the first meiotic prophase.
- Territoriality* the defense of an area against organisms of the same or similar kind.
- Tetraploid* containing four genomes in reproductive cells other than the gametes.
- Tetrasomic* describing an organism with one chromosome in the complement represented four times.
- Thallus* a plant body not sharply differentiated into root and shoot.
- Thelytoky* a form of apomixis in animals in which diploid females are produced from unfertilized eggs.

- Thymine** the pyrimidine (2,4-dihydroxy-5-methylpyrimidine) involved in the structure of DNA but not RNA.
- Transduction** a mechanism of gene transfer in bacteria in which genetic material is transferred from one cell to another by bacteriophage.
- Transformation** a change in the genetic information of a bacterium as a result of exposure to a DNA extract of a bacterium of different genetic constitution.
- Transhydrogenation** the sequential transfer of electrons in cellular oxidation cycles.
- Translocation** see reciprocal translocation.
- Trans state** two mutational alterations in cistrons on different homologous chromosomes; see cis state.
- Trisomic** describing an organism with one chromosome in the complement represented three times.
- Univalent** a chromosome lacking a homologue and therefore unsynapsed at the first meiotic prophase.
- Uracil** the pyrimidine (2,4-dihydroxypyrimidine) involved in the structure of RNA but not DNA.
- Variance** a measure of dispersion obtained by squaring the deviations of the individuals from the mean and dividing the result by the number of individuals; the square of the standard deviation.
- Viability** the capability for living or continuing to develop; often incorrectly used as synonymous with fitness.
- Vivipary** in plants, vegetative reproduction in which propagules replace flowers in the inflorescence; in animals, the production of living young rather than eggs.
- Wild type** the most frequently observed phenotype, or the phenotype arbitrarily designated as "normal."

index

- Abrams, 178, 235
- Acentric fragments, 49
- Achillea*, 213, 230
borcalis, 214
lanulosa, 154, 214
millefolium, 213
- Acrocentric chromosomes, 186
- Adaptation, 157, 311, 312
and gene combinations, 120
- Adaptive peaks, 120, 121
- Adaptive radiation, 264–266
in plants, 266
- Adaptive value, 104
- Adaptive zone, 263–267, 270, 272
access to, 267
- Adenosine diphosphate (ADP), 10, 26
- Adenosine triphosphate (ATP), 10, 12, 26
- ADP, 10, 26
- Adventitious embryony, 199, 200
- African elephant, 254
- Agamic complex, 201, 202, 204
- Agamospermy, 199
- Age, geological, determination of, 260, 261
- Alaska brown bear, 257
- Alcidis agathysus*, 271, 273
- Algae, 73, 166, 167, 194
(See also Blue-green algae; Brown algae;
Green algae)
- Alleles, 38, 42, 92, 93, 111, 118
multiple, 42
- Allen's rule, 213, 232
- Allison, A. C., 145, 158
- Allium*, 31, 74, 198
cepa, 191
fistulosum, 191
- Allometry and antlers, 275
- Allopatric speciation, 247
- Allopolyploidy, 190–195, 202, 204, 206, 247
segmental, 191, 195
- Allotetraploidy, 190, 191, 194
- Alterations of chromosomes, 48–51
- Alternation of generations, 167, 168
- Ameiotic thelytoky, 201, 203
- Amino acids, 6–8, 17, 18
- Amphidiploidy, 186, 191
- Anaphase, 27–30, 33, 34
- Andrewartha, H. G., 83, 88
- Andrews, 255
- Aneupolyploidy, 184–189
- Angiosperms, 83, 84, 270
- Annelida, 196
- Annual plants, recombination in, 183
- Anteater, banded, 265
- Anthropocentrism, 295, 296
- Antibiotics, 148, 150
- Antlers and allometry, 275
- Apes, anthropoid, 67, 252
- Aphids, 201, 205, 206
- Apogamety, 199
- Apomixis, 183, 194, 196–207, 241
in vertebrates, 204, 205
- Apospory, 199, 200
- Apples, 190, 194
- Arachnids, 200
- Arboreal existence of prehominids, 281–283
- Archaeopteryx*, 273
- Archosaurian reptiles, 259, 260, 264
- Aristolochia* swallowtail butterfly, 232
- Aristolochia watsonii*, 87
- Aristotle, 291
- Arrhenotoky, 200
- Artemia salina*, 204
- Artificial selection, 103, 150
- Ascaris*, 245
lumbricoides, 230
suum, 230
- Asclepiadaceae, 258, 271
- Asclepias*, 232
tuberosa, 214, 215, 232–234
- Ascomycetes, 168
- Asexual reproduction, 196, 197, 247, 299
(See also Apomixis)
- Asplenium*, 192–194
bradleyi, 192–194
cbenoides, 192, 194
gravesii, 193, 194
montanum, 193, 194
pinnatifidum, 193, 194
platyneuron, 192, 194
rhizophyllum, 192–194
trudellii, 193, 194
- Assortative mating, negative, 170, 172
positive, 170, 171
- Aster, 27
- Atmosphere, oxidizing, 7
reducing, 6
- ATP, 10, 12, 26
- Australopithecines, 284–287

- Australopithecus*, 67, 284, 285
 Autocatalysis, 8, 10, 11
 Autopolyploids, 190, 191, 195, 202, 206
 Autosomal chromosomes, 28, 47, 178
 Autotetraploidy, 190, 195
 Autotriploidy, 190
Avena, 85
 Axelrod, 277
 Aztecs, 291
- B chromosomes, 187
 Baboons, 282
 Bacillariophyceae, 167
 Back mutation, 101, 114
 Bacteria, 44, 161–166, 169
 chemosynthetic, 10
 green, 26
 lysogenic, 163
 Bacteriophages, 162, 163, 169
 Baker, 233
 Balanced polymorphism, 110–113, 146
 Bananas, 190
 Bar Mitzvah, 290
 Basal granule, 26
 Basidiomycetes, 168
Battus philenor, 87, 232
 Bears, 75, 256, 257
 Bees, evolution of social behavior in, 158, 159
 Beetles, 180
 Behavior, 79–81, 87, 172, 223, 227, 228, 237, 240
 aggregating, 80
 Benzer, 38
 Bergmann's rule, 213, 232
 Biogenetic law, 66
 Biological-species concept, 298
 utility of, 299
 Birch, L. C., 83, 88
 Birds, 224–229, 241, 243–246, 260, 264, 267
 Birds of paradise, 241
Biston, 212, 230
 betularia, 126–131
 Bivalents, 32, 41
 Black bears, 256
 Black flies, 85
Blaps polychresta, 180
 Blood types, distribution of, 252
 Blue-green algae, 26, 166
 Bluegrass, 146, 198, 202
- Bombyx*, 41
 Botfly, human, 84
 Boulenger, 22
 Bowman, R. I., 224–228, 249
Bradypodicola hahneli, 84
 Bradytely, 261–266
Brassica, 85, 186
 Braunshtein, 21
 Breeding size, 95, 96
 Briggs, 63
 Brine shrimp, 204
 Brown, C. W., 219
 Brown, W. L., 249
 Brown algae, 167
 Brown bear, European, 75
 Bryophytes, 168
 Buddha, 291
 Buffering, 59, 60, 166
 Bumpus, 125
 Butterflies, 46, 58, 61, 79, 84, 85, 87, 154, 218, 251, 271
 cabbage, 84
 checkerspot, 75–79, 303–307
 monarch, 58
 North American, 307
 sibling species in, 220, 244
 swallowtail, 147
 tiger, 212
 Butterfly weed, 214
- Cabbage, 190
 Cabbage butterfly, imported, 84
 native, 84
 Cactaceae, 271
Cactospiza heliobates, 225, 227, 228
 pallida, 225, 227, 228
 Cactus, 225, 271
 Cain, 133, 134
Callimantis, 32
 Calvin, M., 7, 8, 10–12, 21
Camarhynchus parvulus, 225, 227
 pauper, 225
 psittacula, 225, 227
Camelina, 147
 Camin, 137, 140, 159
Campanula, 178
 Canalized processes, 58–60
 Carbohydrates, 23, 24
Carex, 186
 Caribou, 87
 Carnivora, 261, 262, 264

- Carson, 159
- Carus, 301
- Caryophyllaceae, 147
- Castes in social insects, 80
- Catalysts, 9
- Caterpillars, 61, 64, 130
- Cell wall, 24
- Cells, 19, 23
- Cellulose, 24
- Centric fragment, 184
- Centric fusion, 186, 195
- Centrioles, 26, 27
- Centromere, 27, 34, 50, 184
- Centrosome, 26
- Cepaea*, 133–136, 212, 230, 247
hortensis, 136
memoralis, 133, 135, 136
- Certhidea olivacea*, 224, 225, 227–229
- Character displacement, 229, 231, 249
- Checkerspot butterflies, 75–79, 303–307
- Cherries, 190
- Chiasmata, 32–34, 183
- Chimpanzees, 282, 286
- Chlorophyll, 11, 26
- Chloroplastids, 26, 165
- Chromatids, 27, 32–34, 41
- Chromosomal deletions, 47, 48
- Chromosome bridge, 176
- Chromosome number, gametic, 34, 183, 184
 zygotic, 184
- Chromosome rings, 50, 182
- Chromosomes, 17, 26–35, 40, 167
 acrocentric, 186
 alterations of, 48–51
 autosomal, 28, 47, 178
 B type, 187
 bridges, 176
 dicentric, 49, 176
 differential segment of, 47, 178
 interstitial segments of, 178
 limited, 187, 188
 maps of, 46, 47
 metacentric, 186
 neo-X, 178
 neo-Y, 178
 pairing segments of, 47, 178
 polytene, 49, 63
 rings of, 50, 182
 salivary gland, 47, 49, 140
 sex, 28, 32, 47, 175
 somatic pairing of, 49
- Chromosomes, spiralization of, 28, 30
 supernumerary, 186
 synopsis of, 32, 41, 176, 187, 190
 X, 47, 48, 178, 180
 Y, 47, 48, 175, 178, 180
- Cichlidae, 220, 244, 265
- Cichlids, 244, 265
- Cilia, 26
- Cis state, 38
- Cistrans, 39
- Cladocera, 205
- Cladocerans, 201
- Cladonia*, 87
- Clarke, 159
- Clarkia*, 180–182, 186, 187
amoena, 180–182
franciscana, 180–182
rubicunda, 180–182
- Clausen, J., 154, 155, 213, 214, 249, 312
- Clays, reactions at surface of, 9
- Cleistogamous flowers, 197
- Cleland, 178, 182
- Clematis fremontii*, 76, 78
- Cleora repandata*, 130, 131
- Climax community, 86
- Clinal variation (*see* Variation)
- Clines, 212, 214–218
- Clone, 74, 196, 205, 248
- Clover, white, 146
- Club mosses, 263
- Cnemidophorus*, 204
- Coacervates, 8, 12, 13, 19
- Coadaptation, 153
- Cobras, 265
- Cockroaches, 178, 270, 295
- Coelacanth fishes, 259
- Coelenterata, 74, 168, 196
- Coenonympha tullia*, 218, 234
- Coenzymes, 9
- Colchicine, 189
- Coleoptera, 200
- Colloid, 12
- Colonial organisms, 74
- Colony, 80, 158
- Communion, 291
- Community, 86
 climax, 86
 closed, 171
 equilibrium in, 86
 evolution of, 87
 open, 171
- Competition, 270, 311

- Complementation, 39
 Complexity, increase in, 275, 276
 Components of variance (*see* Variance)
 Compositae, 185
 Computers, digital, 302, 303
 Confirmation, 290
 Continuous variation, 52
 Convergence, 270, 271
 and parallelism in cultural evolution,
 290
 Cope's rule, 274
 Correlation coefficient, product-moment,
 303-305
 Cotton, 46
Crepis, 185, 202, 204
 foetida, 186
 fuliginosa, 185
 kotschyana, 186
 neglecta, 185
 runcinata, 202
 Crickets, 186
 Crocodiles, 260, 263
 Cross-veinless phenotype in *Drosophila*,
 156
 Crossing-over, 32, 35, 38, 40, 41, 43, 46,
 49, 175
 somatic, 168
 Crotalidae, 265
 Crow, J. F., 123
 Cruciferae, 147
 Cuckoos, 229, 245-247
 gentes in, 229, 245-247
Culex, 31
 Cultural bias and evolutionary theory, 296-
 298
 Cultural diversity, 287
 Cultural evolution, 290, 295
 convergence and parallelism in, 290
 (*See also* Evolution)
 Cultural integration and genetic
 homeostasis, 291
 Culture, 281, 285-292
 Curculionidae, 204
 Cyanophycophyta, 166
 Cybernetics, 60
 Cyclical parthenogenesis and sequence of
 generations, 205, 206
 Cyclical thelytoky, 200
Cyclosia hestinioides, 271, 273
 Cyperaceae, 266
 Cytoplasm, 24-27
 Cytoplasmic inheritance, 26, 165
Dactylis glomerata, 146
 Darlington, C. D., 68, 183-185, 207
 Darwin, 211, 224, 291, 301, 308
 Darwin's finches (*Geospizinae*), 224, 243,
 245, 265, 310
Datura, 180
 Dawn redwood, 252, 259
 Day lily, 74, 196
 Decay of variability, 98-101
 Deletions, chromosomal, 47, 48
 Dendrograms, 304-306
 Deoxyribonucleic acid, 14-19, 27, 44, 57,
 64, 161-164, 167, 170
Dermatobia hominis, 84
 De Robertis, 29, 30, 33, 34, 43
 Development, 42, 166, 167
 Developmental homeostasis, 57-61, 66,
 166, 167, 171
 De Vries, 182
 Diatoms, 167
 Dicentric chromatid, 49, 176
Dichromena, 266
 Dictatorships, 290, 291
 Differential segment of chromosomes, 47,
 178
 Differentiation, cellular, 62-65
 Dikaryosis, 168, 169
Diplococcus, 161
 Diploidy, 45, 165-170, 184
 Diplophase, 61
 Diplospory, 199-201
 Diptera, 49, 187
 Directed alternate disjunction, 178, 182
 Directional selection, 104, 127
 Discordant variation, 252
 Disease and pollution of environment, 289
 Disjunction, 34, 50
 Dispersal, 79, 80, 172
 Disruptive selection, 104, 147, 148, 248
 Dissemination, 83
 Distribution, 75-79
 ecological, 76, 79, 84
 geographic, 75, 76
 of individuals, 79, 80
 DNA (*see* Deoxyribonucleic acid)
 Dobzhansky, T., 16, 55, 139-145, 159, 218,
 235, 236, 249, 293, 298, 309, 312, 314
 Domestication, 238
 Dominance, 39, 45, 103, 104, 130
 ecological, 276
 Dominance component of variance, 53
 Dominance-recessiveness, 45

- Dowdeswell, 132
- Dragonfly, 62
- Drift, genetic, 97–100, 102, 146
- Drosophila*, 32, 41, 46, 47, 49, 50, 52, 58, 59, 139–145, 148, 151, 152, 156, 158, 175, 177, 186, 238, 248
- chromosome inversion types in, 140–145
- cross-veinless phenotype in, 156
- melanogaster*, 64, 145, 151, 156, 175
- miranda*, 180
- paulistorum*, 219, 238, 299
- persimilis*, 144, 242
- pseudoobscura*, 140, 143–145, 242
- tropicalis*, 113, 144
- virilis*, 180
- Dubois, 259
- Ducks, 241
- Dunker religious community, 146
- Dunn, L. C., 16, 55
- du Noüy, Lecompte, 295, 314
- Duplications, 49
- Dusky flycatcher, 240
- Earthworms, 204
- Ecological distribution, 76, 79, 84
- Ecological dominance, 276
- Ecological succession, 86
- Ecosystems, 84, 86, 165, 276
- Ecotypic variation, 213
- Effective population size, 232, 235
- Effector substances, 65
- Egg mimics, 229, 233, 245, 246
- Ehrlich, P. R., 77, 88, 137, 140, 159, 306, 308, 314
- Elapidae, 265
- Elephants, 254
- Elephas maximus*, 254
- Elodea*, 196
- Emberiza citrinella*, 128
- Embryology, experimental, 63
- Emigrantes, 205
- Emigration, 102
- Empidonax*, 240
- oberholseri*, 240
- wrightii*, 240
- Endoplasmic reticulum, 25, 27
- Endopolyploidy, 31, 64, 200
- Energy, 5, 9–12
- English sparrows, 84, 125
- Ensatina*, 217, 219, 221, 238
- Environment and recombination, 170, 171, 183, 206
- Environmental factors, classification of, 83
- Enzymes, 9, 46
- Epigenetic system, 60
- Epigenotype, 60, 67, 75, 83
- Epiphytes, 84
- Epistasis, 42
- Epling, 235, 236
- Equational division, 28
- Equilibrium in communities, 86
- Erebia calcarius*, 224, 245
- cassioides*, 220, 223, 224, 244
- iranica*, 245
- nivalis*, 220, 223, 224, 244
- tyndarus*, 220, 223, 244
- Erickson, 76, 78
- Erythacus rubecula*, 128
- Erodium*, 85
- Escherichia coli*, 163
- Ethics, 292
- Euchromatin, 50, 184
- Eugenics, 108
- Euphorbiaceae, 271
- Euphydryas*, 303–306
- chalcedona*, 303–306
- editha*, 75–77, 79, 82, 303–306
- Eupolyploidy, 184, 189–196
- Europe, Western, culture of, 291, 296–298
- Evening primrose, 177
- Evolution, as an aspect of human culture, 295
- belief in, 310
- of brain in man, 286, 287
- cultural, 285–292, 295
- and biological, comparison of, 287, 288–292
- interaction between, 289–292
- (See also Cultural evolution)
- of eyes, 157
- modes of, 259, 260, 264–266, 270
- phyletic, 260, 261
- quantum, 260, 263
- rates of, 260–264, 266, 267
- of social behavior in bees, 158, 159
- teaching of, 309, 310
- trends in, 274–276
- Evolutionary momentum, 275
- Evolutionary success, standards of, 295, 296
- Evolutionary theory, and cultural bias, 296–298
- and language, 296
- Exchange, four-strand, 41, 43
- two-strand, 41, 43

- Expressivity, 44, 167
 Extinction, 251, 252, 254–256, 260–264,
 270, 272, 292
 Exiles, 205
 Eyes, evolution of, 157
- Falconer, D. S., 53, 55
 False dandelion, 185, 202
 Feedback mechanisms, 59, 60, 66, 82, 86
Festuca pratensis, 191
 Fisher, 45, 100, 102, 123, 131, 132
 Fishes, 204, 205, 270
 species swarms in, 220, 244
 Fitness, 104, 112, 113, 152, 153, 161, 171,
 183
 Fixation, 97–100, 114, 117–119
 Flagella, 26
 Flagellates, 167
 Flax, mimicry of, 147
 Flight, 264, 265
 Flowering plants, 168, 194
 (See also Angiosperms)
 Ford, 130–132
 Fossilization, 259
 Founder principle, 136, 243
 Fox, 7
 Foxes, arctic, 232
 Frank, P., 314
 Fringillidae, 224, 243
 Frog, 63, 84
 (See also *Rana*)
 Fruit flies (see *Drosophila*)
 Fundatrices, 205, 206
 Fungi, 73, 166–168, 194, 272
 Fungus gnat, 28, 187–189
- Galápagos finches (Geospizinae), 224, 243,
 245, 265, 310
 Gall wasps, 201, 205
 Galton, 37
 Gametes, 31, 32, 44, 49, 79, 93, 167
 random union of, 35
 wastage of, 169, 182
 Gametogenesis, 167
 Gametophyte generation, 61, 168, 199
 male, 168, 172
 Gametophytic apomixis, 199
 Gene combinations and adaptation, 120
 Gene flow, 234–236, 289
 Gene frequency, 54, 92–95, 97, 98, 101,
 102, 110, 114, 116
 rate of change in, 106
 Gene pool, 92
 Generation, length of, and recombination,
 79
 spontaneous, 5
 sporophyte, 168, 199
 Genes, 14, 38, 42, 44, 45, 175
 complementary, 42
 epistatic, in chickens, 42
 hypostatic, in chickens, 42
 lethal, 182
 loss of, 117, 118
 modifier, 42, 46, 130, 148
 oligo-, 52
 operator, transcription of, 64, 65
 random fixation of, 121, 235
 random loss of, 235
 regulator, transcription of, 64, 65
 structural, transcription of, 64, 65
 switch, 52
 (See also Supergenes)
 Genetic assimilation, 61, 156
 Genetic code, 13–19, 63, 64
 (See also Genetic information)
 Genetic drift, 97–99, 133, 170, 171, 243
 Genetic homeostasis, 153, 154, 167, 171
 and cultural integration, 291
 Genetic inertia, 95
 Genetic information, 13, 19, 26, 28, 59, 62–
 64, 75, 92, 281
 Genetic isolation, 218, 236
 Genetic load, 112, 113
 Genetic material, 35, 37, 49, 57, 58
 (See also Genetic information)
 Genetic systems, 35, 49, 58, 85, 161, 169,
 183, 207
 Genome, 183
 Genomic chromosome number, 183
 Genotype, 57, 59, 64, 83
 Genotype frequency, 93, 94, 120
 Gentes of cuckoos, 229, 245–247
 Geographic distribution, 75, 76
 Geographic variation, 212, 214, 219, 230
 Geological age, determination of, 260, 261
Geospiza conirostris, 225, 226
 difficilis, 225, 227
 fortis, 224, 226, 227, 311
 fuliginosa, 224, 226, 311
 magnirostris, 224, 226, 227, 229, 311
 scandens, 225, 226, 227

Geospizinae, 224, 243, 245, 265, 310
 Germ line, 31, 57, 187
 Gerris, 31
 Gibbons, 283
 Gibson, J. B., 248, 249
 Gill pouches, 67
Ginkgo, 252, 255
 biloba, 252, 255
 Ginkgoales, 252
 Glass, 146
 Gliding, 264, 265
 Gloger's rule, 213
 Goldschmidt, 218
 Golgi material, 25
 Gorillas, 282
 Grackles, 241
 Gramineae, 266
 Grana, 26
 Granick, 11
 Grant, 171, 266, 268
 Grasses, 266
 Grasshoppers, 178, 186
 Grasslands, 84
 Gray flycatcher, 240
 Green algae, 167
 Green bacteria, 26
 Grizzly bears, 256
 American, 75
 Grosbeaks, 241
 Growth, 58
 Gulls, 241
 Guppies, 238
 Gymnosperms, 168, 270
 Gynogenesis, 205
 Gypsy moth, 218

Haeckel, 66
 Haldane, 45, 46, 123
 Haldane's rule, 218
Haplochromis, 220, 222, 244
 Haplo-diploidy, 200
 Haploid apogamety, 199
 Haploid parthenogenesis, 199, 200
 Haploidy, 166–168, 184
 Haplophase, 61
 Hardin, 310
 Hardy, 123
 Hardy-Weinberg equilibrium, 93, 95, 101,
 102, 143, 144
 Hare wallabies, 265
 Harlow, 286, 287

Harrison, 151, 154
 Heer, 255
 Heiser, 241
Helianthus, 241
 annuus, 241
 bolanderi, 241
Hemerocallis fulva, 74, 196
 Hennig, W., 314
 Herbaceous plants, recombination in, 171,
 183
 Heritability, 53
 Hermaphroditism, 166, 204
 Heterochromatin, 41, 47, 50, 178, 184, 187
 Heterogametic sex, 47, 48
 Heterokaryosis, 168
 Heterosis, 53
 Heterozygosity, 40, 45, 110–114, 152, 171,
 201
 Hiesey, 154, 155, 213, 214, 249
 Higher categories, 251, 272, 273
 Hitler, 291
 Holm, R. W., 88, 308, 314
 Home range, 80
 Homeostasis, developmental, 57, 66, 167,
 171
 genetic, 153, 154, 167, 171
Homo erectus, 259, 284, 285
Homo sapiens, 61, 172, 252, 281, 284, 285,
 295
 (See also Man)
 Homogametic sex, 47, 48
 Homiotherms, 232
 Homologous chromosomes, 32
 Homoptera, 200
 Homozygosity, 40, 45
 Honeyeaters, 241
 Horizontal speciation, 259
 Horotely, 261, 263, 265
 Horses, 274
 Host preference, 229
 Howler monkeys, 80
 Hybridization in grosbeaks, 308
 Hybrids, ecology of, 241, 242
 selection against, 242
 Hydra, 74
 Hymenoptera, 61, 200
Hypericum, 180

Ideopsis daos, 271, 273
 Immigration, 102
 Inbreeding, 116, 170, 171

- Inbreeding depression, 53, 171
 Incest taboos, 289
 Incompatibility systems, 172
 Indian elephant, 254
 Indians, American, culture of, 291
 Individual, 73–75, 82
 Individuals, number of, 80
 size of, and recombination, 79
 Induction, 63
 Industrial melanic moths, 247
 Industrial melanism, 46, 125–131
 Infection, 165
 Information, genetic (*see* Genetic information)
 nongenetic, 281
 Insecticides, 148, 150
 Insects, 200, 267
 Interclone selection, 248
 Interference, 41, 46
 Intergroup selection, 122
 Intersexuality, 218
 Interspecific territories, 240
 Interstitial segment of chromosomes, 178
 Intragroup selection, 122
 Intrapopulation variation, 213
 Introggressive hybridization, 240–242
 (*See also* Hybridization)
 Inversion type in *Drosophila*, Arrowhead
 (AR), 140–145
 Chiricahua (CH), 140–145
 Pikes Peak (PP), 144–145
 Standard (ST), 140–145
 Inversions, chromosomal, 47, 49–51, 139–
 145, 176, 177, 180
 paracentric, 176, 180
 pericentric, 177, 182
 Ionizing radiation, 113, 292
 Irish elk, 275
 Island model, 116
 Isolation, 237
 behavioral, 223, 237
 by distance, 116
 sexual, 242
- Jacob, 64, 65, 68
 Japanese iris, 190
 Java man, 284, 285
 Jaw structure, evolution of, 66
 Johnson, 240
 Joining, 260
- Kangaroos, 265
 Kappa particles, 164
 Karyotype, 175, 180
 Keck, D. D., 154, 155, 213, 214, 249
 Kemp, 146
 Kettlewell, 126–130, 312
 Killer strains of *Paramecium*, 164, 165
 King, 63
 Kinship systems, 287
 Kiriakoff, 312*n*.
 Koalas, 265
 Koopman, 242
 Kräusel, 255
- L (limited) chromosomes, 187, 188
Lacerta saxicola, 204
 Lack, 224, 249
 Lamotte, 133, 136, 159
 Language, 287, 288, 296–298
 Eskimo, 287, 297
 and evolutionary theory, 296
 Gaucho, 297
 Hopi, 297, 298
 Indo-European, 297
Latimeria, 258
 Lederberg, 163
 Leopard frog, 215
 Lerner, 59, 152, 153, 159
 Lethal genes, 182
 Lethal screen, 200
 Lewis, 180–182
 Lewontin, 128*n*.
 Li, C. C., 95, 105, 123
 Lichens, 73, 225, 299
 Life cycle, diploid, 167
 haploid, 167
 Limited chromosomes, 187, 188
 Linaceae, 147
Linanthus, 236
 parryae, 234–236
 Linkage, 40, 41, 47, 50, 117, 148, 162, 163
 Linnaeus, 37
 Linton, R., 291, 293
Linum, 147
 Lipids, 23, 24, 26
 Liverworts, 168
 Living fossils, 258
 Lizards, 204
Lolium perenne, 191
 Lorkovič, 220, 223

Loss of genes and random fixation, 97–101, 121, 235
 Louse, human, 229, 245
 rabbit, 245
Loxodonta africana, 254
 Lumbricidae, 204
 Lycaenidae, 251
Lymantia dispar, 218
 Lysogenic bacteria, 163

 Macroevolution, 251, 258
 Macromolecules, 14, 23
 Maidenhair tree, 252
 Malaria, 61, 145
 Mammals, 260, 281
 Man, 47, 58, 67, 84, 146, 151, 229, 230, 238
 bipedal posture of, 283
 brain size in, 285
 care of young by, 282
 evolution of brain in, 286, 287
 fossil record of, 284
 Java, 284, 285
 Neanderthal, 284
 Peking, 284, 285
 population increase in, 292
 postnatal growth of, 285
 reasoning power in, 286
 reticulate evolution in, 284
 sense of smell in, 282
 sexuality in, 282
 terrestrial existence of, 283
 use of fire by, 284
 use of tools by, 284
 vision in, 282
 Mangrove finch, 227
 Mangroves, 225
Maniola, 132
 jurtina, 132, 154
 Mantids, 178
 Marmosets, 283
 Marsupial moles, 265
 Marsupials, 265, 270
 Mather, 151, 154
 Mating systems, 170
 Mating types, 168
 Mayr, E., 159, 249, 298
 Meadow fescue, 191
 Meaning, 73
Megaceros, 275
 Meiosis, 31–35, 40, 41, 165, 167, 201
 Meiotic drive, 175, 176
 Memory, 19, 286
 Mendel, 37–39
 Mendelian populations, 91
 Messenger RNA, 17, 18, 27, 64, 65
 Metacentric chromosomes, 186
 Metalloenzymes, 11
 Metaphase, 27, 29, 30, 32
Metasequoia, 258
 glyptostroboides, 252
 Metz, 189
 Mice, 300
 Michener, 158, 159
 Microevolution, 251, 258
 Microhabitat of *Cepaea nemoralis*, 133
 Micropterygids, 272
 Microsomes, 17, 25
 Migration, 79, 93, 114–118, 146
 Milkweeds, 258
 Miller, S. L., 6, 7, 21
 Mimicry, 147–149, 157
 of eggs, 245, 246
 Mitochondria, 25–27, 165
 Mitosis, 27–29, 62, 63
 Modifier genes, 42, 46, 130, 148
Mollienesia, 204
 formosa, 204, 205
 latipinna, 204, 205
 Mollusks, pelecypod, 261–264
 Momentum, evolutionary, 275
 Monarch butterfly, 58
 Monkeys, 283
 Monod, 64, 65, 68
 Monotremes, 270, 272
 Montagu, A., 293
 Moore, J. A., 216–218
 Moore, R. C., 239
 Morphogenesis, 66
 Morrison, J. H., 35
 Mosquitoes, 61, 84, 150
 Mosses, 168, 194
 Moths, 46, 125, 128, 130, 131, 271
 industrial melanic, 125, 247
 sloth, 84
 Mourant, 253
 Multicellular organisms, 57
 Multivalents, 190
 Multivariate comparisons, 302
Muscicapa striata, 128
 Mushrooms, 168
 Muskrat, 83
 Mustard, 84
 Mutagenic agents, 44
 Mutant, 38

- Mutation, 38, 44, 46, 48, 53, 59, 93, 101, 102, 114, 117-119, 175, 237-291
 back, 101, 114
 Mutation rate, 44, 79, 263
 Mutational load, 113
 Mutons, 38
 Mythologies, 290
- Narwhals, 275
Natrix, 212, 247
sipedon, 137, 230
 Natural selection, 13, 42, 60, 86, 103, 150
 cultural analogue of, 291
 Navigation in California newts, 79, 81
 Neanderthal man, 284
 Needham, A. E., 21
 Neighborhoods, 116
Nemobius fasciatus, 186
Neophasia, 254
menapia, 254
terlooti, 254
 Neoteny, 67
 Neo-X chromosomes, 178
 Neo-Y chromosomes, 178
Neurospora, 46
 Newts, California, navigation in, 79
 Nondisjunction, 187
 Nowinski, 29, 30, 33, 34, 43
 Nuclear division, 27
 Nucleic acids, 8, 14
 (See also Deoxyribonucleic acid; Ribonucleic acid)
 Nucleolus, 26, 27
 Nucleotides, 15-18, 38
 Nucleus, 25-28
 Numerical taxonomy, 260, 302, 305, 307, 312
 Nuthatches, 128, 229
Nymphalis, 256
antiopa, 256
californica, 256
milberti, 256
polychloros, 256
urticae, 256
vau-album, 256
xanthomelas, 256
- Oak-hickory forests, 87
 Oaks, 171
 Oats, wild, 84
Oenothera, 177-180, 182
biennis, 179, 182
erythrosepala, 182
hookeri, 179, 182
lamarckiana, 182
 Oligogenes, 52
 Onagraceae, 180
 Onions, 94, 191, 198
 Oparin, A. I., 6, 13, 21
 Operator genes, transcription of, 64
 Operon, 64
 Opossums, 263
Opuntia, 225
 Orangutans, 283
 Orchard grass, 146
 Orchids, 84
Oreopithecus, 284
 Organizers, 63
 Overdominance, 154
 for fitness, 109, 113
 Oxidation, biological, 10
- Paeonia*, 178, 180
 Pairing segments of chromosomes, 47, 178
 Panmixis, 91, 92
Papilio dardanus, 147, 149, 246
glaucus, 212, 232
laglazei, 271, 273
 Parallelism, 271
 in cultural evolution, 290
Paramecium, 164, 165, 169
 Parasitism, 229, 245
 Parthenogenesis, 189, 199, 200, 204-206
 Pasynskii, 21
 Pattee, 14, 15
 Pavlovskaya, 21
 Peacocks, 275
 Peck order, 80
Pedicularis dudleyi, 82
Pediculus, 245
humanis, 229, 245
 Peking man, 284, 285
 Pelecypoda, 261, 262, 264
 Penetrance, 42
 Perception, 73
 Perennial plants, recombination in, 171, 183
Peromyscus gossypianus, 300
leucopus, 300
 Phaeophycophyta, 167
 Phage, 162
 temperate, 163

Phalangers, 265
 Phenocopies, 154
 Phenotype, 58, 59
 Phlox family, 266
Phoenicurus phoenicurus, 128
 Phosphate bonds, 9, 10, 12
 Phosphorylation, oxidative, 10
 Photophosphorylation, 10, 12, 26
 Phycomycetes, 168
 Phyletic evolution, 260, 261
 Phylogeny, reticulate, 299
 Pieridae, 254
Pieris protodice, 84
 rapae, 84
 Pimentel, 248, 249
Pinaroloxias inornata, 225
 Pines, closed-cone, 254
 Pinocytosis, 24
Pinus attenuata, 254
 linguiformis, 254
 masoni, 254
 muricata, 254
 radiata, 254, 256
 remorata, 254
 Pioneer organisms, 171
 Pipe vine, decumbent, 87
Pipilo erythrophthalmus, 240
 ocai, 240
 Pit vipers, 265
Pithecanthropus, 259
 Placental mammals, 265, 270
Plantago erecta, 76, 79
 Plantain, 76, 79
 Plants, adaptive radiation in, 266
 Plasma membrane, 23
 Plasmodesmata, 24
Plasmodium, 61
 Plastids, 26, 165
 Plateau in selection response, 152
Platycnemis, 62, 63
Platyspiza crassirostris, 224, 225, 227
 Pleiotropy, 44, 64
 Pleistocene glaciations, 238
 Pneumococcus, 162
Poa, 198, 202, 206
 pratensis, 146
 Polar bear, 257
 Polemoniaceae, 266, 268, 269
 Pollen, 61, 168
 Pollination, 83, 171, 172, 258, 266, 268, 269, 275
 Pollution of environment, 131, 289
 Polygenes, 52, 169
 Polygenic inheritance, 53
 Polygenic systems, 54, 169
 Polymorphism, 110
 balanced, 110–113, 146
 Polypeptides, 8, 44
 synthetic, 7
 Polyploidy, 182, 183–196, 201, 202, 241
 Polyyps, 74
 Polytene chromosomes, 47, 63
 Pomoideae, 194
 Population biology, 73
 Populations, 75, 80
 fitness, 112, 311
 fusion of, 238
 mendelian, 91
 monomorphic, 113
 size of, 80, 82, 95
 effective breeding, 96, 232, 235
 structure of, 79, 114
 Porphyrins, 9, 10
 Portuguese man-of-war, 74
 Potential interbreeding, 300
 Primates, 283
 Primrose, 190
Primula, 191
 kewensis, 190
 Probability density function, 115
 Prometaphase, 27, 29, 30
 Prophase, 163
 Prophase, 27, 29–33, 41
 Protective coloration, 157
 Protein synthesis, 9, 64
 Proteinoids, 8
 Proteins, 6, 8, 24, 26
 Protozoa, 74, 167, 196
 Pseudocopulation, 84, 275
 Pseudogamy, 199, 200
 Puberty rites, 290
 Puff, 63
 Punishment, concept of supernatural, 292
 Punnett, 149, 273
 Purine, 17
 Pyrimidine, 17
 Q matrix, 304, 305
 Quadrivalents, 50
 Quantitative variation, 52
 Quantum evolution, 260, 263

- R matrix, 304
 Race, 252
 Radish, 190
 Rain forest, 84
Rana, 218
 catesbiana, 216
 pipiens, 215–218, 234, 300
 sylvatica, 216, 217
 Random fixation and loss of genes, 97–101, 121, 235
 Random mating, 91, 170
 Random segregation, 34
Raphanobrassica, 190, 191
 Rates of evolution, 260–264, 266, 267
 Rats, 85
 Raven, 180–182
 Recapitulation, 66, 67
 Recessive, 40
 Reciprocal translocation, 47, 49, 50, 177, 180, 183, 184, 186
 Recombination, 13, 35, 38, 40, 46, 79, 162, 163, 234
 in annual plants, 183
 and environment, 170, 171, 183, 206
 of genomes, 191
 in herbaceous plants, 171, 183
 index of, 183
 length of generation and, 79
 in microorganisms, 164
 in perennial plants, 171, 183
 reduction of, 169
 size of individual and, 79
 in woody plants, 171, 183
 Recons, 38
 Redstarts, 128
 Redwood trees, 58
 Reindeer moss, 87
 Religions, 287, 288, 290, 291
 Religious belief, origins of, 288
 Renner complexes, 182
 Rensch, B., 274, 277
 Repressor substances, 65
 Reptilia, 186, 251, 264, 267, 270
 Reticulate phylogeny, 299
 Reticulate variation, 258
 Rh locus, 146
Rhoeo, 177, 180
 Rhynchocephalia, 251
 Ribonucleic acid, 14, 15, 17–19, 65
 messenger, 17, 18, 27, 64, 65
 transfer, 18, 27
 Ring of chromosomes, 50, 182
 Ribosomes, 17, 25
 River model, 116
 RNA (*see* Ribonucleic acid)
 Robins, 128
 Roe, 128*n*.
 Root grafting, 74
 Rosaceae, 194
 Rotifers, 200, 201, 205, 247
Rubus, 202, 204
 Ryan, F. J., 55, 207
 Rye grass, perennial, 191
 Saez, 29, 30, 33, 34, 43
 Sagan, C., 21
 Sager, R., 55, 207
 Salamanders, 190, 218, 219
 Salivary gland chromosomes, 47, 49, 140
Salmonella, 163
 typhimurium, 164
 Sampling error, 95, 100, 237, 243
 Scale insects, 74
 Scallions, 191
 Scarlet tiger moth, 131
 Schmieder, 301*n*.
Sciara, 28, 177
 coprophila, 187–189
 Scientists, faith of, 312
 responsibility of, 313
 Scorpions, 178
 Sedges, 266
 Sedlmair, 159
 Segmental allopolyploidy, 191, 195
 Segregational load, 113
 Selection, 45, 46, 48, 64, 93, 102, 117, 118, 230, 237
 artificial, 103, 150
 coefficient of, 105
 creative aspect of, 102–104
 directional, 104, 127
 disruptive, 104, 147, 148, 248
 interclone, 248
 intergroup, 122
 intragroup, 122
 natural, 13, 42, 60, 86, 103, 150
 cultural analogue of, 291
 plateau in response to, 152
 pressures, change of, 289
 relaxation of, 152, 153
 stabilizing, 104, 125, 153
 Self-fertilization, 170, 206
 Self-pollination, 183

- Septobasidium*, 74
Sequoia, 252
Sequoiadendron, 252
 Sequoias, 61, 263
 Sex, differentiation of, 47, 172
 Sex-chromosome mechanisms, 178
 multiple, 178
 XO type, 48
 Sex chromosomes, 28, 32, 47, 175
 Sex determination, 200, 201
 Sex linkage, 47
 Sex ratios, 96
 Sexual isolation, 242
 Sexual reproduction, 166
 Sexuales, 205, 206
 Sexuality in man, 282
 Sexuparae, 205, 206
 Sheppard, 131, 133–135, 148, 159
Shigella dysenteriae, 164
 Sibling species in butterflies, 220, 244
 Sickle-cell anemia, 145, 230
 Significance, statistical, 128*n*.
Silene, 147
 Silkworms, 41
 Simpson, G. C., 128*n*., 259–265, 274, 275,
 277
 Sinnott, E. W., 16, 55
 Siphonales, 167
Sitta europaea, 128
 neumayer, 229
 tephronota, 229
 Size, overall body, increase in, 274, 275
 Slobodkin, L. B., 88, 248
 Sloth, 84
 Sloth moth, 84
 Snails, polymorphic land, 133–136
 (See also *Cepaea*)
 Snakes, 265
 Sneath, P. H. A., 314
 Social behavior, evolution of, in bees, 158,
 159
 Social hierarchy, 80
 Social insects, 74, 80, 158
 Social sanctions, 288
 Sokal, R. R., 314
 Somatic pairing of chromosomes, 49
 Song thrush, 128, 133
 Speciation, 211, 230
 allopatric, 247
 horizontal, 259
 sympatric, 247, 248, 311
 vertical, 259
 Species, 211, 272, 298, 302
 Species swarms in fishes, 220
Spergula, 147
Sphenodon, 252, 256
 punctatus, 251
 Spindle, 27
 Spindle fibers, 26
 Spiralization of chromosomes, 28, 30
 Spleenwort, 194
 Splitting, 259, 261
 Spontaneous generation, 5
 Sporogenesis, 168
 Sporophyte generation, 168, 199
 Sporozoa, 168
 Spotted flycatchers, 128
 Spuhler, 123
 Stag beetles, 275
 Standard deviation, 52
 Stationary frequency distributions, 114, 115
 Stebbins, G. L., 88, 159, 167, 170, 171, 183,
 185, 191, 194, 195, 207, 249, 277
 Stebbins, R. C., 219, 221
 Storksbill, 84
 Streams, 248, 249
 Strepsiptera, 267
Styx, 252
 infemalis, 251
 Succession, ecological, 86
 Succulent plants, convergence in, 270
 Sunflower, 241
 Supergenes, 144, 148, 175–177, 183
 Supernumerary chromosomes, 186
 Survivorship curves, 260, 261, 263
 Swallowtail butterfly, 147
 Swanson, C. P., 35
 Switch genes, 52
 Sycamore, 75
 Symbiosis, 74, 84
 Sympatric speciation, 247, 248, 311
 Sympatry, 240
 Synapsis of chromosomes, 32, 41, 176, 187,
 190
 Syngamy, 165, 166
 Taboos, 291
 Tachytely, 261, 263, 265, 267, 272
 Tadpoles, 63
 Tanager-like finch, 225
 Tarsiers, 283
 Tasmanian devil, 265
 Tasmanian wolves, 265

- Tatum, 163
 Taxonomy, structure imposed on nature, 307
 Tecumseh, 291
 Telophase, 28-34
 Temperate phages, 163
 Template, 19, 20, 21
 Terminalization, 32, 34
 Termites, 229
 Territoriality, 80
 Territories, interspecific, 240
Tetracoccus ilicifolius, 82
Tetraneura ulmi, 205
 Thelytoky, 200, 205
 Thoday, J. M., 248, 249
 Thysanoptera, 200
 Tiger lilies, 190
 Tiger swallowtail butterfly, 212
 Tinbergen, 128
 Tobacco, 291
 Tobgy, 185
 Tools, use of, 285
 Towhees, 240
 Trans state, 38
 Transduction, 163, 164
 Transfer RNA, 18, 27
 Transformation, 161, 164
 Transient polymorphism, 131
 Translocation, reciprocal, 47, 49, 50, 177, 180, 183, 184, 186
 Tree kangaroos, 265
 Tree shrews, 283
Treponema pallidum, 87
Trifolium repens, 146
 Triplets, 17, 18, 20, 21
 Trophic levels, 86
 Tuatara, 251, 256
 Tulips, 190
Turdus ericetorum, 128, 133
 Twitty, 79, 81
- Ultraviolet light, 9
 Unicellular organisms, 57
 Unique events, 73
 Univalents, 32, 190, 191
Ursus americanus, 256
 arctos, 257
 horribilis, 256
 maritimus, 257
 middendorffi, 257
- Variance, components of, additive genetic, 53
 dominance, 53
 environmental, 52, 53
 epistatic, 53
 gene-environment interaction, 53
 genetic, 52, 53
 nonadditive, 53
 phenotypic, 52
 remainder, 53
- Variation, 37
 clinal, 232
 in animals, 215
 in plants, 214
 continuous, 52
 discordant, 252
 ecotypic, 213
 geographic, 212, 214, 219, 230
 intrapopulational, 213
 patterns of, 307
 quantitative, 52
 reticulate, 258
- Vaurie, 231
 Vegetative reproduction, 31, 74, 190, 196
 Verbal communication, 286
 Vertical speciation, 259
 Violets, 197
 Vipers, pit, 265
 Virgin births, 290
 Virginia deer, 87
 Viruses, 162, 164, 165
 RNA type, 164
 Vivipary in plants, 198
 Vocalization in sympatric birds, 240
- Waddington, C. H., 60, 68, 156, 159
 Wagner, 192-194
 Wald, 8
 Warbler finch, 224, 229
 Wastage of gametes, 169, 182
 Water molds, 168
 Water snakes, 137, 151
 Water striders, 31
 Watson-Crick model, 16
 Weevils, 204, 275
 Weinberg, 123
 West, D. A., 308, 314
 Western Europe, culture of, 291, 296-298
 Whales, 270
 White, M. J. D., 43, 189, 203, 207
 Whooping cranes, 82

Whorf, B. L., 297, 314
Wild type, 58
Wilson, E. O., 249
Wilson, G. B., 35
Wolves, 87
Woodson, R. E., 214, 215, 234, 249
Woody plants, recombination in, 171, 183
Worms, 201
Wright, S., 45, 46, 103, 115, 116, 118–121,
123, 195, 235
Wynne-Edwards, V. C., 88
X chromosome, 47, 48, 178, 180
Y chromosome, 47, 48, 175, 178, 180
Yarrow, 213
Yeast, 61, 74, 169
Yellow hammers, 128
Zca, 47
Zinjanthropus, 284, 285
Zygotes, wastage of, 169, 182
Zygotic chromosome number, 184

