COMPARATIVE VERTEBRATE NEUROANATOMY

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Evolution and Adaptation

Second Edition

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Dedication

This dedication is in four parts: to those special friends, mentors, and family members who are now deceased, to those special persons still living who have taught and guided us in our careers, to a special friend of the field, and to our families.

In recognition of those special persons who are now deceased, Ann Butler dedicates her contribution to this work to the memory of Alexander and Ethel Benedict Gutman, Raymond C. Truex, and B. Raj Bhussry; William Hodos dedicates his contribution to the memory of his parents, Morris and Dorothy Hodos, and Walle J. H. Nauta.

In recognition of those special persons in our lives who have been teachers and mentors as well as friends and colleagues, we also dedicate this book to Warren F. Walker, Jr., Theodore J. Voneida, R. Glenn Northcutt, Ford F. Ebner, Sven O. E. Ebbesson, C. Boyd Campbell, and Harvey J. Karten. Additionally, we dedicate this work to Harold J. Morowitz, James L. Olds, Robert F. Smith, and William S. Hall in acknowledgement of their outstanding support and encouragement.

We also dedicate this book to Dr. Thomas Karger in appreciation of his generous and steadfast support of the field of comparative neurobiology, as particularly evinced by his sponsorship of the J. B. Johnston Club and its yearly Karger Symposium. His beneficence has substantially promoted the dissemination of new data and theories in the field and thus materially aided the preparation of this second edition.

Finally, we dedicate this book to our families, Thomas and Whitney Butler and Nira, Gilya, and Tamar Hodos, who have always given us their loyal support, their patience, and their ceaseless encouragement.

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THE FOREBRAIN: TELENCEPHALON

Preface

What Is This Book About?

This book is about the central nervous system of those animals that possess backbones—the vertebrates—and how evolution has shaped and molded their bodies and their nervous systems, allowing them to thrive in their particular environments or to take advantage of new environmental opportunities. Thus, it is a book about the relationship between structure and function and about survival through effective design. It is a book about the past as well as the present and about the history of vertebrate nervous system evolution, to the extent that we can read that history from the present state of these animals.

Who Is This Book For?

This book has been written first and foremost for neuroscience students at the graduate or advanced undergraduate level. We have presumed that the reader will have taken one or more introductory undergraduate biology courses or otherwise be familiar with this material. In a more general sense, this book is also for anyone who is interested in the anatomy of the nervous system and how it is related to the way that an animal functions in its world, both internal and external.

This book is intended as an introductory work rather than as a handbook or reference work that scientists might refer to in their professional writing. We have modeled this book on several textbooks designed for advanced undergraduate to graduate levels: *Functional Anatomy of the Vertebrates: An Evolutionary Perspective* (Second Edition) by W. F. Walker, Jr. and K. F. Liem (Saunders College Publishing, Fort Worth, TX, 1994); *Hyman's Comparative Vertebrate Anatomy* edited by M. H. Wake (The University of Chicago Press, 1979); *The Human Brain and Spinal Cord* by L. Heimer (Springer-Verlag, New York, 1983); *Core Text of Neuroanatomy* by M. B. Carpenter (Williams and Wilkins, Baltimore, 1991); *An Introduction to Molecular Neurobiology* by Z. W. Hall (Sinauer Associates, Sunderland, MA, 1992); and *Principles of Neuroscience* (Third Edition) by E. R. Kandel, J. H. Schwartz, and T. M. Jessell (Appleton and Lange, Norwalk, CT, 1991). In keeping with the format of these texts, we have not cited references in the body of the text, but at the end of each chapter we have listed the references from which we drew material and additional papers that may interest the reader. Our aim has been to introduce the reader to the field and to synthesize information into a coherent overview, rather than to present an extensive catalog of individual data.

In keeping with the introductory nature of this work, we largely have omitted details on whether and/or where particular projections cross the midline of the nervous system. In some cases, where this information is of particular importance, we have included it. However, in most cases, we leave it to the interested reader to glean such details from other sources.

This is a book that we hope will be of interest to the general scientific reader and the nature enthusiast, as well as to advanced undergraduate or beginning graduate students in the neurosciences. Physicians and others with knowledge of the human central nervous system should also find much of interest here. To our colleagues who are specialists in the field of comparative neuroanatomy, we say that this is not the book that you might write; this is the book that students should read to give them the background to read your book and other scholarly publications in neuroanatomy and brain evolution.

Apropos of this aim and since the time of the first edition of this textbook, a truly remarkable contribution to the literature of comparative neuroanatomy was made by Rudolf Nieuwenhuys, Hans ten Donkelaar, and Charles Nicholson with the publication of their comprehensive and encyclopedic set of three volumes on *The Central Nervous System of Vertebrates* (1998, Springer-Verlag, Berlin). These volumes cover the subject and the literature in far greater depth and breadth than could or should be included in a textbook. We have benefited greatly from the material in these volumes in writing the second edition of this book. In updating material, there is the constant temptation to add more and more detail, and in the process, forsake the original purpose. We thus have endeavored to tread a fine line between updating and maintaining the introductory level. We hope that this book will continue to fill its intended role as an introductory work, allowing the reader to then delve into the Nieuwenhuys et al. volumes as well as the primary literature for much more extensive and detailed treatments of a multitude of topics.

What Can Be Learned About the Human Brain From a Book About the Brains of Many Different Vertebrates?

During the past four decades, a great explosion of information about the anatomy of the brains of nonhuman and especially nonmammalian vertebrates has taken place. One of the lessons to emerge from this wealth of new data has been the reversal of the nineteenth century view that a dramatic change in brain evolution occurred with the evolution of mammals in

general and humans in particular. In other words, once the powerful tools of modern neuroanatomy were applied to the brains of birds, fishes, reptiles, and amphibians, many of the same patterns of cell groups and their interconnections that were known to be present in mammals (including primates) were found to be present in nonmammalian vertebrates as well. Thus, comparative neuroanatomists came to recognize that the evolution of the vertebrate central nervous system had been far more conservative than earlier investigators had realized.

To be sure, great differences in specialization of the brain exist between animals that have become adapted to very different modes of existence. Indeed, those differences in form and function are what make the study of comparative neuroanatomy and brain evolution so fascinating—a fascination that we hope to share with you. In spite of these differences, however, all vertebrate central nervous systems share a common organizational scheme so that someone who is familiar with the brain of any vertebrate will also be on familiar ground when first encountering the brain of any other species. Someone who has read this book and retained the general principles of brain anatomy and organization that it presents will have little difficulty reading a medical school textbook of human neuroanatomy because much of it will be familiar both in overall conception and in many of the details.

What Is New in This Book and How Does It Differ from Other Texts?

The first edition of this book incorporated several new approaches to the subject matter of comparative neuroanatomy and the orientation with which we study it. These new approaches, which have been maintained and/or further developed in this second edition, include

- A recent reevaluation of the cranial nerves of vertebrates and their derivation and organization
- A new organizational approach to the various groups of vertebrates based on the degree of elaboration in their central nervous systems rather than the traditional, *scala naturae*-like ranking
- New insights into the organization and evolution of the dorsal thalamus and dorsal pallium in the forebrain
- A new and comprehensive overview of brain evolution in vertebrates that encompasses many of the evolutionary and developmental topics covered in the rest of the text

The first of these new approaches is based on the work of Northcutt, Baker, Noden, and others, on the organization of the cranial nerves. While constituting a radical departure from the established, traditional list of twelve cranial nerves with their functional components, we feel that this new approach is a marked improvement for two reasons: First, it takes into account additional cranial nerves, both long known and newly recognized ones, that are found in many vertebrates but are not included in the "traditional twelve." Second, it is based on embryological development, including gene expression patterns, and thus provides a coherent accounting of the segmentation of the head itself and of its component parts, including both the brain and other tissues (particularly the neural crest, epithelial placodes, and paraxial mesoderm). Chapter 9 on the embryology of the cranial nerves in relation to head segmentation covers this newly developed approach to cranial nerve organization and is crucial to understanding the subsequent chapters on the cranial nerves themselves.

The second departure from tradition that we took in the first edition and have retained here is the order in which various groups of vertebrates are considered in the chapters on the various regions of the nervous system. This approach is based on the range of variation in brain structure within each of the major groups of vertebrates. It is intended to overcome the erroneous but culturally ingrained idea of a single, simple-to-complex, linear series of evolutionary stages leading from fish to frog to rat to cat to monkey to human, i.e., the myth of a *scala naturae.* Chapter 4 specifically addresses this issue.

A great diversity in brain organization has been achieved independently at least four separate times within four separate radiations of vertebrates; our approach is designed to highlight both the diversity itself and its multiple, independent development. Thus, in a number of the chapters on brain regions and systems, particularly in the midbrain and forebrain, we first consider and compare those species within each radiation in which the brain has relatively simple cellular organization, as for example, lampreys, dogfish sharks, gars, and frogs. We then consider and compare those species within each radiation in which the brain has relatively complex cellular organization, as for example, hagfishes, skates, teleost fishes, and amniotes (mammals, reptiles, and birds). We hope to convince the reader that the development of a more complex brain has been accomplished not just once for the "ascent of man," but multiple times. Moreover, we will show that mammals (including primates) do not always have the most sophisticated brain systems.

In line with this point, other chapters, including "Evolution and Variation," "Evolution and Adaptation of the Brain, Behavior, and Intelligence," and "Theories of Brain Evolution," seek to dispel further the myth of *scala naturae* and to deal with the actual range of variation in line with the known facts and processes involved. In this context, we hope that the reader will come to understand that, whereas some vertebrates have simpler brains than others, all living vertebrates are equally successful in that they are alive and adapted to their environments.

A third new approach taken for the first edition and maintained here concerns the evolution of two major parts of the forebrain, the dorsal thalamus and the dorsal pallium, particularly in amniote vertebrates. Two fundamentally different divisions of the dorsal thalamus recently have been recognized in all jawed vertebrates: one that predominantly receives direct, lemniscal sensory and related inputs, called the lemnothalamus, and one that predominantly receives sensory inputs relayed to it via the roof of the midbrain, called the collothalamus. These lemnothalamic and collothalamic divisions of the dorsal thalamus have recently gained validation from differential patterns of gene expression during development. Correspondingly, two major divisions of the pallium in amniote vertebrates that receive their respective inputs predominantly from the lemnothalamic and collothalamic divisions of the dorsal thalamus have been recognized as well. The way in which a number of the chapters on the forebrain have been

organized and the material presented in them are based to some extent on these new concepts of forebrain evolution. Finally, new insights into the evolution of the brain, not just in vertebrates but among some of the invertebrate chordates as well, are presented in the last chapter of this book. Recent findings on genetic patterning of central nervous system structure and on the anatomy of the brain and head region in the cephalochordate *Branchiostoma*, as well as anatomical evidence from the recently found fossils of the chordate *Haikouella*, allow for some of the features of the brain in the earliest vertebrates to be identified. A new survey of brain evolution is presented. For context, brain organization in some invertebrates is surveyed, particularly in terms of gene expression patterns, which are strikingly similar to those in vertebrates. Then vertebrate brain evolution is discussed, beginning with a few but significant features that can be identified in the common ancestors of cephalochordates and vertebrates, identifying additional features that were present in the earliest vertebrates, including two novel tissues of the head (neural crest and placodes) and a number of cranial nerves associated with them, and then tracing the separate evolutionary histories of the brain in the major radiations of extant vertebrates.

For the second edition, a recently proposed model of the transition to vertebrates that specifies the gain of paired eyes and elaboration of the diencephalon and hindbrain before most of the elaboration of neural crest and placodal tissues occurred to produce the peripheral nervous system has been included. This model was recently given strong support by newly discovered fossil evidence from the chordate *Haikouella*. Also, the striking similarities of patterning gene expression across all bilaterally symmetrical animals studied, from mice to fruit flies, and their implications for the evolution of rostrocaudally and dorsoventrally organized central nervous systems are discussed.

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Part One

EVOLUTION AND THE ORGANIZATION OF THE CENTRAL NERVOUS SYSTEM

1

Evolution and Variation

INTRODUCTION

One of the primary fascinations of the natural world is the vast diversity of living organisms within it. Diversity of organisms and their many body parts is a hallmark of biology. Biological diversity has been produced by the process of **natural selection**, part of which is a reflection of changing climates, geophysical phenomena, and habitats. The pressures of natural selection act on spontaneous variations of the phenotypes that occur within a population and are the result of mutational changes within the genes.

For the study of biological diversity, we need to recognize the natural groupings to which individual organisms belong. A **species** is usually defined as a naturally interbreeding set of individual organisms or set of populations of organisms. The English words "species" and "special" derive from the same Latin term *specialis*, and in fact each species is distinguished by its particular, special feature(s) that is/are unique to it. The next level of phylogenetic classification is that of **genus**, which is a set of species that are more closely related to each other than to species outside the genus. Additional examples of levels are those of **family**, **order**, **class**, and **phylum**. Also, various intermediate levels, such as subfamily, infraorder, supraorder, and so on, are employed as appropriate. Even within a species, various subspecies can be recognized. The term **taxon** applies to any defined, natural group of organisms, such as a species, order, or class. The term **clade** can also be used to refer to such defined natural groups. The terms taxon and clade are usually and best used to apply to **monophyletic groups**, which are groups that include all of the descendants of a specified common ancestor and no other members. In practice, often only the **extant** (living) descendants are addressed.

Our current understanding of biological diversity began with the theory put forth by Charles Darwin (and independently by Alfred Russel Wallace) in 1858–1859. This theory states that a process of evolution by natural selection has produced the variation that is documented by the fossil record and among extant species. The source of the variation upon which natural selection acts was not identified until the science of genetics was established by the pioneering work of Gregor Mendel, who in 1865 formulated the principle of particulate inheritance by the means of transmitted units or genes, and the later work of Theodosius Dobzhansky and others in the first half of the twentieth century.

Modern evolutionary theory embodies the work of Darwin in the context of genetics, molecular biology, and other relevant sciences. This interrelationship of disciplines was termed an **evolutionary synthesis** by Julian Huxley in 1942; it refers to the recognition that both gradual evolutionary changes and larger evolutionary processes, such as speciation, are explainable in terms of genetic mechanisms. Since that time, a substantial body of work in genetics, systematic biology, developmental biology, paleontology, and related fields has yielded new and more complex insights on this subject. The title of a recent book by Niles Eldredge (1985), *Unfinished Synthesis*, reflects the continuing debate within the field.

Until Darwin's publication of his views, most Western scientists believed that most or all species of wild animals living at that time had been unchanged since their creation by a deity. Darwin's idea that living creatures had evolved over long periods of time was accepted fairly readily. Some resisted the

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idea of humans being animals in continuity with nature, that is, that humans are related to any other animals, such as apes and monkeys. That evolution is a directionless process employing natural selection is a concept that has been accepted by some but resisted with vigor by others, even today.

The idea that evolution is progressive in the sense that progress or continuous improvement occurs over time is seductive and comforting. It is seductive in its appeal to the egocentricity of our species and comforting as a source of moral principles. The Aristotelian concept of a ***scala naturae*** that living animals can be arranged in a continuous, hierarchical, ladder-like progression with humans at the pinnacle embodies this appeal, as does the Judeo–Christian tradition of creation that culminates with the human species. Julian Huxley promoted the idea that, although evolution was without purpose, it was progressive. He believed that ethical principles and the meaning of human existence could be derived from the position of humans at its pinnacle.

The *scala naturae* concept of progressively ascending scales of life forms, such as the fish–frog–reptile–rat–cat–monkey–human sequence, is seen as intuitively correct. The pervasive flaw in all such rankings is that they are made from an anthropocentric point of view. The anthropocentric scale, however, is of no greater scientific value in an evolutionary context than one based, for example, on our assessment of the animals' beauty. The appeal of the idea of progress over evolution is based on the fact that progress itself, like beauty, is a human concept and value; it is not, however, a biological principle.

Inherent in the notion of a scale of nature is the idea that each animal has a natural rank on this scale. The more "advanced" animals (humans and the ones seemingly closest to humans) occupy ranks high on the scale, and those that seem to bear less resemblance to humans are relegated to the lower ranks. Thus, we have come to refer to some animals as "the higher vertebrates" and others as "the lower vertebrates," or "the submammalian vertebrates." Unfortunately, terms like "higher," "lower," and "submammalian" represent only homocentric value judgments; they are thus inappropriate ways of comparing animals and have no place in the vocabulary of evolutionary biology. Many extant species of vertebrates are only distantly related to humans and resemble them very little; nevertheless, these animals are just as successful and well adapted to their environments as humans and their closest relatives are to their own environments. The simple fact that animals are different does not confer any rank to them relative to each other.

Many humans consider the human species as "special," different in some way and standing apart from all other species. As noted above, the word "special" and "species" are derived from the same Latin term, so in that sense, *all species are special*. Thus, to the extent that we are a species, we are special by definition. The perspective of William S. Gilbert and Sir Arthur Sullivan, in their operetta The Pirates of Penzance, is relevant here: "If everybody's somebody, then no one's anybody." Scala naturae thinking that views any one species as superior to all others is in fact one of the greatest impediments to understanding the biological world and to appreciating the place of our own species within it. Evolution does not create superior and inferior taxa; it simply creates diversity.

DIVERSITY OVER TIME

Biological diversity is a result of natural selection acting on random variations within populations of organisms. The degree of biological diversity has increased over time in some ways. For example, twice as many species of marine animals (invertebrate and vertebrate) exist today as existed in the Paleozoic era. In other ways, however, biological diversity has dramatically decreased over time. In the Paleozoic era, the number of groups of higher taxonomic rank (more inclusive categories) was far greater than the number that exists today. Diversity in the range of basic body plans has decreased, whereas the diversity of species having any of the few, extant, basic body plans has increased. The greater number of extant species is grouped within the fewer number of higher categories.

One explanation for this more complex pattern of evolutionary change focuses on processes that tend to eliminate extremes in variation, such as competition under conditions of natural selection. Animals with the more successful body plans would ultimately survive, and the number of higher categories thus decreases over time. A second explanation involves the random process of **extinction**. To consider this possibility, we need to examine evolutionary history in terms of the extreme physical forces that shape it.

Extinctions of varying degree repeatedly occur and profoundly affect biological evolution. Some extinctions are of modest degree and limited extent, happening to isolated populations due to normal environmental fluctuations or accidental factors. Species most resistant to environmental fluctuations tend to be those with individuals that have larger bodies, longer lives, and a greater degree of social interaction related to breeding behaviors. Other extinctions are of greater consequence and related to **habitat fragmentation** caused by such factors as tectonic shifts, temperature changes, alteration in rainfall patterns, and changes in oceanic level. When habitat fragmentation occurs, species more resistant to extinction are those that are herbivorous versus carnivorous and, among carnivores, of smaller body size. Those species with more strictly defined habitat requirements—**habitat specialists**—are more prone to extinction than species that are **habitat generalists**. Species with populations of smaller size or lesser density are likewise more prone to extinction than those of greater size and/or density.

Of the greatest consequence are mass extinctions of hundreds or thousands of species, such as those that occurred at the end of the Permian and the Cretaceous periods. Not only are mass extinctions dramatic and of momentous impact on biological flora and fauna, but they appear to occur with a regular periodicity. Mass extinctions have recurred on a cycle of about 26 million years for at least the last 225 million years. The Cretaceous extinction occurred 65 million years ago. To account for a cycle on such a long time scale, extraterrestrial causes, such as asteroid or comet impacts, have been considered, and evidence from the distribution of iridium, a relatively rare element of extraterrestrial (meteoritic) origin, in the earth's surface supports this possibility. A recurring disturbance of the Oort cloud—the cloud of comets that circle the sun—could release comets that could then impact the earth with catastrophic results.

In mass extinctions, some species and groups of species have better chances of survival than others. Categories of taxa that have a greater number of species (**species-rich clades**) tend to be composed of habitat specialist species, species that have become specialized for survival in a particular habitat, which are thus more susceptible to extinction if the habitat changes suddenly. In contrast, the habitat generalist species tend to be in taxonomic categories with a fewer number of species (**species-poor clades**), have wider geographic ranges, and can more readily shift habitats if conditions change.

In normal times, species-rich clades undergo a net increase in species number, offsetting losses due to limited environmental fluctuations, accidents, and habitat fragmentation. This speciation has a pattern of punctuated equilibrium—rapid change followed by a longer period of little or no change, as discussed below. Species-poor clades, on the other hand, have a lower rate of speciation but are more resistant to environmental and habitat assaults. This balance permits both types of clades to flourish in the intervals between mass extinctions. In mass extinctions, the species-rich clades are more vulnerable, and thus over time, fewer higher categories survive. More species arise in at least some of the remaining higher categories due to new waves of speciation following each period of mass extinction. Biological evolution is thus the net result of multiple independent processes.

EVOLUTIONARY MECHANISMS

Evolution can be defined simply as a *change over time*. In biological systems, random genetic variation occurring within a population allows for phenotype variation, which natural selection can then act upon. Darwin recognized that evolution occurs as a consequence of two separate processes. The first process, which we know today to encompass mutations and genetic recombinations as well as other factors, is a random process that produces variability. The second process, natural selection, is not random but rather opportunistic, and it acts on this variability. Natural selection acts on populations, affecting the frequency of particular genes within the population, rather than on individuals.

Genetic Factors

Mutations and changes in the frequency of certain gene alleles, that is, alternate forms of the gene (dominant vs. recessive), account for diversity within an interbreeding population. The individual members of the population are similar but not identical. Because a gene may exist in a large variety of allelic forms but an individual animal has only one pair of alleles for each gene, any given individual possesses only a small fraction of the total genetic variation that is stored in the population as a whole.

The relative frequencies of alternative alleles and genotypes reach equilibrium and then tend to remain constant in a large, randomly mating population. Despite this tendency, changes in the frequencies of different alleles do occur over succeeding generations. In addition to mutations, factors that affect the frequency of alleles in a species include **genetic recombination, gene flow**, and **isolating mechanisms**.

Gene recombination assembles an existing array of allelic forms of different genes into a variety of combinations. This does not increase the frequencies of these alleles but does increase variability. While mutation is the ultimate source of genetic variation, recombination generates numerous genotypic differences among individuals in a population. Consequently, recombination provides a large number of the variations acted upon by natural selection.

Gene flow is a change in the frequency of particular alleles caused by individuals of the same species migrating into and interbreeding within a given population. Gene flow is essential to maintaining various populations as members of a single species, since the most important aspect of the definition of a species is that it consists of a set of populations that actually or potentially interbreed in nature. Gene flow is responsible for genetic cohesion among the various populations that form the species. This process is a stabilizing influence on genetic variation and is responsible for the relatively slow rate of evolution that occurs in common, widespread species.

Biological mechanisms that isolate one population from another reproductively are in direct contrast to gene flow and define the limit of the species. Geographic isolation, such as islands separated from each other by the ocean or a peninsula being isolated as an island due to a rise in the level of the ocean, can result in changes in gene frequencies between the two populations. A small number of individuals that becomes isolated from the rest of the population will not necessarily have the same alleles in the same frequency distribution as the whole original population, resulting in a shift in allelic frequencies in the isolated population. Examples of such isolated populations are various species of birds on various islands in the Galapagos, Hawaiian, and other similar island groups. If the geographic isolation eventually ceases, reproductive isolation may nevertheless be maintained by newly established mechanical incompatibilities of the male and female or by behavioral isolation caused by differences in mating ritual or species recognition cues that exclude some formerly potential mates.

Natural Selection

Natural selection acts on the variability and establishes certain variant types in new frequencies within a given population. Natural selection is the increase in frequency of particular alleles as a result of those alleles enhancing the population's ability to survive and produce offspring. The **fitness** of a variant is a measure of how strongly the variant will be selected for, that is, how adaptive it is. Thus, a novel variant that enables a population to capitalize on a vacant niche may rapidly establish itself. Alternatively, selective pressures that are too strong, such as a relatively sudden decrease in ambient temperatures during an ice age, may result in extinction of populations. In such a case, the variability within the population is simply not extensive enough to fortuitously have the number of variants that would allow for selection of adaptations to the cold.

If a mutant allele appears infrequently in a large population, the initial frequency of the allele will be low and will tend to remain low. If a mutant allele appears in a single individual and has no selective advantage or disadvantage, it can by chance alone readily become extinct. On the other hand, if it

even slightly enhances the ability of its bearer to live and reproduce, it will increase in frequency. Selection is the most important means by which allele frequencies are changed. Natural selection can be considered to consist of the differential, nonrandom reproduction of particular alleles. As alleles are parts of whole genotypes, selection can also be thought of as the differential and nonrandom reproduction of particular genotypes.

Darwin considered natural selection to mean differential mortality. Contemporary evolutionists look upon it as differential reproduction. Although natural selection does frequently take the form of differential mortality, other strategies occur as well, such as increasing the number of offspring produced or improving the chance of successful mating by increasing efficiency in getting food or evading predators. Differential mortality can be regarded as one form of differential reproduction, if, for example, some animals do not survive long enough to reproduce.

Gene alleles most often have multiple effects, that is, they are **pleiotropic**. Some of the characteristics determined by an allele may be advantageous to the individual, while others may be disadvantageous. An individual carrying an allele (A) might have a selective advantage over another individual carrying its matching allele (A′), but might be inferior to the phenotype of the second individual in some other character produced by allele A. If individuals carrying the allele A have a net superiority over individuals carrying the allele A′, then allele A will increase in frequency despite its deleterious side effects.

The discussion thus far has been primarily concerned with selection of single alleles, but the same principles can be extended to encompass combinations of two or more genes. Many adaptations are based not on single genes but on multiple genes or gene combinations and the resultant phenotype on which selection acts. Populations of organisms exist in a particular environment to which they must be fitted or adapted in order to live and reproduce successfully. If the environment remains stable and the population is highly adapted, selection operates primarily to eliminate peripheral variants and offtypes that arise by mutation or recombination. If a change occurs in the environment, one or more of the peripheral variants may be better adapted to the new conditions than those with the more normal genotype. Selection now takes a different form, favoring the formerly peripheral variants and eliminating some of the standard genotypes.

Since natural selection acts on a population rather than any individual, traits such as "altruism" can be selected for. For example, in many species, an individual animal may do work or even sacrifice itself in the service of offspring that are related but not its own. By so doing, the animal is protecting the genes that it has in common with those offspring. Thus, rather than being truly altruistic, such acts are actually self-serving in that they are a mechanism to protect at least some genes that are the same as the animal's. The genetic basis for the potential to act in support and defense of related offspring is thus likely to be retained in the population.

Darwin believed that the course of evolution resulted primarily from natural selection acting on variations within populations. In his view, this process produced gradual changes that could, over long periods, account for all the organic diversity that we observe today. The modern synthesis has incorporated the new knowledge of mechanisms provided by genetics, including that from the recent advances in molecular biology. Nevertheless, emphasis is still placed on the role of natural selection acting at the level of the population, as advanced by Darwin. The term **microevolution** refers to such divergences of populations within a given species, resulting in races or breeds. Microevolution involves the gradual accumulation of small changes over time, the way Darwin envisioned the evolutionary process. Another type of gradual evolutionary change is **phyletic evolution** (also called **anagenesis**). In phyletic evolution, a single lineage, without branching into divergent lineages, undergoes change over time. The ancestral and descendant portions of the lineage can become sufficiently different that they are recognized as different species.

In 1972, Niles Eldredge and Stephen Jay Gould, after examining evidence from the fossil record of marine invertebrates, pointed out that in this group at least, few examples exist of species that undergo significant change gradually through time. In most cases, a particular morphology is retained for millions of years and then changes abruptly over a short period of time. Eldredge and Gould used the term **punctuated equilibrium** to describe this pattern. Punctuated equilibrium is similar to the concept of saltatory evolution, the sudden origin of new taxa by abrupt evolutionary change, held by some of the nineteenth century biologists. The process by which new taxa are formed, from the specials level on up through the higher taxic categories, is called **macroevolution**. The formation of new species can also be referred to as **speciation** or **cladogenesis**. The term speciation is used to describe a process in which a single species gives rise to a branch that becomes established as a new, sister species or splits into two new lineages that both become new species, that is, are reproductively isolated from each other.

Darwin and a number of other biologists thought that the microevolutionary process of gradual morphological change brought about by the accumulation of genetic mutations could also explain the origin of the so-called higher taxonomic categories of species, families, orders, and classes. However, the morphological differences between various orders and families, and even those that distinguish individual species within a genus, can be considerable. After all, morphological differences are the major basis for defining these various higher categories. The new synthesis of evolution and developmental biology that is now underway reemphasizes macroevolutionary events and their crucial significance for evolutionary divergences and the formation of new taxa. Changes in the developmental process—such as **heterochrony**, a change in the relative timing of potentially related developmental events, and allometric alterations, a change in the proportional growth of a structure and/or its elements—can have dramatic effects on the phenotype. Such changes in the developmental process intervene between genotype and adult phenotype and can produce the types of substantial and rapid morphological changes that typify saltatory evolutionary events. As discussed in Box 1-1, these kinds of changes involve **developmental fields**, also called **morphogenetic fields**, **embryonic fields**, or **anlagen** (singular: **anlage**), which are the fundamental evolutionary units of macroevolutionary change. Darwin himself recognized the crucial interrelationship of embryology and evolution.

BOX 1-1. Morphogenetic Fields and the New "Evo-Devo" Synthesis

Over the past decade, it has become compellingly clear that development and evolution interact with each other, and the new synthesis occurring in biology is based on this premise. The new amalgamation of these fields of study has been dubbed "**Evo-Devo**" for short. Natural selection acts on the phenotype of the developing embryo just as it acts on the adult. The translation from the genes to the adult phenotype depends on the proper expression of the genetic instructions. Expression of various patterning genes results in expression of other genes, which in turn affect and recruit additional genes and so on, through a precisely choreographed developmental process, affecting developmental events. For example, the length of cell proliferation periods determines the number of daughter cells that form a structure and thus its volume. Whether cells of a particular set migrate to another location or remain piled up in the immediate vicinity of where they were proliferated determines the location of the structure. If the cells migrate, the order in which they do so determines their relative arrangement within the structure. All such events must occur at the proper time and to the proper degree to produce the genetically programmed phenotype. Changes in the expression levels of the patterning genes can have dramatic affects on the phenotypic outcome. Many changes can be deleterious and result in the death of the embryo, either during development or at shortly after birth. Some changes, however, can cause a substantial change in the phenotype without being lethal. Such changes, if they produce an alternate phenotype that is advantageous in terms of selective pressures, will be selected for. Major evolutionary divergences as well as lesser ones within smaller taxic groups may arise from these mechanisms.

In 1996, Scott Gilbert, John Opitz, and Rudolf Raff published a review of the new perspective that has emerged on the interplay between developmental biology and evolution. Views of homology (discussed below) and of evolutionary mechanisms are now being reevaluated, and the full biological continuum of genes-embryological development-adult phenotype is being reconciled with evolutionary mechanisms. The key to this new synthesis is the **morphogenetic field**. Gilbert et al. define morphogenetic fields as "discrete units of embryological development . . . produced by the interactions of genes and gene products within specific bounded domains." The fields are "modular entities [that] are genetically specified, have autonomous attributes and hierarchical organization, and can change with regard to location, time, and interactions with other modules." Essentially, morphogenetic fields are the building blocks of development, and they interact in highly complex ways.

The expression parameters of the key patterning genes affect the morphogenetic fields and determine the variability of their products. Altering the timing of the formation of a morphogenetic field (called heterochrony) or altering other attributes of the field can affect other fields or whether the field in question is able to produce its adult phenotypic structure(s). Limb buds, for example, give rise to limbs in most vertebrates. However, in snakes, the limb buds do not produce limbs. Alteration of the properties of the limb buds results in this alteration of the normal tetrapod pattern. Thus, "the morphogenetic field (and not the genes or the cells) is seen as a major unit of ontogeny whose changes bring about changes in evolution."

As Gilbert et al. discuss, morphogenetic fields had been a major focus of biology in the first half of the 20th century, but interest in them was eclipsed by the synthesis of genetic and evolutionary theory. The significance of morphogenetic fields has now come to be appreciated once again. Changes in them can account for saltatory, macroevolutionary events. Thus, both gradual, microevolutionary changes and the rapid, macroevolutionary changes observed in the fossil record now can be accounted for with satisfactory biological explanations.

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Evolution of the Vertebrate Central Nervous System

Extant vertebrates currently comprise diverse groups, each with diverse and numerous species. Nevertheless, in the subsequent chapters of this book, we will encounter many features of the central nervous system of vertebrates that are remarkably constant from one group to another. We will also encounter many that vary considerably. The features that are constant as well as those that are diverse have resulted from the pressures of natural selection, themselves derived from climatic and geophysical factors, acting on the randomly derived variation in the frequency of gene alleles in interbreeding populations. Patterning genes in turn affect the morphogenetic fields, which, as discussed in Box 1-1, are the basic units of development.

Variation in the structure of the central nervous system of vertebrates has resulted from changes in the developmental program over evolution. The most salient and defining differences in brain structure and organization have resulted from alterations in the behavior of various morphogenetic fields—relatively simple changes in the length of the cell proliferation periods and the migration patterns of the neuronal precursors underlie the basic and substantial differences in organization

between mammalian brains and those of birds and reptiles, for example. Other alterations can result in the production of new cell types. Major differences within each of the major vertebrate groups as to how elaborate the brains of different taxa are also depend on proliferation and migration behaviors of various morphogenetic fields.

In a sense, the morphogenetic field is the nub of the answer to the riddle of brain evolution: complexity is most often derived from simplicity, that is, great diversity and great complexity have arisen because they both are merely the result of a few, simple random mutational events that affect the behavior of particular morphogenetic fields, the phenotypes of which have been favored highly by natural selection. Comparative neuroscience addresses the questions of how brains can change as new species evolve and how much a given part of the brain can change over evolution. To assess the variation, we first need to be able to recognize the same structures in different brains and then to compare their similarities and differences. Defining what is meant by the word "same" in this context has been an important keystone of comparative neuroanatomical analysis.

SAMENESS AND ITS BIOLOGICAL SIGNIFICANCE

Analogy

Most of this section will focus on phyletic continuity of structures across taxa and/or on the phyletic continuity of the genes and/or morphogenetic fields that produce them. The concept of **analogy** is different in that it addresses similarity of *function*, irrespective of phyletic relationships or continuity. Structures with quite different morphology, phyletic origin, and embryological origin can have quite similar functions. In other words, structures can be analogous if they serve the same function, whether they are the same or different in terms of phyletic inheritance from a common ancestor. As we will discuss below, the wing of a bird and the wing of a bat are homoplastic (independently evolved) as wings, but they are both historically homologous (inherited from a common ancestor) as forelimb derivatives and analogous as both wings and forelimb derivatives. They share the same function of flying. An elephant's trunk and a raccoon's hand have nothing in common phyletically or embryologically, yet they are analogous as organs for manipulating objects in the external environment. As we also will discuss for cases of both homology and homoplasy, the analogy must be specified to make sense. The wings are analogous as both wings and forelimb derivatives because they are used in the same way at both these levels. They are not analogous as feathered appendages, since bat wings have membranous surfaces rather than feathers.

Historical Homology

The concept of "same" is expressed in biology by the term **homology**. This term was first introduced by the influential British anatomist Richard Owen in 1843. Owen defined **homologue** (i.e., **homologous structures**) as "the same organ in different animals under every variety of form and function." Owen's definition preceded Darwin's theory of evolution, and modern concepts of homology have been affected by the revolutions in evolutionary biology and genetics that subsequently occurred.

Leigh Van Valen defined homology as "correspondence caused by continuity of information," a definition that has been as criticized for its vagueness as it has been praised for its flexibility and utility. Another definition, proposed by George Gaylord Simpson, states that "homology is resemblance due to inheritance from common ancestry." These definitions both refer to **similarity**—"resemblance" or "correspondence"—but some structures that are present in related groups of animals and that have been inherited from a common ancestor may lack any vestige of resemblance. For example, the middle ear bones of mammals (the malleus and the incus) are very unlike the articular and quadrate jaw bones of other tetrapods and from which they are ancestrally derived. Only the data provided by the fossil record allow us to recognize the common derivation of these structures.

Other definitions of homology stress **phyletic continuity**. Edward Wiley proposed that "A character of two or more taxa is homologous if this character is found in the common ancestor of these taxa, or, two characters (or a linear sequence of characters) are homologous if one is directly (or sequentially) derived from the other(s)." In this usage, the concept of homology is rooted in phylogeny. This usage can be referred to as **phyletic homology** or **historical homology**. Inheritance of the character from a common ancestor with consistent expression of the character through the various descendant lineages and across all or most members of the lineage is required to meet the definition. However, as new information accumulates and an improved understanding of the relationship of genes and developmental processes to evolutionary change is achieved, the concept of homology is changing. The newer concepts will be considered below.

A similar definition for historical homology was proposed by Michael Ghiselin: "Structures and other entities are homologous when it is true that they could, in principle, be traced back through a genealogical series to a (stipulated) common ancestral precursor."The required stipulation is the basis of the homology. Without the stipulation, that is, **specification**, of the homology, any statement of homology is incomplete. Consider, for example, the following two statements, both of which are true:

- The wing of a bird is homologous to the wing of a bat.
- The wing of a bird is not homologous to the wing of a bat.

These two statements, although both true, are both incomplete and hence are seemingly in conflict. The wing of a bird is homologous to the wing of a bat *as a derivative of the forelimb*. The common ancestors of birds and bats possessed forelimbs of a similar basic construction, from which the wings are derived in both cases. The wing of a bird, however, is not homologous to the wing of a bat *as a wing*, since the forelimbs of the common amniote ancestors of birds and bats did not have the form of wings. Saying that A is homologous to B is as incomplete a statement as saying that "Harriet is more than Jane." More what? More intelligent? More athletic? More sophisticated? In statements of homology, unless the specification is obvious and unmistakable, the specific characteristic being

compared must be included in the statement for the statement to be meaningful.

Several different types of historically homologous relationships can be recognized. Hobart Smith gave clear and concise definitions of them in his 1967 paper on biological similarities. The most common type might be called a **discrete homology**, defined as "common ancestry of structures which can be compared individually. . . ." Alternate terms for discrete homology are **strict homology** or **one-to-one homology**. The wing of a bird being homologous to the wing of a bat as a forelimb derivative is an example of a discrete homology, in that a discrete structure in each of two or more taxa is being compared. Additional types of homology, as specified by Smith, are also applicable to neuroanatomical studies. A **serial** or **iterative homology** (also called homonomy) involves structures that are derived from the same ontogenetic division of two or more segments in a single individual organism, such as the wing of a bird and the leg of the same individual bird, as serially derived tetrapod limbs. Vertebrate ribs, vertebrae, and spinal cord segments are additional examples of serial homology. Also involving development is the concept of **field homology**, which applies to structures that are derived from the same ontogenetic source, i.e., the same morphogenetic field (see Box 1-1), across taxa. An example of a field homology is the five digits of a human hand being homologous as a set of derivatives of a common morphogenetic field to the set of the lesser number of distal forelimb divisions in a variety of other mammals. The topic of field homology is discussed further in Box 1-2.

Since the features of any given structure may be altered in different lineages, fossil evidence has played a significant role in identifying homologous parts of the musculoskeletal system among vertebrates. The brain does not fossilize, however, so other criteria for proposing hypotheses of historical homology are needed for neuroanatomical work. These criteria are based on the degree of similarity and were proposed by Simpson in 1961. They include the **minuteness of the resemblance** and the **multiplicity of the similarities**. In neuroanatomical studies, the features that can be compared for a given group of neurons in two different extant taxa include:

- Topological similarity.
- Topographical similarity.
- Similarity of axonal connections.
- Similarity in their relationships to some consistent feature of the two species.
- Similarity of embryological derivation.
- Similarity in the morphological features of individual neurons that form the group.
- Similarity in the neurochemical attributes of the neurons.
- Similarity in the physiological properties of the neurons.
- Similarity in the behavioral outcomes of neuronal activity.

Not all of these criteria can be met in every case. Some would argue strongly against including the last two criteria, noting that comparisons should be structural only and never functional. Nevertheless, the more of these criteria that can be satisfied, the stronger the support for an hypothesis of historical homology, that is, phyletic continuity. In those cases in which structures that are homologous also meet most or all of the above criteria for similarity, the term **homogeny**, or its adjective **homogenous**, can be applied, although these terms are rarely encountered in the literature.

Homoplasy

Homoplasy is the opposite of historical homology. The term is used to refer to structural similarity without phyletic continuity, and its adjective is **homoplastic**. Structural similarity can occur in divergent lineages as a result of similar adaptive responses to similar environmental pressures rather than as an inheritance from ancestors. The wing of a bird and the wing of a bat are not homologous as wings; they are homoplastic as wings. Note again that the relationship must be specified to make sense. Structural similarity without phyletic continuity can also result from changes in the expression of particular patterning genes, with alterations in the fate and behavior of morphogenetic fields.

Three different types of homoplasy are recognized: **convergence**, **parallelism**, and **reversals**. Convergence refers to the process of similar responses to similar adaptive pressures, but the responses are based on entirely different genes and morphogenetic processes. Convergence has been defined by Wiley as "the development of similar characters from different preexisting characters." Convergence usually occurs in remotely related animals, and the degree of similarity and the minuteness of the resemblance are limited and generally superficial.

Parallelism, in contrast, usually occurs in closely related taxa, and the degree of similarity and minuteness of the resemblance tend to be extensive. Wiley defined parallelism as "the independent development of similar characters from the same plesiomorphic [i.e., ancestral] character." In other words, the descendant character is not present in the common ancestor of two taxa, but each of the descendant taxa develops the descendant character after the time of their evolutionary divergence. One implication of parallelism is that the genetic and/or morphogenetic material that produces the structures in the different taxa is the same, i.e., inherited from a common ancestor with phyletic continuity. In both homology and parallelism, similar structures are present in closely related animals with similar survival problems that have adapted in similar ways. Historical homology differs from parallelism only in the consistency with which the structure is phenotypically expressed along the phyletic lineage or across the phylogeny of extant taxa.

When such instances of similar structures being present in closely related species occur, distinguishing between parallelism and historical homology can sometimes be difficult. In these circumstances, assuming historical homology is regarded as the preferable tactic. The German scientist Willi Hennig codified this method in his **auxiliary principle**: "Never assume convergent or parallel evolution; always assume homology in the absence of contrary evidence." As we will discuss below, this method is based on the idea that it is simpler for a common ancestor to acquire a given structure once than for each of two descendent groups to acquire it independently. Also, the biological basis for the structure is the same for historical homology and parallelism. For understanding evolutionary processes, identifying shared genetic and morphogenetic bases of structure is more important than distinguishing between historical homology and parallelism. Tables 1-1 and 1-2 offer

BOX 1-2. Field Homology

Field homology involves structures that are embryologically derived from the same developmental field. In a 1967 paper, Hobart Smith defined it as "derivation of structures, however similar or dissimilar, from a common anlage, or in other words, from the same ontogenetic source of the same or different segments, of any two or more compared individuals or groups of individuals." Interestingly, Smith recognized the seminal importance of embryology for the concept of homology; he defined homology itself as "commonness in phylogenetic *or embryonic* origin of two or more specific compared structures, irrespective of similarity of structure or function [our italics]."

The concept of field homology rests on the concept of the developmental, or morphogenetic, field itself (see Box 1-1). With the new, "evo-devo" synthesis and the rediscovered appreciation of the morphogenetic field, the legitimacy of the field homology concept has been accepted by a number of comparative neurobiologists. For a field homology to be valid, it is required that the morphogenetic fields themselves be homologous, either historically or as defined by evo-devo perspectives (as discussed below).

It is important to note that the field homology concept is generally used to compare a set of derivatives in the adult phenotype in one taxon with the corresponding set of derivatives in the adult phenotype of another taxon. It is not appropriate to make "diagonal" comparisons of noncorresponding developmental stages in two different taxa. In other words, the comparison should be "horizontal," as across the rungs of a ladder, with the side rails representing time and each rung connecting comparable developmental stages. That is to say, homologous morphogenetic fields need to be compared at similar stages of their development rather than comparing an early field in one taxon to a later and more differentiated field in another taxon. Glenn Northcutt has argued against the use of the morphogenetic field homology concept, partly on the basis of improper "diagonal" comparisons, and this point is a crucial one, since one must try to distinguish between homologous field derivatives and the appearance of a truly new structure—an **evolutionary innovation**.

In Figure 1, Northcutt's diagram is shown in A, which shows three taxa descended from a common ancestor. This common descent applies to the examples shown in B and C as well. In A, two structures, E_1 and E_2, have developed in Taxon 3 as derivatives of an additional developmental stage that has no homologue in Taxa 1 and 2, i.e., the E morphogenetic field that produces E_1 and E_2 is not homologous to the D field of Taxa 1 and 2. The field homology concept, as currently applied by others, would also invalidate this comparison. It would require that a homologous morphogenetic field E be identified in Taxa 1 and 2 for the comparison of derivatives to be valid, as shown in the example in B. In both A and B, it is implied that E developed from D, but another possibility, that of evolutionary innovation, must also be considered, as shown in the example in C. In this situation, an entirely new, autonomous morphogenetic field, indicated by the asterisk, enters the picture in Taxon 3, which is independent of the temporal series of development of the field A-B-C-D-(E) in Taxa 1 and 2. Such a scenario is illustrated by distal limb development in tetrapods (Taxon 3 in this example), as Günter Wagner and Chi-hua Chiu have discussed. This diagram oversimplifies the actual history of tetrapod limb evolution (see Chapter 7), but the point to be made here is that a new component, produced by a new morphogenetic field, cannot be included in the set of deriv-

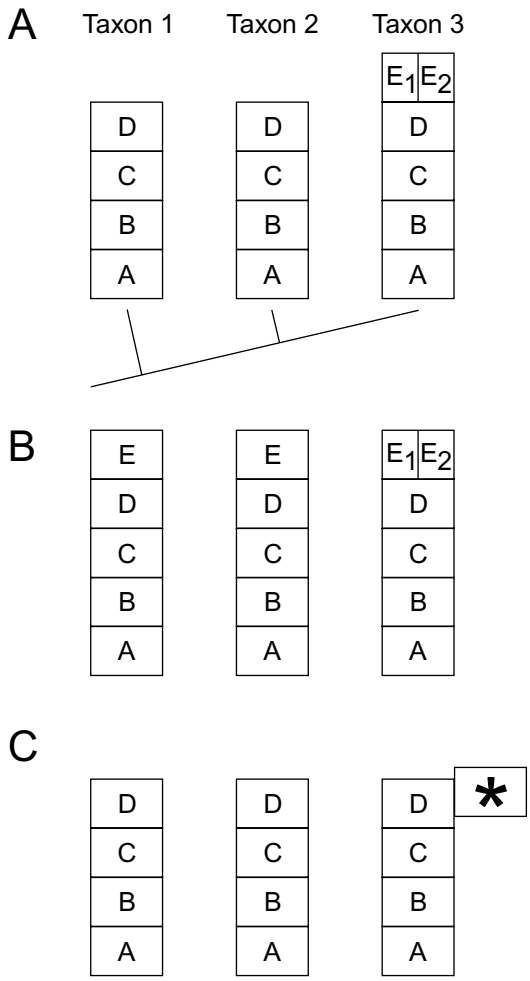

FIGURE 1. Examples of successive stages in the development of a morphogenetic field in three taxa. (A) after Northcutt (1999) showing noncomparability of E_1 and E_2 in Taxon 3 to D in Taxa 1 and 2. (B) correct field homology hypothesis of E_1 and E_2 in Taxon 3 to E in Taxa 1 and 2. (C) evolutionary innovation, indicated by * in Taxon 3, which is not derived from D and must be excluded from comparison with the derivatives of D among all three taxa.

BOX 1-2. Field Homology—cont'd

atives of another field, D, and then compared to the derivatives of D in another taxon. In other words, one must be precise in determining the derivatives of any given morphogenetic field for a hypothesis of field homology to be valid. This point is of particular importance for illuminating the evolution of various parts of the brain across vertebrates.

It should also be noted that, although development from a common morphogenetic field is an important criterion for recognizing homology, it is not absolute. Other criteria must also be weighed. While most historical homologues arise from historically homologous morphogenetic fields, some arise from nonhomologous fields. Such exceptions are few but do occur. The lens of the eye, for example, can be derived from different sources.

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TABLE 1-1. Comparisons With a Human Hand

Basis of the Relationship	Hand of a Monkey	Hand of a Raccoon	Forepaw of a Rat	Wing of a Bat	Wing of a Bird	Wing of a Moth
Historically homologous as a hand?	Yes—their common ancestor had hands	No—their common ancestor had forepaws, not hands	No—their common ancestor had forepaws, not hands	No—their common ancestor had forepaws, not hands	No—their common ancestor had forepaws, not hands	No—an insect wing is not related to a hand
Homoplastic as a hand?	No—they are historically homologous	Yes—it looks roughly like a human hand	Yes—in some respects but not to the same degree as in the case of the raccoon	No—it does not resemble a human hand	No—it does not resemble a human hand	No—it does not resemble a human hand
Historically homologous as a forepaw?	Yes	Yes	Yes	Yes	No—bird wings are forelimbs, not forepaws	No—an insect wing is not related to a forepaw
Homoplastic as a forepaw?	No—they are historically homologous as forepaws	No—they are historically homologous as forepaws	No—they are historically homologous as forepaws	No—they are historically homologous as forepaws	No—bird wings are forelimbs, not forepaws	No—an insect wing does not resemble a forepaw
Analogous?	Yes—used for manipulation	Yes—used for manipulation	Yes—used for manipulation	No—used for flight, not manipulation	No—used for flight, not manipulation	No—used for flight, not manipulation

some opportunities to see whether you understand the differences between historical homology, homoplasy, and analogy. They also point out the importance of specifying the relationship.

Reversals are instances of a character appearing, subsequently disappearing, and still later reappearing along the descendants in one lineage. Since the character is not consistently expressed in the phenotype, it cannot be considered to be historically homologous. Because most and perhaps all cases of reversal are based on expression of the same underlying gene and/or morphogenetic field and processes, inherited down the lineage from the common ancestor, they are closely related to parallelism.

Biological Homology

A number of other approaches to homology have been taken by various scientists. The historical homology concept does not satisfy some situations, due to its failure to recognize the importance of genetic and morphogenetic continuity as the bases for sameness. Its insistence on consistent phenotypic expression of a particular character in all or most members

TABLE 1-2. Comparisons With an Eagle's Wing

Basis of the Relationship	Wing of a Sparrow	Wing of a Crow	Wing of a Bat	Wing of a Moth
Historically homologous as a wing?	Yes—their common ancestor had wings	Yes—their common ancestor had wings	No—their common ancestor did not have wings	No—their common ancestor did not have wings
Homoplastic as a wing?	No—they are historically homologous	No—they are historically homologous	No—it does not resemble a bird wing	No—it does not resemble a bird wing
Historically homologous as a forelimb derivative?	Yes	Yes	Yes	No—an insect wing is not related to a forelimb
Homoplastic as a forelimb derivative?	No—they are historically homologous	No—they are historically homologous	No—it does not resemble a bird wing	No—an insect wing does not resemble a forelimb
Analogous?	Yes—used for flight	Yes—used for flight	Yes—used for flight	Yes—used for flight

of a taxon is at odds with biological reality, which includes cases of inconsistent phenotypic expression. Two alternative approaches discussed here are **biological homology** and **generative homology**, or **syngeny**. One could say that, although historical homology focuses on phyletic continuity, biological homology focuses on morphological identity, and generative homology focuses on genetic and morphogenetic identity. These concepts are not mutually exclusive. In fact, they overlap considerably. These concepts are each best suited for a different research interest—historical homology for phylogenetics and systematics, biological homology for character evolution, and generative homology for comparative developmental biology.

Biological homology is an alternative approach that addresses how characters evolve and become stabilized within a taxon and the mechanisms of character evolution. Biological homology focuses on developmental pathways and the behavior of morphogenetic fields to account for variability of character expression but does not define sameness by them. It attempts to link historical homology to developmental processes and constraints. Biological homology was defined by Leigh Van Valen in 1982 as "resemblance caused by a continuity of information" and by Louise Roth in 1984 as based on "sharing of pathways of development . . . controlled by genealogically related genes." In 1989, Günter Wagner stated that "Structures from two individuals or from the same individual are homologous if they share a set of developmental constraints, caused by locally acting self-regulatory mechanisms of organ differentiation. These structures are thus developmentally individualized parts of the phenotype." This concept of homology seeks to understand why individualized parts of the body behave as units that maintain their structural identity. Gerd Müller and Günter Wagner more recently defined biological homology as "the establishment and conservation of individualized structural units in organismal evolution." Most if not all cases of biological homology are also cases of historical homology.

Generative Homology or Syngeny

A number of approaches to the problem of parallelism have been taken, including the concepts of **latent homology** put forward by Gavin deBeer in 1971. He proposed that this term should refer to characters that occur within only some members of a taxon but that may not have been expressed in the common ancestor and are not expressed in a substantial number of the other members of the taxon. Other similar concepts have been put forward, but they have focused on parallelism (and reversals) rather than addressing the close relationship of historical homology to these phenomena.

The discovery of a particular cell group in the brain of teleost fishes prompted Ann Butler and William Saidel to scrutinize current concepts of homology and to propose a new concept—that of generative homology, or syngeny. The cell group in question, nucleus rostrolateralis, will be discussed in Chapter 21. This nucleus has a very sporadic and far-flung phylogenetic distribution within ray-finned fishes, and it is absent in many taxa that are in phylogenetically intermediate positions to those where it occurs. Nevertheless, where present, it has many and minute similarities. It is an example of very distant parallelism, due to inconsistent expression of its underlying genetic and morphogenetic bases. This unusual pattern of expression of what is clearly the "same" nucleus was the impetus for reexamining the issues of homology and for formulating the concept of generative homology, or syngeny.

The term syngeny means "same genes," since the concept addresses the issue of phyletic continuity of genes and morphogenetic pathways and fields rather than of the adult phenotype per se. Generative homology is closely allied to biological homology, but it specifically states that the recognition of sameness is based on shared genetic/morphogenetic pathways that are inherited with continuity across the members of a taxon. Whether expression of the character is consistent (historical homology) or inconsistent (parallelism or reversals) is not of importance in recognizing the biological relationship of sameness. Thus, generative homology comprises parallelism, reversals, and most cases of historical homology. It is a unifying concept that separates these three phenomena from convergence. The latter is referred to as **allogeny**, meaning "different genes."

The historical homology/homoplasy conceptual stance divides characters along artificial lines with its insistence on

TABLE 1-3. Historical Homology Versus Generative Homology

	Components	Biological Basis	Phenotypic Expression	Opposite
Historical Homology	Historical homology cases only	Inheritance from common ancestor of the character itself	Required to be consistent along and/or across the taxon	Homoplasy: parallelism, reversals, and convergence
Generative Homology	Most cases of historical homology plus parallelism and reversals	Inheritance from common ancestor of genetic and/or morphogenetic basis for the character	Can be either consistent or inconsistent along and/or across the taxon	Allogeny (= convergence)

consistent phenotypic expression. The syngeny/allogeny conceptual stance recognizes that historical homology, parallelism, and reversals all share the inherited underlying genes and morphogenetic processes and thus form a natural conceptual group. Convergence, similarity due to different, noninherited genes and morphogenetic processes, stands alone as the opposite phenomenon. The difference in these two concepts is highlighted in Table 1-3.

The generative homology concept will be of particular relevance in dealing with the plethora of recent findings on patterning genes and the stunning similarity of their expression patterns in some taxa of bilaterally symmetrical animals. As we will discuss further in Chapter 31, many of the same genes that specify basic developmental events in vertebrates, including those for the central nervous system, also occur in invertebrates and have the same roles. Many of the genes that specify the basic divisions of the brain and the formation of the eye, for example, are the same in fruit flies and mice. In such cases, the word "homology" is sometimes used. However, because the common ancestor clearly did not possess a comparable brain or eyes, these structures in mice and flies cannot be historically homologous. Nonetheless, even their designation with the same words, "brain" and "eye," denotes recognition of a basic level of sameness, and, as products of the same patterning genes that were present in the common ancestor, they are indeed the same. The brains of flies and mice as whole brains and the eyes of flies and mice as whole eyes are examples of generative homology; they are **syngenogues** to the extent that they are products of the same set of genetic and morphogenetic processes.

ANALYSIS OF VARIATION

Recognizing similar structures present in different taxa is the first part of the process of reconstructing evolutionary history, which, in the absence of a corroborating fossil record—as is the case with most features of the central nervous system—is essentially a guessing game. Although we may come up with sophisticated theories that seem to account for the data, there is no guarantee that these theories are correct. This is a problem that exists in many areas of science, such as astronomy, geology, psychology, and economics, to name a few. An approach to evolutionary reconstruction of the central nervous system that has been used with considerable success is a methodology called **cladistics**.

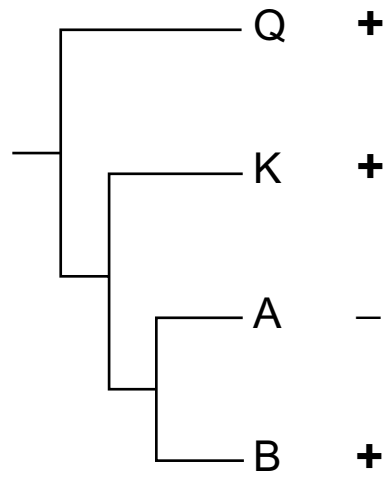

FIGURE 1-1. Cladogram showing the distribution of a trait, indicated by +, among the theoretical extant taxa Q, K, A, and B.

Cladistic Analysis

Cladistics is a formal method of analysis for classifying animals according to their inferred phyletic relations, based on sets of shared similar traits. This approach is the embodiment of the historical homology concept. It can be applied to analyzing the variable occurrence of a given trait among different taxa. In the latter case, a highly corroborated hypothesis of phylogenetic relationships of the taxa under consideration is needed. This phylogenetic hypothesis should be one that is derived from sets of traits not related to the trait being analyzed and also is based on a large number of such traits. It is usually structured in the form of a **cladogram** or **dendrogram**, that is, a tree-like diagram of the species representing their genealogy, produced using cladistic methods of inference. For example, hypotheses of phylogeny, such as those presented in Chapter 4 and based predominantly on fossorial and osteological data, are appropriate to use in the analysis of the distribution of central nervous system traits. Traits that are **plesiomorphic**, that is, are similar to those present in a particular ancestral stock, need to be distinguished from traits that are **apomorphic**, that is, derived specializations within a particular taxon.

The observed distribution of the trait to be analyzed is plotted on the terminal branches of the cladogram, an example of which is shown in Figure 1-1. The pattern of distribution of

the trait in various ancestral groups that can account for the observed distribution in the living (terminal branch) taxa via the *fewest* number of phylogenetic transformations is then inferred. This process thus generates an hypothesis about the evolutionary history of the trait based on its distribution in extant taxa. In our example (Fig. 1-1), we are considering four taxa: A, B, K, and Q. All are descended from a common ancestral stock, but A and B are more closely related to each other than to K. Also, the taxon K and the group of A and B are more closely related to each other than to Q. Taxon B has a particular trait, indicated by the + sign, but the related taxon A does not. Did the common ancestor of A and B have the trait, with the line leading to A subsequently losing it, or did the common ancestor lack the trait and the line leading to B alone gain it?

Cladistic analysis uses **out-group comparisons**, that is, comparisons of the trait in sister taxa, which are taxa more closely related to the taxon being studied than to any other taxon. In our example, we thus first examine taxon K, the out-group, or sister taxon, to the group of B and A, for the presence or absence of the trait and find that it is present in K. One possible scenario, which would require two transformations, is that the trait was gained at some point in the common ancestor of K, A, and B (transformation 1) and was subsequently lost in A (transformation 2). The alternative scenario is equally likely, since it would also require two transformations—the absence of the trait in the common ancestor with its independent gain in K (transformation 1) and B (transformation 2). Thus, on this information alone, we cannot decide which possibility to choose for our working hypothesis. To resolve the question, we can examine taxon Q, the out-group to K, A, and B. We find that the trait is present in Q. Thus, the scenario with the least transformations is that the trait was acquired in the common ancestor of all these taxa (transformation 1) and was subsequently lost only in A (transformation 2). This hypothesis requires fewer transformations than the alternative of three independent acquisitions of the trait in Q, K, and B. It also requires fewer transformations than the other alternative scenario of absence of the trait in the common ancestor, its gain in Q (transformation 1), its independent gain in the common ancestor of K, A, and B (transformation 2), and its subsequent loss in A (transformation 3). Cladistics thus provides a rigorous method for inferring the likely nature of structures in common ancestors and, therefore, which structures are plesiomorphic (ancestral) and which are apomorphic (derived).

Could an alternate scenario to the one with the least transformations actually have occurred? Of course! That is why it is so crucial to employ the scientific method of continually challenging and testing hypotheses. Also, the more taxa that one can examine for the presence or absence of a trait, the less likely is the possibility of error in formulating the hypothesis. It is also why the principle of parsimony serves us well.

Parsimony

Generating an hypothesis of historical homology based on the smallest number of phylogenetic transformations is in accordance with the **principle of parsimony**. In its simplest form, this principle states that if one is confronted by several competing theories or explanations, the simplest one (or the one with the fewest assumptions) is most likely to be correct. Please note that the principle states the simplest explanation is *most* likely to be correct. Parsimony is no guarantee of correctness. In biology, nonetheless, simple explanations seem to be supported by subsequent facts more often than more complex explanations. In the case of the distribution of a trait in Q, K, and B but not A, as shown in Figure 1-1 for example, we would have no grounds to assume that if the common ancestor of A and B had the structure, then a subsequent ancestor of A lost it, another subsequent ancestor of A regained it, and yet another subsequent ancestor lost it again. Unless there were specific evidence to support this having happened, most biologists would find such an elaborate hypothesis to be quite unconvincing. Hence, the value of parsimony: it tends to rule out overly elaborate hypotheses, which is a justified result in most cases. The more elaborate hypothesis described in this example, however, would be a case of reversal, which, as noted above, refers to the gain, loss, regain, and so on of a trait subsequently along a lineage through time. Reversals, although not frequent, do occur, and the cladistic method is not well suited to reveal them.

The principle of parsimony is in accord with current ideas about the mechanisms of evolution for most situations. Any given species does not have a good chance of success if it gains new traits that do not give it an advantage in maintaining itself or if it loses traits that were beneficial to survival. If a new trait allows for a new niche or adaptive advantage, the trait will be selected for and maintained in the phenotype. Most, but not all traits, fit this model. Also in most cases, changes in the genome conform to the principle of parsimony. The simpler the alteration of the genome to produce a variant, on which natural selection can then act, the greater the probability of its occurring and becoming established in a population. This is the **principle of minimum increase in complexity**, as delineated by Peter Saunders and Mae-Wan Ho.

Let us extend our example of using the principle of parsimony in an **out-group analysis** by analyzing the variation of a hypothetical trait with some real taxa, as shown in Figure 1-2, in order to better demonstrate the correct method of analysis and the importance of being rigorous in applying it. Figure 1-2 shows a somewhat simplified cladogram of the major taxa in the vertebrate radiation (which will be discussed in Chapter 4). A plus sign is placed to the right of each taxon where the trait is present and a minus sign where it is absent. We first note that the trait is present in the amniote vertebrates—mammals, reptiles, and birds—but is absent in amphibians. Was it present or absent in the common ancestor of amphibians and amniotes? The out-group to amphibians and amniotes, that is, tetrapods, is the crossopterygian *Latimeria*, and in our example, *Latimeria* lacks the trait, as do the lungfishes. We therefore hypothesize that the trait was absent in the common ancestor of lungfishes, *Latimeria*, and tetrapods. This would mean that only one transformation occurred over evolution among these groups: the acquisition of the trait in the ancestral stock of amniotes. We can also conclude that the trait was not acquired in the common ancestor of tetrapods, because such a change would then have to be followed by another change (the loss of the trait in extant amphibians), and this scenario is not parsimonious. Two changes are more complicated than one, so the hypothesis of two changes must be discarded.

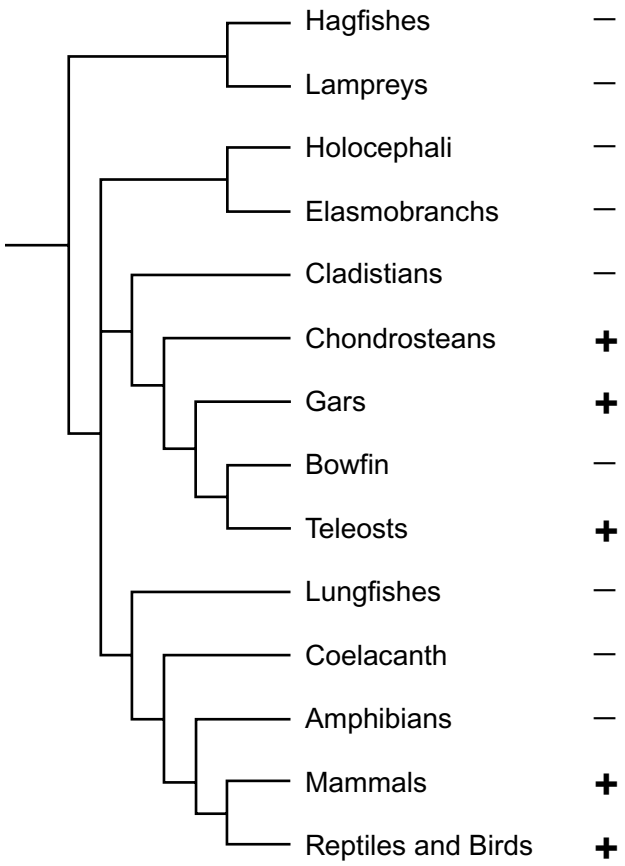

FIGURE 1-2. Cladogram showing the distribution of a trait, indicated by +, among extant groups of vertebrates. (The groups themselves will be discussed in Chapter 3.)

We now turn to the ray-finned fishes and find that a similar trait is present in teleosts, absent in the bowfin, present in gars and chondrosteans, and absent in cladistians. Comparing only teleosts and the bowfin, we do not know whether the trait was present or absent in their common ancestor. Gars and chondrosteans are the out-groups to the bowfin and teleosts, and they have the trait. Therefore, we hypothesize that the trait was present in the common ancestor of these four groups and that it has been lost once—in the bowfin. The trait is absent, however, in cladistians. Was it present or absent in the ancestral stock of ray-finned fishes? The out-group to the ray-finned fishes is the cartilaginous fishes, and the trait is absent in both groups of cartilaginous fishes—holocephali and elasmobranchs. Thus, we hypothesize that the trait was absent in the common ancestors of cartilaginous and ray-finned fishes. It was gained in the ancestral stock of chondrosteans, gars, the bowfin, and teleosts and was subsequently lost in the bowfin.

Jawless vertebrates (hagfishes and lampreys) also lack the trait, so we can extend and summarize the above hypotheses to the following: the trait was absent in ancestral vertebrates, was gained once in the common ancestral stock of chondrosteans, gars, the bowfin, and teleosts (transformation 1), was lost in the bowfin (transformation 2), and was independently gained a second time in amniotes (transformation 3). Three is thus the minimum number of changes that can satisfy this distribution. If, on the other hand, we were to ignore parsimony and hypothesize that the trait was gained in the ancestors of ray-finned fishes and then lost in reedfishes, in the bowfin, in the coelacanth, in lungfishes, and in amphibians, we would have to ascribe to six transformations, twice the number that accounted for the pattern in the more parsimonious hypothesis.

Using the principle of parsimony has important implications for distinguishing historically homologous structures from homoplastic ones. Given the distribution of the trait in our example, we must conclude that the trait in some of the ray-finned fishes and the trait in the amniotes are homoplastic and not historically homologous, even if they resemble each other closely. If two structures are homoplastic, we can examine to what degree they are similar and assess what constraints may be operating and how much potential exists for the development of new structures over evolution. If multiple and minute resemblances exist between structures in phylogenetically far-flung taxa, a hypothesis of generative homology would be justified, as in the case of nucleus rostrolateralis discussed above. Again, the homology must be specified. For example, the eyes of fruit flies are generatively homologous to the eyes of mammals as whole eyes engendered by a specific set of patterning genes. They are not generatively homologous at a finer morphological level, since the ommatidial units of the fly eye are specified by different genes than the mammalian retina and are very different in structure.

Tests of Homology

In 1982, Collin Patterson published an influential paper on homology, in which he noted three different types of homology generally recognized at that time, including historical homology. In this paper, he offered a set of three tests that could be applied to any question of homology. These tests stand today as highly useful for evaluating hypotheses of homology—historical, biological, or generative. The first test is that of similarity. This has been discussed above. Most homologous structures show evidence of similar features, including developmental, topological, and morphological ones. The second test is that of congruence, which specifically applies to cases of historical homology. It specifies that the character in question be distributed in a pattern that is congruent with another, unrelated synapomorphy (advanced character). The third test, which we have not yet discussed, is a useful one to keep in mind. It is the test of **conjunction**, which states that "If two structures are supposed to be homologous, that hypothesis can be conclusively refuted by finding both structures in one organism." For example, if a particular neural cell group in one organism is proposed to be homologous to a certain neural cell group in another organism, finding the latter cell group to be present also in the first organism would nullify the hypothesis.

A Word of Caution

We need to return to the example shown in Figure 1-2 to consider one last important point. A major pitfall can arise when using cladistic analysis that we need to be aware of. This pitfall involves ignoring the presence of out-groups to

why is the traditional view of vertebrate brain evolution "from fish to man" wrong? 1) humans didn't evolve from fish 2) evolution of the brain didn't happen linearly 3) humans do not have the largest brain. what are the five parts of the brain that all vertebrates have? 1) medulla oblongata 2) cerebellum 3) mesencephlaon (tectum/colliculi suprior and inferior, tegmentum, pons) 4) diancephalon (epithalamus, hypothalamus, thalamus) 5) telencephalon (pallium/cortex, subpallium,subcortex). what is negative brain allometry? larger animals tend to have relatively smaller brains.Â This set is often saved in the same folder as Comparative Neuroanatomy: Nervous System. 46 terms. gokimgo. Comparative Neuroanatomy: Sensory Systems & Auditory System. 51 terms. @article{Farsad1996ComparativeVN, title={Comparative Vertebrate Neuroanatomy: Evolution and Adaptation}, author={Khashayar Farsad}, journal={The Yale Journal of Biology and Medicine}, year={1996}, volume={69}, pages={365 - 366} }. Khashayar Farsad. Published in. The Yale Journal of Biologyâ€¦ 1996. Immunology: A Short Course, Third Edition is an extensively revised and updated version of their previous edition. According to the authors, every chapter has been either extensively revised or rewritten since the 1991 publication of their second edition. Much of the updated information is in the real