Science and Evolution as Science

I

1 The Nature of Science and Evolution, and Evolution as Science

KEY CONCEPTS

- Science can investigate events that occurred in the past.
- Science can investigate evolution.
- The scientific method can be applied to evolution.
- Evolution is a science.
- The word *evolution* has had different meaning over time.
- Evolution acts on individuals and on populations but in different ways.
- Individuals in the same species can adapt differently to different parts of their geographical range.
- Organisms modify the environment in which they live.
- Genes are defined and studied in different ways.

Overview

Above: The wonders created by the relentless action of wind and water.

The scientific method is a universal means of proposing a hypothesis, designing experiments, collecting data to test that hypothesis, interpreting the data in the context of past knowledge, and accepting or rejecting the hypothesis. New conclusions may add evidence to support existing scientific knowledge or they may overthrow an existing theory and replace it with a new theory that changes the way we view the world. Isaac Newton's discovery of **gravitation** and Charles Darwin's discovery of **evolution by natural selection** are two examples of theories that changed our understanding of how the world and its organisms function.

Much scientific investigation relates to events that occurred in the past. The origin of the universe and how volcanoes form are two examples. Evolution as a science is no different. The science of evolution investigates past and ongoing processes concerning how organisms arise and change over time. The origin of stars and of glaciers and the process of evolution were all revealed in the same way — using the scientific method.

In addition to examining the scientific method and evolution as a science, this chapter lays out a brief history of evolution as a term and as a concept, and introduces **natural selection**, **variation**, and **inheritance** as three fundamental principles and processes underlying evolution. The different ways in which evolution "sees" individuals and populations are outlined. The nature of the unit of inheritance — the **gene** — is introduced, as is the special way in which organisms relate to their environment — the **niche**.

The Scientific Method

The essential nature of science is discovery through application of a method — the **scientific method** — that allows discoveries to be made. The discovery may be a previously unknown object — a previously unknown type of organisms from the ocean deeps — or a new explanation — how such organisms survived and evolved at depth.

Our quest for discovery, whether by the scientific method or through exploration, invention, or just plain thirst to understand the unknown, has never been better treated than by Daniel J. Boorstein in *The Discoverers,* first published in 1983.

The scientific method consists of

1. producing a hypothesis;
2. designing and performing controlled experiments or making observations that allow data relevant to the hypothesis to be collected;
3. analyzing the data in an objective way against the background of existing knowledge; and,
4. drawing conclusions that support or refute the hypothesis.

Through the repeated application of this method, science progresses by accumulating evidence consistent with one interpretation and inconsistent with others.

When possible, experimentation is an important way to test hypotheses. However, when experimentation is not possible, data can be collected and hypotheses accepted or rejected without experimental verification. The scientific method thus is applied to astronomy, geology, and past evolutionary events because the scientific method is sufficiently precise to allow explanations of past events. If those explanations contradicted present events, new hypotheses would be generated and new data obtained. As a consequence, astronomy, geology and evolution are sciences.

Careful observation, recording and systematic analysis are important ways of applying the scientific method. Comparative study of systems that are alike in many respects but differ in others is another important application of the scientific method. We thus can compare ants and termites as two types of social insects, or we can compare chimpanzees and modern humans as closely related primates. We can go further and compare ants and humans as two groups of social organisms. Through systematic application of the scientific method, unsupported hypotheses are eliminated and a single interpretation emerges as the one best explaining the data. This process may take years or centuries, as it did for the discovery of the relationship between the orbits of Earth, other planets and the Sun (FIGURE 1.1), and for the discovery of deoxyribonucleic acid (DNA) as the molecule of inheritance carrying the genetic code from generation to generation.

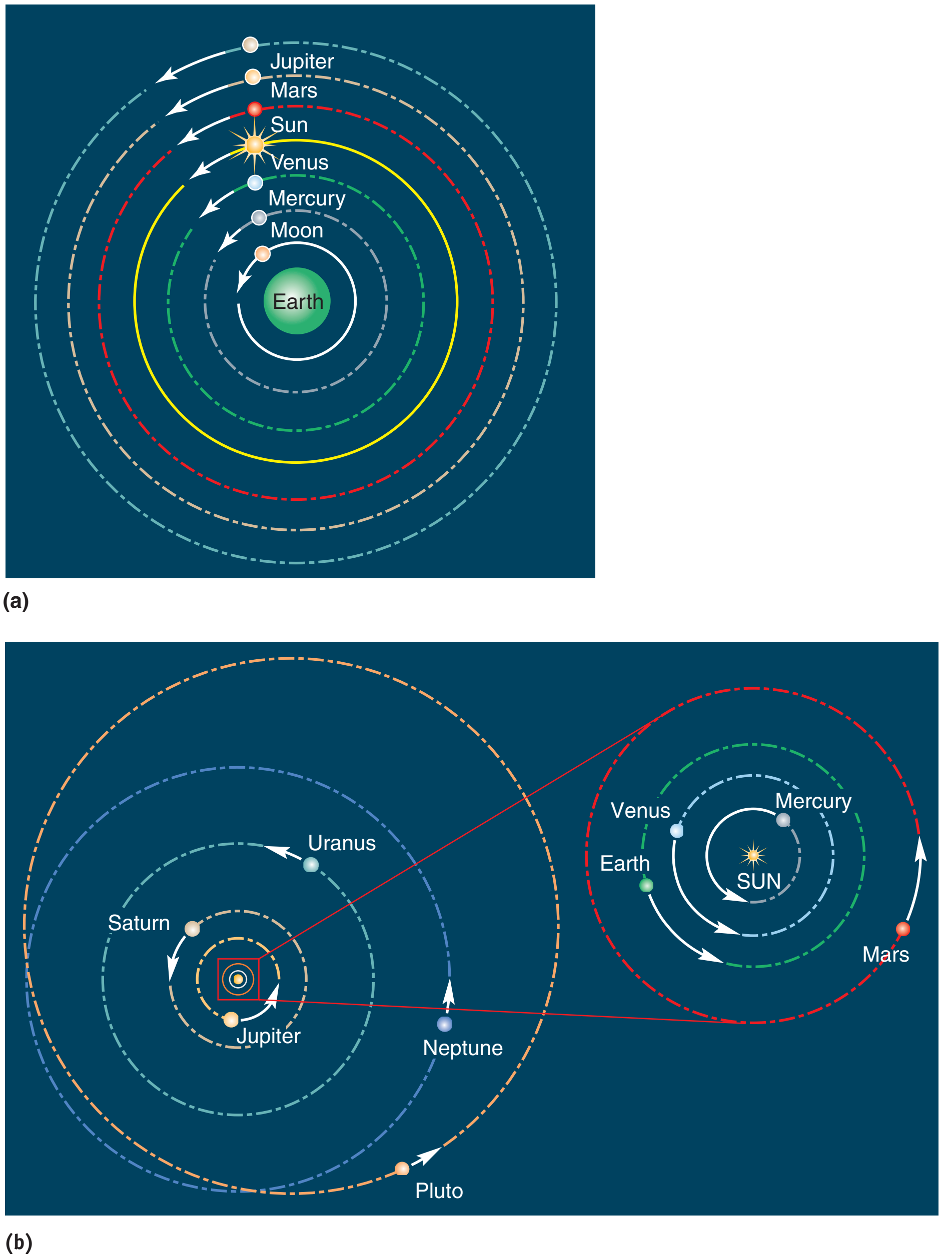


FIGURE 1.1 Two hypotheses reflecting theories of the orbits of the planets, one in which the planets orbit Earth (**a**), the other in which the planets orbit the Sun (**b**).

Other discoveries may be, or appear to be, instantaneous: The apple falling on Newton's head led him to the discovery of the law of universal gravitation; the rising level of the water in his bath led Archimedes to the discovery of the principle of buoyancy. Even such "Eureka moments" cannot be isolated from past knowledge or the way of thinking of the society in which the discoverer resides. This is so even when the discovery totally changes how we view natural phenomena, as when Albert Einstein discovered that matter and energy are not separate but interconvertible, expressed in the formula $E = mc^2$ (energy equals mass times the speed of light squared [multiplied by itself]). Even though the formula revolutionized our thinking, it did not arise in a vacuum. Earlier theories of matter and energy existed.

Archimedes' principle is that, "Any body fully or partially submerged in a fluid is buoyed up by a force equal to the weight of the fluid displaced."

Newton's law of universal gravitation: "I deduced that the forces which keep the planets in their orbs must be reciprocally as the squares of their distances from the centers about which they revolve" (Newton, 1687).

The social context in which science is conducted — indeed, whether science is conducted at all — what is considered an appropriate topic for analysis using the scientific method, how scientific knowledge is used, and the proportion of the population engaged in or benefiting from scientific discovery, vary among and within modern human societies. A century ago, psychology was regarded as "no more than" a social science (and some objected to the word science in the phrase "social science"). Today, psychologists utilize the scientific method, expect variation around the norm, propose and test hypotheses, and use sophisticated statistical methods to inform their conclusions.

Science and Events in the Past

Can we apply the scientific method to understand and explain events that happened in the past? Can we, for example, design experiments and/or collect data to investigate how Earth arose, how gravity originated, how cells evolved? Yes, we can. All sciences concerned with the past — astronomy, cosmology, geology, paleontology and evolution — make use of observations to refute or support proposed hypotheses. This entire book is devoted to obtaining scientific evidence for various aspects of evolution, not only biological evolution but evolution of the Universe, the Solar System and Earth.

Furthermore, we can gather data to explain events that occurred in the past, even if they occurred only once. The latter is of special interest in historical sciences where the emphasis may be on understanding a particular sequence of historical events rather than discovering general laws such as those of physics and chemistry. The evolutionary biologist and popularizer of science Stephen J. Gould (1941–2002) was especially prominent in promoting the view that past events condition present and future change. Topics of historical science include events that led to our solar system, to the separation of South America from Africa, and to the origin of humans, recognizing that these events are singular and may not apply to all stars, all continental separations, or the evolution of all species. Sciences that deal with the past make use of general laws such as those of gravity, mechanics and biochemistry with the aim of discovering the causes of diversity and uniqueness as well as the principles and laws that apply uniformly to all matter or all life. The ability to extrapolate from processes or events that affect all organisms — the existence of variation, mutation, changing environments — and to explain the role of past history, is central to the dynamic interdisciplinary nature of the study of evolution, and makes it a robust and testable field of inquiry. Does this make evolution a science?

Evolution as a Science

A criticism sometimes raised against evolution as a science that can be studied and understood using the scientific method, is that evolutionary explanations (hypotheses) cannot be tested and supported (or falsified) in the same way as hypotheses in physics and chemistry.

The claim is sometimes made that because evolution deals with events that occurred in the past — events that are generally impossible to repeat in a laboratory — evolutionary biology can never reach the status of the sciences of physics and chemistry. As discussed in the previous section, we can explain historical events as rationally as we explain other scientific events. In particular, evolution that occurred in the past can be observed, documented, studied and tested. Evidence to test evolutionary hypotheses exists in the fossil record, and evolution can be tested experimentally.

Ways of Knowing. A New History of Science, Technology and Medicine, by J. V. Pickstone, 2001, contains a unified argument against such criticisms in an analysis of the development of the scientific method in science, technology and medicine — an analysis described by one of the ablest historians of science and medicine, the late Roy Porter (1946–2002) as, "the most exciting synthesis we now possess."

- The sequence of primate-like hominins (humans and their closest relatives) in the fossil record supports the hypothesis that humans have a primate origin (see Chapter 19).
- Correspondence in the basic chemical sequences of myoglobin and hemoglobin, two classes of iron-containing molecules that bind and transport oxygen, supports an evolutionary relationship between them (see Chapter 8).

Because either hypothesis could be disproved by finding, for example, frog- or reptile-like hominid fossilized ancestors or by discovering a species that lacks chemical sequence similarities between myoglobin and hemoglobin, such hypotheses are scientific. The fact of past evolutionary events can be tested scientifically.

The ever-present influence of past evolutionary history is far more than a theoretical postulate. Evolution can be demonstrated experimentally. One example is when replicated populations of the fruit fly, *Drosophila melanogaster*, are returned to a common ancestral environment and allowed to breed for 50 generations. These populations undergo changes to an ancestral state, but do not all revert to the same universal state. The changes we see depend upon the particular **character** analyzed, a reflection of **mosaic evolution** in which characters in the same species evolve at different rates. This important experiment illustrates that we can demonstrate past evolutionary history on a character-by-character basis.

The terms **character(s)** and **feature(s)** are used interchangeably for any distinguishable attribute of an organism, whether morphological (blue eyes), behavioral (burrows), functional (breathes oxygen) or molecular (has the gene for hemoglobin).

In a second example described by Jeffrey Barrick and his colleagues in the journal *Nature* on October 29, 2009, all mutations occurring over 20 years (40,000 generations) in the bacterium *Escherichia coli* were recorded. After 20,000 generations, a mutation in a gene involved in repairing DNA resulted in an acceleration of the rate at which mutations became established in the populations — 45 mutations in the first 20,000 generations and 600 in the second 20,000 generations.

The properties of different hydrogen atoms can be explained on a common physical basis. The properties of different organisms — the organization and function of their component parts — only can be understood in the context of their history, which includes adjustments to specific lifestyles at particular times that influence (and have influenced) the type of change possible in the future (BOX 1.1). The adjustment of an organism to its environment (including adjustment to other organisms in that environment) is measured by the biological attribute **fitness**, which differs from organism to organism, population to population, and species to species. Nevertheless, when historical conditions are repeated, and different organisms are subjected to similar selective evolutionary forces, some common responses can be predicted; geographi-

Fitness can be defined as the measure of the ability of an individual to survive and transmit its genes (genotype) to the next generation, relative to the ability of other individuals in the same population (see Chapter 15).

BOX 1.1

Environment-Organism Interactions

Climate, terrain, prey and/or predators are often reflected in the features of organisms. If a species is distributed over a wide north–south range, adaptations in northern populations often allow us to distinguish northern from southern individuals. Adjustment to similar environments can bring forth parallel evolutionary changes in different species, as seen on a local scale, as in cave-dwelling animals (see Figure 1.2) or on a continental scale, as seen in American and Australian mammals (see Figure 6.6).

A well-known pattern of inherited response to a specific environment is the relationship in warm-blooded vertebrates between body size and average temperature, a relationship known as **Bergmann's rule.** Individual members of a species in cooler climates tend to be larger than individuals of the same species in warmer climates. This relationship exists primarily because bodies with larger volumes have proportionately less exposed surface area than do bodies with smaller volumes. Because heat loss relates to surface area, larger bodies can retain heat more efficiently in cooler climates. Smaller bodies can eliminate heat more efficiently in warmer climates.

Patterns of adaptation also can be detected in the fossil record. Body size of bushy-tailed woodrats (*Neotoma cinerea*) closely follows climatic fluctuations from the time of the last glacial period about 25,000 years ago to the present with larger body size in colder periods and smaller body size in warmer periods. Similarly, among populations of modern humans, we can compare thick-chested, short-limbed Inuit in the north with slender Africans in equatorial regions.

Karl Georg Lucas Christian Bergmann (1814–1865), a German anatomist, physiologist and biologist developed this rule in 1847.

cally widely separated populations and species of fish, amphibians, spiders and insects adapted to cave conditions, consistently show rudimentary eyes and loss of pigmentation (FIGURE 1.2). Predictability is an essential element of a scientific theory.

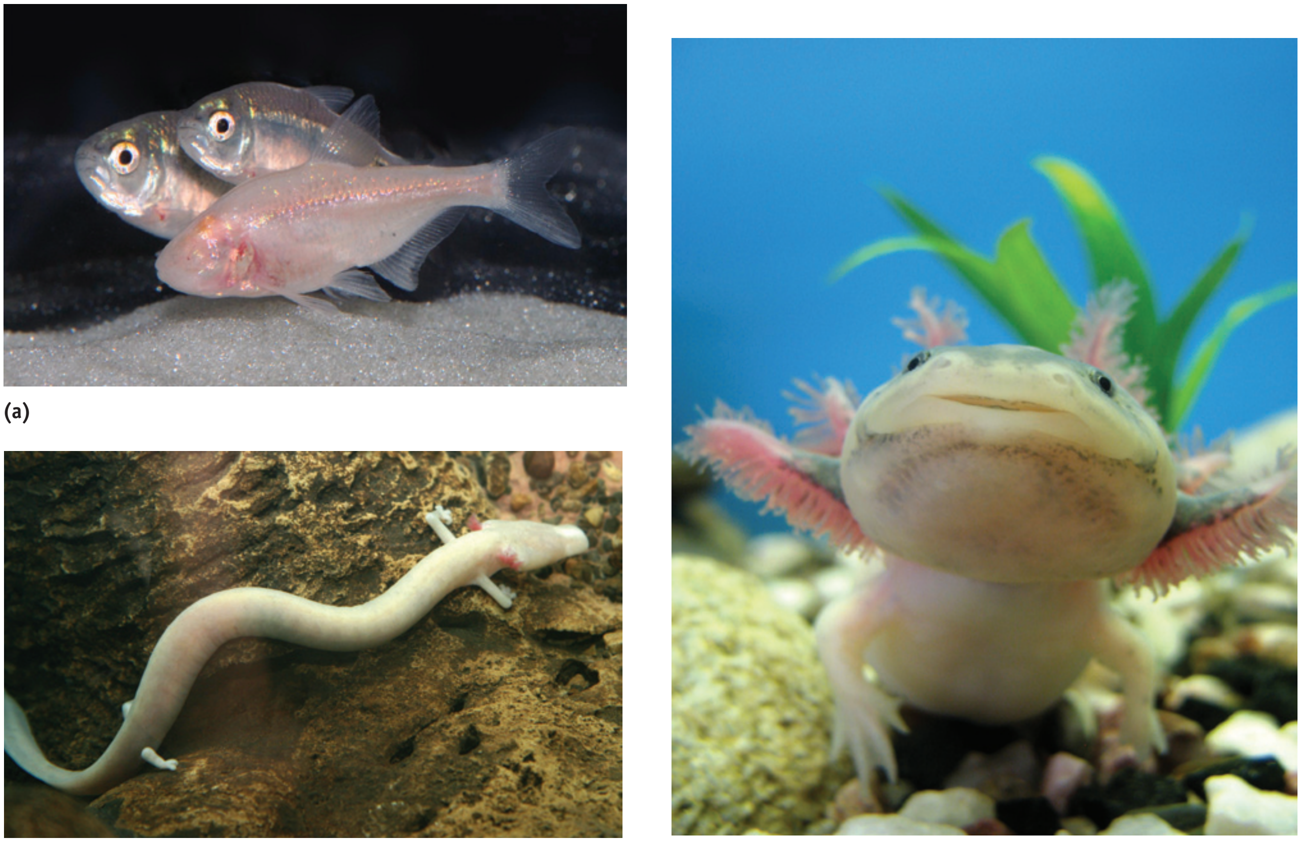
Evolution as Only a Theory

It is sometimes proposed that because we cannot see evolution happening, evolution will always be a theory and not a "fact."

Any of the foundational theories in science — the atomic theory, the theory of relativity, the universal theory of gravitation — account for events we cannot see in everyday life. Nevertheless, we experience the effects of these forces of nature daily. The atomic theory is accepted by scientists because it explains chemical reactions, although atoms are not visible to the naked eye. The universal theory of gravitation is accepted as explaining why objects remain tethered to Earth even though we cannot see the gravitational waves that cause the effect.

Similarly, the theory of evolution accounts for the historical sequence of past and present organisms by explaining their existence in terms of factors that cause changes in the genetic inheritance of organisms over time.

The facts of evolution come from the anatomical similarities and differences among organisms, the places where they live, the metabolic pathways they use, the embryological stages through which they develop, the fossil forms they leave behind, and the genetic, chromosomal, and molecular features that relate them. The theory of evolution (inherited changes over time) is a coherent explanation of the historical course of biology (facts) in terms of natural processes, such as mutation, selection, genetic drift, migration and altered gene regulation (see Chapters 12–15). These



(a)

(b)

(c)

FIGURE 1.2 Adaptations to life in the dark. (**a**) Surface-dwelling (eyed, pigmented) and cave-dwelling (blind, non-pigmented) forms of Mexican cave fish. (**b, c**) Blind and non-pigmented (albino) cave-dwelling axolotls shown from the top (**b**) and from the front (**c**). Note prominent gills in (**c**).

explanations are consistent with all observations made so far. Such an approach is not different from the *fact* that an apple dropped on Newton's head, an event Newton explained by developing a *theory* of gravity.

For our purposes, an appropriate way to present the science of evolution is to document the facts of evolution — the historical record available to us in fossils, molecules, and living organisms — and to seek to understand, through application of the scientific method, the evolutionary processes by which the historical record of evolutionary change came about.

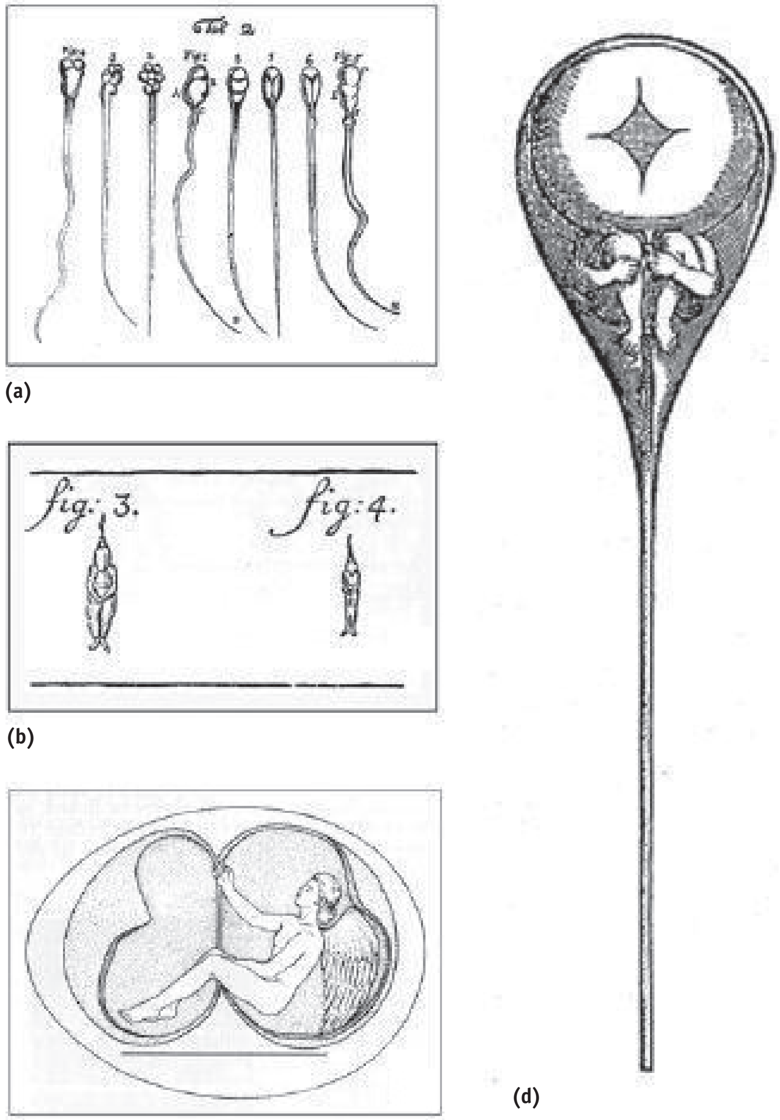
A good place to begin is to consider the meaning of the word *evolution*.

Evolution: an Overview of the Term and the Concept

The word *evolution* had different meanings in the past to the way we use the word today.

Evolution as the Development of an Individual

The first meaning — evolution as the development of an organism — reflects the original 17th century definition, when the word evolution (from the Latin *evolutio*, unrolling) was used for the unfolding of the parts and organs of an embryo to reveal



(a) (b) (c) (d)

FIGURE 1.3 Four views of adult humans as preformed within sperm (**a, b, d**) and within the body of the female (**c**).

a preformed body plan (FIGURE 1.3, and see Box 7.2). Here evolution applies to individuals. Evolution as development can be traced to the Swiss botanist, physiologist, lawyer, and poet, Albrecht von Haller (1708–1777), who in 1774 used evolution to describe the development of the individual in the egg:

> But the 17th century theory of evolution proposed by Jan Swammerdam and Marcello Malpighi prevails almost everywhere: all human bodies were created fully formed and folded up in the ovary of Eve and that these bodies are gradually distended by alimentary humor until they grow to the form and size of animals (Haller, 1774, cited from Adelmann, 1966, pp. 893–894).

Another Swiss lawyer, Charles Bonnet (1720–1793), further solidified evolution as preformation in his theory of encapsulation (*emboîtment*). Bonnet wrote that all members of all future generations are preformed within the egg: cotyledons within the seeds of plants; the insect imago inside the pupa; future aphids in the bodies of parthenogenetic female aphids, and so forth (see Box 7.2).

Evolution as the Transformation of Populations between Generations

Only in the 19th century did evolution come to mean transformation of a species or transformation of the features of organisms, both of which occur within populations, not individuals (see the latter part of this chapter). It is as transformation that we use the term evolution in a wide variety of contexts other than biological evolution: the evolution of an argument, the evolution of the computer, the evolution of heart valves. Charles Darwin (1809–1882), who proposed a theory of evolution as descent with modification from generation to generation (see Chapter 6), provided only one figure of the process in his book titled, *On the Origin of Species* (FIGURE 1.4) and only used the word *evolution* once, as the last word of the book.

> There is grandeur in this view of life, with its several powers, having been originally breathed by the Creator into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved.

Given the nature of the evidence they discovered and worked with, geologists were among the first to use the term evolution for transformation of species and progressive change through geological time. Robert Grant (1793–1874), the first Professor of Comparative Anatomy at University College London, used the term evolution in

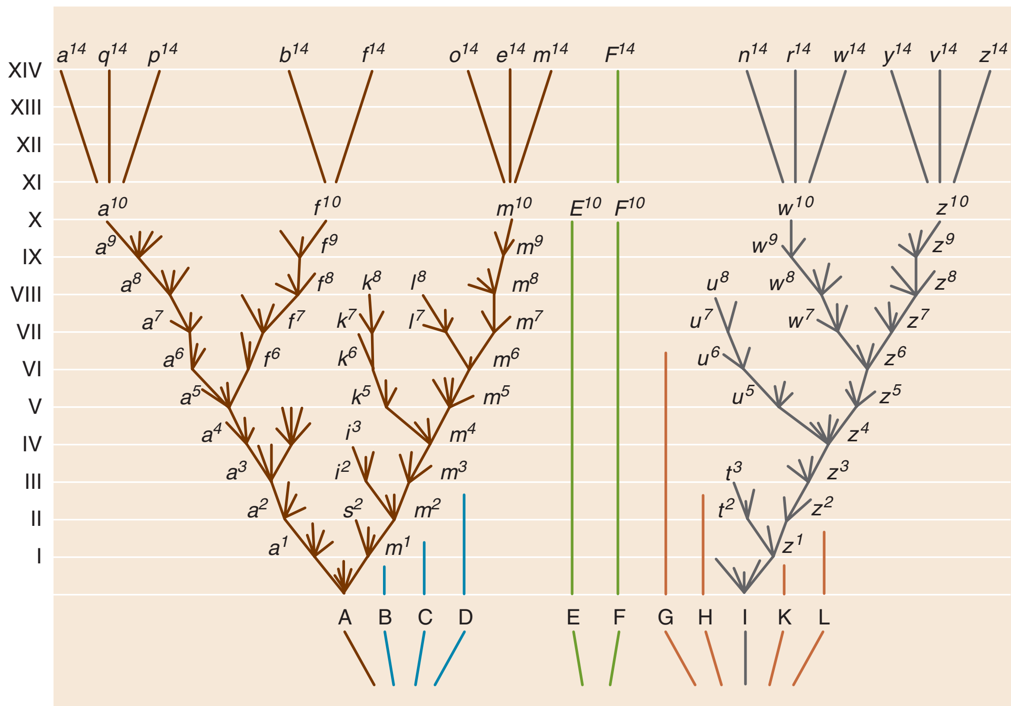


FIGURE 1.4 The illustration Charles Darwin used in his book, *On the Origin of Species* to represent progressive divergence within individual species (a^1–a^{10}; m^1–m^{10}; z^1–z^{10}) and the splitting of species into multiple lineages (S^2, i^2, i^3 from m^1 and m^2, for example).

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1826 for the gradual origin of invertebrate groups. Charles Lyell (1797–1875), one of the founders of geology and a close friend of Charles Darwin, used evolution in 1832 for gradual improvement associated with the transformation of aquatic to land-dwelling organisms: "the testacea [shelled animals] of the ocean existed first, until some of them, by gradual evolution, were improved into those inhabiting the land." Even here, an argument can be made that both Grant and Lyell were using evolution in the sense of change during development.

Transformation and Descent with Modification: 1859–Now

This section contains a very brief overview of major changes in the way evolution has been studied, changes that reflect advances in understanding biology at deeper and deeper levels.

From the publication of *On the Origin of Species* in 1859 until 1900, evolution was studied as

- the origination and transformation of species (one species of horse → another species of horse);
- the transformation of major groups/lineages of organisms and the search for ancestors (invertebrates → vertebrates; fish → amphibians); and
- the transformation of features such as jaws, limbs, kidneys, nervous systems within lineages of organisms.

Origination is used throughout the text in the same sense as in the *Oxford English Dictionary*'s definition of evolution, that is, for the first appearance or origin of.

A new genetic approach to evolution followed the rediscovery in 1900 of Gregor Mendel's experiments breeding pea plants and the development of Mendelian genetics (see Chapter 7). Geneticists began to work with inbred lines of organisms, with animals maintained in laboratories or with plants in greenhouses. The discovery of mutations — changes in a sequence of DNA — further focused attention on genes as fundamental to the evolutionary process.

Two discoveries in the early 20th century placed the emphasis on mechanisms of evolutionary change within populations. In 1908, Geoffrey Hardy (1877–1947) in England and Wilhelm Weinberg (1863–1937) in Germany independently derived a formula for calculating gene frequencies in populations under natural selection (soon named the *Hardy-Weinberg law* or *principle*; see Chapter 14). In 1918 the brilliant English mathematician R. A. Fisher (1890–1962) fused Mendelian inheritance with population genetics (see Chapter 7). By the 1930s, speciation was seen as resulting from genetic changes within a lineage as reflected in changes in gene frequency (see Chapter 14). In the 1940s, the synthesis of population genetics, systematics, and adaptive change forged what we know as the **modern synthesis** or the **modern evolutionary synthesis.**

Fisher, along with his fellow Englishman J. B. S. Haldane (1892–1964) and the American geneticist Sewall Wright (1889–1988) are the acknowledged founders of the modern synthesis of evolution based on population genetics (see Chapter 14).

Population genetics does not provide a complete theory of evolution, however. **Evolution now is recognized as hierarchical**; genes, structures, populations, species and ecosystems all evolve. To a considerable extent hierarchical evolution is a reflection of the hierarchical organization of life itself, a concept outlined in Box 4.1.

Perhaps the most well recognized hierarchy of life is that from

genes → molecules → organelles → cells → tissues → organs → organisms → populations → species

Hierarchical systems aid and stabilize evolution, enabling organisms to evolve, incorporate and maintain new functional properties. A hierarchical approach to understanding evolution has emerged and consolidated over the past 40 years, replacing or running parallel with the reductionist approach, which proposes that explanations for events on one level of complexity can and should be reduced to (deduced from) explanations on a more basic level. The biological hierarchy extends across many levels, from atoms to molecules to cells to tissues to organs to individuals to populations to species to cultures, each with specific functional properties.

Why does evolutionary biology not reduce to a reductionist approach? In no small part we require a hierarchy of mechanisms to explain emerging properties and increasing complexity because properties at one level are insufficient to explain properties at higher level(s). Evolution operates on at least four levels.

1. The **genetic** level, through mutations, changes in gene number and regulation, and changes in gene networks.
2. The **organismal** level, seen as individual variation and differential survival through adaptation and the evolution of new structures, functions and/or behaviors.
3. Changes in populations of organisms, operating through mechanisms that limit gene flow between populations.
4. The subsequent origin, radiation and adaptation of **species**.

From this list you may have inferred that the term *gene* (*genes*) must be being used differently at levels 1 and in 3: a unit that mutates (1) and a unit that can flow through a population (3). Current concepts of what we mean by a gene are outlined in BOX 1.2.

Because evolution acts at genetic, organismal and population levels, an ideal definition should reflect evolution at all three levels. In many respects, Darwin's phrase descent with modification, illustrated in Figure 1.4, remains an inclusive definition of biological evolution. Evolution as descent with modification encompasses evolutionary change at genetic, organismal and population levels, although integration of all three levels is required to fully comprehend evolution.

BOX 1.2
What Is a Gene?

It may surprise you to find that there are several definitions for the basis unit of inheritance, the *gene*. In large part, this is because different specialists study the gene in different ways and at different levels. Reflecting these different approaches, a gene can be defined as one or more of the following (an example of each is provided).

- a region of DNA, the activation of which leads to the formation of a feature or character (the gene for blue eyes);
- a region of DNA, the activation of which leads to the formation of a protein or RNA (the gene for the protein collagen);
- a region of DNA encompassing coding and non-coding segments (exons and introns) (a definition that applies only to eukaryotes);
- a unit of inheritance located on a chromosome (the gene for muscular dystrophy in humans mapped to chromosome 9);
- a set of nucleotides reliably copied and transferred from generation to generation (the unit of heredity).

How our views of evolution originated and have changed, and how evolution operates at the three levels of genes, organisms and populations are the topics of this book. Some themes that will emerge are

- We cannot predict the continued evolutionary success of a particular group on the basis of its dominance at a particular earlier time.
- Crucial evolutionary advantages may accrue to groups that already have characteristics adaptable to new circumstances.
- Long-term evolutionary replacement among groups is not predictable.
- New modes of biological organization can enhance group survival.
- New levels of organization occur because of coordinated changes in many traits over long intervals of time.
- Once such new levels have been attained, widespread radiation often begins.
- Extinction is common if not inevitable because of constraints on the potential of a species to adapt to large or rapid environmental changes.

Individuals, Populations and Evolution

Natural selection reflects the differential survival and reproduction of individual organisms with particular features. Differential survival and reproduction are mechanisms of evolution. Natural selection is the outcome. Although selection reflects the fate of individuals, the response to selection lies in the information content of the genomes of all individuals in the population, information that can change because of mutation or random processes (see Chapters 6, 12, and 15).

It is important to have a clear view of individuals and populations with respect to evolution (TABLE 1.1), not merely because use of the word evolution has shifted

TABLE

1.1 Comparison of Characteristics of Individuals and Populations

Characteristic	Individual	Population
Life span	One generation	Many generations
Spatial continuity	Limited	Extensive
Genetic characteristics	Genotype	Gene frequencies
Genetic variation	Expressed in one lifespan	Expressed in evolutionary change
Evolutionary characteristics	No changes, because an individual has only one genotype and is limited to a single generation	Can evolve (change in gene frequency), because evolution occurs between generations
Selection	Operates on phenotype in one generation	With mutation, leads to change in genotype from generation to generation
Mutation	Somatic influence individual	Gametic inheritance/gametic mutation transferred through reproduction
Variation	Phenotypic not inherited Genotypic transferred through reproduction	Genotype inherited

from individuals to populations, but because individuals respond to selection but populations evolve. Because this is important, the essential differences between individuals and populations as far as evolution is concerned are outlined as 12 points below. Each is presented as a statement of fact. You can regard them as conclusions, the evidence for which is provided in the remainder of the book. You also can read them as a summary of the evolutionary process.

1. Organisms exist as **individuals**. Individual multicellular organisms (animals, plants, fungi) develop, grow, mature, reproduce, senesce (in most cases) age and die. Individual unicellular organisms (bacteria in everyday language) reproduce and die.
2. **Natural selection** acts on individuals but individuals do not evolve. Individuals pass on their genes (see Box 1.2) along with mutations in those genes to individuals of the next generation.
3. In most species of uni- and multicellular organisms, individuals exist in **populations** that inhabit discrete ecological **niches** (BOX 1.3). Populations of multicellular organisms have a structure that usually includes different age classes of a single generation and often includes overlapping generations, especially in species with short reproductive cycles and long lives.
4. Populations of a sexually reproducing organism consist of individuals that are **not identical** to one another — they are not clones. In a population of a species in which individuals reproduce asexually, for example by budding or fission, all individuals in a population may be identical.
5. **Resources are often limited** with the consequence that not all individuals in a population will survive to reproduce and contribute offspring to the next generation.
6. **Populations do not reproduce, individuals reproduce.** Populations pass to the next generation(s) a gene pool from some of the individuals who reproduced.
7. **Variation** is an essential prerequisite for evolution to act: natural selection allows some variants to survive and others not.
8. Because resources are limited, natural selection results in survival to the next generation through reproduction of the individuals (variants) that are best suited to the conditions of their existence.
9. Because the genetic background of individual sexually reproducing organisms differs, those that are selected on the basis of their fit to the environment will preferentially pass their genes to the next generation. Those individuals that are less well fitted to the environment will tend not to pass their genes to the next generation.
10. Because of differential reproduction the genetic composition of a population will change gradually from generation to generation. Genetic changes also accumulate because of random **drift** of genes from generation to generation and/or because spontaneous **mutations** change the genetic composition of populations.
11. Populations may **subdivide** into smaller groups. Differences that emerge in the subgroups can provide the basis for speciation.
12. Populations or subsets or populations may "**crash**" or become **extinct** because of environmental catastrophes.

In one species of frog, the adults die soon after producing their offspring whose embryonic life is prolonged. Consequently, for much of the year this species exists only as embryos.

BOX 1.3

What Is a Niche?

Niche or **ecological niche** is defined in various ways in the literature of ecology and evolutionary biology. Most definitions emphasize the role of the organism (population, species) in its environment, that is, the niche is not defined as a place but by a set of interactions. Each has a particular emphasis, illustrated by the italicized words in the following definitions.

1. Where a living thing *is found* and what *it does there* (FIGURE B1.1)
2. The *role* of an organism in an ecosystem
3. The *role* of a species within a community
4. All the *functional roles* of an organism in a biological community
5. A *unique ecological role* of an organism in a community
6. The environmental *habitat* of a population or species, the *resources* it uses and its *interactions* with other organisms
7. The *status* of an organism within its environment and community as it affects the survival of the species
8. The *role* or functional position of a species *within the community* of an ecosystem
9. The physical and functional *role* of an organism *within an ecosystem*

FIGURE B1.1 Several species of lichens (distinguishable by color, shape, size and habit) occupy and utilize different niches on the rock outcrop.

As you can see, most definitions consider the niche in relation to organisms, although definitions 3 and 8 emphasize the species. All except 1, 6 and 7 use *role* as the primary aspect of the definition. Number 4 emphasizes functional role, number 5 ecological role, and number 9 physical and functional roles. Numbers 1 and 6 are the most general or all encompassing; number 7 is the most specific (it ties niche to species survival). Four uses the word *community* without defining what a community is. Number 6 uses *habitat* without a definition. However defined, ecological niches are now being reconstructed in phylogenetic analyses and shown to be conserved over long periods of evolutionary time (Donoghue, 2008).

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Recommended Reading

Allen, G., and J. Baker, 2003. *Biology: Scientific Process and Social Issues*. Wiley Blackwell, Hoboken, NJ.

Appleman, P. (ed.), 2001. *A Norton Critical Edition. Darwin: Texts, Commentary*, 3d ed. Philip Appleman (ed.). W. W. Norton, New York.

Barrick, J. E., S. Y. Dong, S. H. Yoon, et al., 2009. Genome evolution and adaptation in a long-term experiment with *Escherichia coli*. *Nature*, 481, 1243–1247. (See pp. 1219–1221 for commentary.)

Biological Sciences Curriculum Study (BSCS) contains much on evolution, including a virtual tour activity of the Galapagos Islands that allows computer-based collection and analysis of organisms. See http://www.bscs.org/.

Boorstein, D. J., 1983. *The Discoverers*. Random House, New York.

Bowler, P. J., 1996. *Life's Splendid Drama: Evolutionary Biology and the Reconstruction of Life's Ancestry, 1860–1940*. The University of Chicago Press, Chicago.

Bowler, P. J., 2003. *Evolution: The History of an Idea*, 3d ed. University of California Press, Berkeley, CA.

Donoghue, M. J., 2008. A phylogenetic perspective on the distribution of plant diversity. *Proc. Natl. Acad. U.S.A.*, **105**, 11549–11555.

Mayr, E., 2001. *What Evolution Is. With a Foreword by Jared Diamond*. Basic Books, New York.

Pickstone, J. V., 2001. *Ways of Knowing. A New History of Science, Technology and Medicine*. The University of Chicago Press, Chicago.