PART 1

Evolution and Species

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CHAPTER 1

Intellectual Origins of the Theory of Biological Evolution

CHAPTER SUMMARY

Many intellectual threads are woven into the fabric of the modern theory of evolution, a theory that requires recognition that Earth is ancient, that all organisms share a common inheritance, and that natural events can be explained by discoverable natural laws. It took a long time for the concept of change of species over time—evolution—to take hold. Idealistic philosophies that saw species as unchangeable and arranged in a hierarchical order from most imperfect to most perfect (expressed as the *Great Chain of Being*) discouraged any thought of species change. Widespread belief in the spontaneous generation of organisms hindered any thought that one organism could be transformed into another. Only in the late sixteenth and early seventeenth centuries did the recognition of inexplicable gaps in the chain of nature prompt European philosophers to propose that the universe might go through successive intermediate stages on the way to perfection. Not until the mid-nineteenth century, when Charles Darwin and Alfred Russel Wallace proposed a mechanism—evolution by natural selection—was species change tied to interactions between organisms and to interactions between organisms and their environment. It was then that the science of evolutionary biology was born.

NATURAL SELECTION *is the sum of the survival and fertility mechanisms that affect reproductive success, as measured by the differential survival and reproduction of individual organisms with particular features.*

UNIVERSAL PROPERTIES OF ORGANISMS

All organisms are bound together by three essential, shared universal properties:

1. A common mechanism of inheritance based on the genetic code carried in DNA.
2. An organization built upon cells.
3. The accumulation of inherited changes over billions of years of existence on Earth.

Only after Darwin and Wallace developed and published their theories of **species transformation in response to natural selection** did biological evolution become an acceptable scientific concept. Acceptance that organisms could change over time and that new types of organisms could arise from existing ones revolutionized the way we viewed the world and the way we understood and explained natural phenomena. Neither Darwin nor Wallace coined the term *evolution,* nor was either of them the first to propose that organisms changed over time. This chapter looks at the word and concept of '*evolution*' before Darwin and Wallace when the idea of evolution was applied to the **development of individual organisms** and not for transformation between generations.[1] We then turn to the concept **of evolution as transformation of species between generations**. A brief history of evolutionary views before Darwin and Wallace is followed by an outline of the evolutionary theory they proposed, and a discussion of how that theory has matured over the past 150 years. The chapter ends by discussing how the **theory of evolution is supported by the science of evolutionary biology**.

EVOLUTION AS DEVELOPMENT OF INDIVIDUALS

> *Evolution*. **1** the process by which different living organisms are thought to have developed or diversified from earlier forms during the history of the earth. **2** the gradual development of an organism, especially from a simple to a more complex form: *the forms of written language undergo constant forms of evolution.* **3** *Chemistry* the giving off of a gaseous product, or heat. **4** a pattern of movements or maneuvers: *silk ribbons waving in fanciful evolutions.* **5** *Mathematics, dated* the extraction of a root from a given quantity. (*Oxford Dictionaries Online,* Copyright ©, 2012).

As this dictionary definition indicates, the word evolution has many different meanings. The concept of evolution can be applied to a wide variety of phenomena; the evolution of an argument, the evolution of the computer, the evolution of heart valves . . .

Using "evolution" to describe the development of an organism stems from the original seventeenth century use of the word. It began with the Latin term *evolutio*, which means unrolling, and was used to describe the unfolding of the parts and organs of an embryo to reveal a preformed body plan. An example would be the (mistaken) belief that a caterpillar "unfolds" into a butterfly as it emerges from the chrysalis (**FIGURE 1.1**), much as the shape of an umbrella is revealed when it is unfolded. Only in the nineteenth century did evolution come to mean transformation of a species or transformation of the features of organisms between generations.

Evolution as embryonic development can be traced to the Swiss botanist, physiologist, lawyer, and poet Albrecht von Haller (1708–1777). In Haller's time, it was presumed that the adult human was preformed in the egg. In 1774, Haller used evolution to describe the preformed development of the adult in the egg: "But the theory of evolution proposed by Swammerdam and Malpighi prevails almost everywhere . . . that there is in fact included in the egg a germ or perfect little human machine . . ."[2]

[1] Bowler (2003) and Hall and Olson (2003) are good source books for changing views of evolution.
[2] Haller (1774) cited from H. B. Adelmann, 1966, *Marcello Malpighi and the Evolution of Embryology.* Cornell University Press, Ithaca, NY, pp. 893–894.

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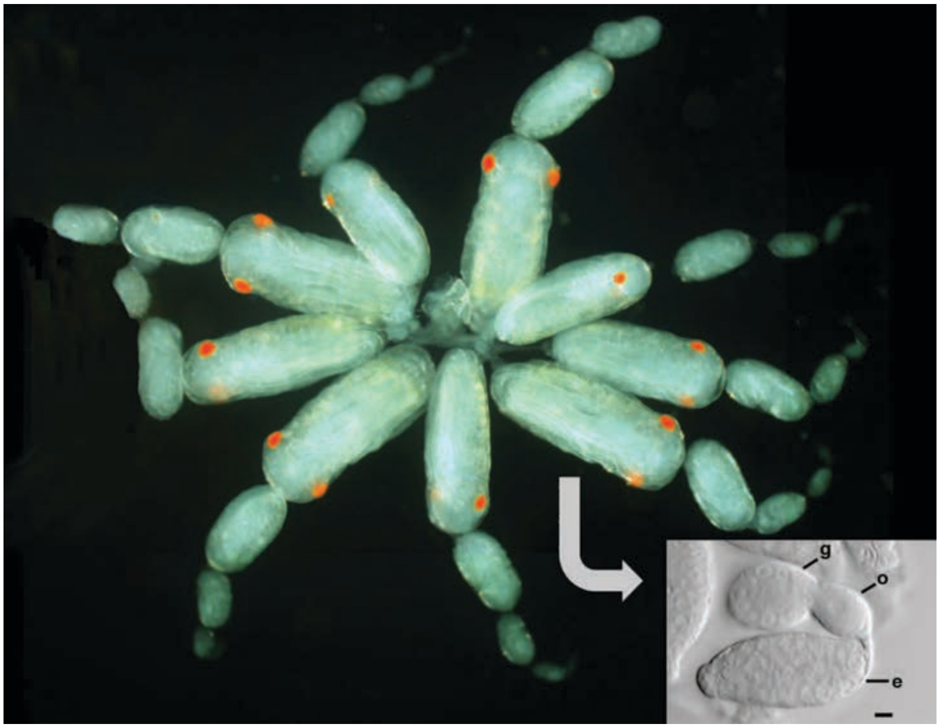
FIGURE 1.1 The butterfly that appears to "unfold" from the chrysalis has, in fact, undergone a metamorphosis from a pupal stage.

Another Swiss naturalist and philosopher, Charles Bonnet (1720–1793), built on and developed this concept of **preformation**. Bonnet wrote that *all members of all future generations* are preformed within the egg: cotyledons within the seeds of plants; insect imagos inside pupae; future aphids in the bodies of parthenogenetic female aphids (**FIGURE 1.2**).[3] Some preformationists like Bonnet (now known as *ovists*) proposed that the miniature adult was contained within the egg. Others (now known as *spermists*



(a) (b)

Courtesy of Gregory Davis, Bryn Mawr College

FIGURE 1.2 The ovaries of a female pea aphid (*Acyrthosiphon pisum*) spread out **(a)** to show embryos in various stages of development from the oldest (with orange eyespots) at the center to the youngest at the distal tips of each ovariole. **(b)** Dissection of one of these older embryos reveals that it possesses ovaries in which each ovariole contains an embryo (e), a developing oocyte (o) and an associated germarium (g) containing nurse cells and future oocytes.

[3] As you can see from Figure 1.2, "seeing" generations of embryos in female aphids in the eighteenth century would have been quite a challenge. My thanks to Greg Davis for the superb specimen shown in Figure 1.2.

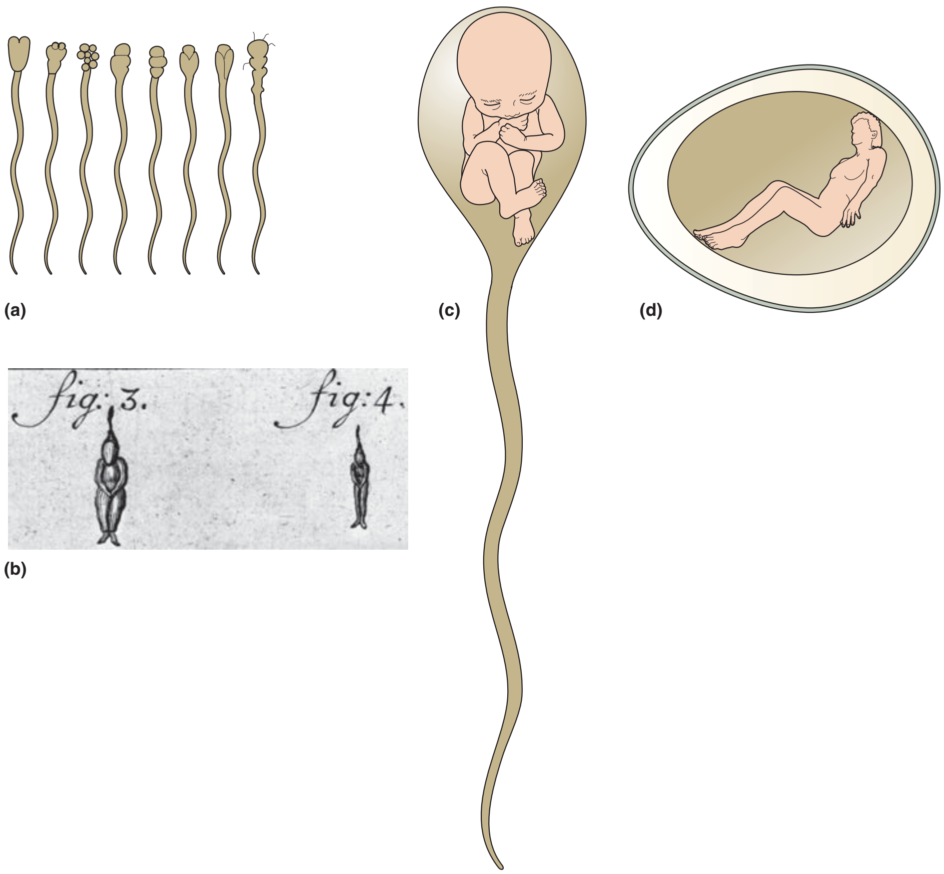


FIGURE 1.3 Four views of adult humans as preformed within sperm **(a, b, c)** and within the body of the female **(d)**.

[(a) Adapted from Antoni van Leeuwenhoek. Philosophical Transactions, 1678; (b) Courtesy of National Library of Medicine; (c) Adapted from Nicholas Hartsoeker; (d) Adapted from Needham, J. *History of Embryology*. Cambridge University Press, 1959.]

or animalculists) proposed that the adult in miniature was contained within the male seminal fluid. Indeed, they "saw" and drew adults within sperm (**FIGURE 1.3**). In its most highly developed form, preformationism held that the initial member of a species had within it the preformed "germs" of ***all* future generations**; Eve's ovaries contained the entire preformed human species nested like an infinite set of Russian dolls (**FIGURE 1.4**). Preformationism, therefore, reinforced the fixity of species and left the origin of species to an unknowable creation and/or creator.

FIGURE 1.4 Russian dolls illustrate nesting.

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EVOLUTION AS SPONTANEOUS GENERATION

From the 1700s until the middle of the nineteenth century, it was a common belief that, although most large organisms reproduced by sexual means, smaller organisms arose spontaneously from mud or organic matter. According to some folklore, when larger organisms died, they decomposed into smaller ones. Over 400 years ago the Belgian physician and chemist Johann van Helmont (1577–1644) offered a classic expression of this belief of **spontaneous generation**:

> If you press a piece of underwear soiled with sweat together with some wheat in an open mouth jar, after about 21 days the odor changes and the ferment, coming out of the underwear and penetrating through the husks of wheat, changes the wheat into mice. But what is more remarkable is that mice of both sexes emerge, and these mice successfully reproduce with mice born naturally from parents . . . But what is even more remarkable is that the mice which come out of the wheat and underwear are not small mice, not even miniature adults or aborted mice, but adult mice emerge!

Two serious and somewhat contradictory obstacles to the development of evolutionary concepts therefore prevailed at this time:

- The concept of species constancy raised the question of the origin of species, but insistence on species fixity prevented any consideration of transformations between species.
- Acceptance of spontaneous generation seemed contrary to species fixity and cast doubt on any permanent continuity between organisms.

If species could arise *de novo* at any time or be capriciously changed into another species could there ever be a rational mechanism to explain the origin or sequence of appearance of species? In fact, experiments disproving spontaneous generation were published as early as during the seventeenth century as these contradictions began to be considered (**BOX 1.1**).

EVOLUTION AS TRANSFORMATION BETWEEN GENERATIONS

Not surprisingly (in hindsight), and given the nature of the fossil evidence discovered in the 1820 and 1830s, geologists were among the first to use the term evolution for the transformation of species and for progressive change through geological time.

One of the foremost naturalists, anatomists and geologists in Great Britain in the early nineteenth century was Robert Grant (1793–1874). Grant used the term evolution in 1826 to describe the gradual (and progressive) origin of invertebrate groups in successive strata of rock that "have evolved from a primitive model" by "external circumstances." Charles Lyell (1797–1875) used evolution in the second volume of *Principles of Geology* (1832) to illustrate gradual "improvement" of aquatic organisms to land-dwelling organisms recorded in the fossil record: "[shelled invertebrates] of the ocean existed first, until some of them, by gradual evolution, were *improved* into those inhabiting the land."[4] However, after Darwin published his theory of evolution, Lyell was one of the few geologists who did not embrace Darwin's theory but maintained that the distribution of organisms on Earth was explained by the geological history of the Earth.

[4] R. E. Grant, 1826. Observations on the nature and importance of geology. *Edinburgh New Philos. J.* **14**, 270–284; C. Lyell, 1830–1833. *Principles of Geology, Being an Attempt to Explain the Former Changes of the Earth's Surface by References to Causes Now in Operation.* J. Murray, London. (The quotation is from volume 2, page 11.) Both Grant and Lyell supported Lamarck's theory of evolution.

BOX 1.1 Early Experiments Disproving Spontaneous Generation of Insects

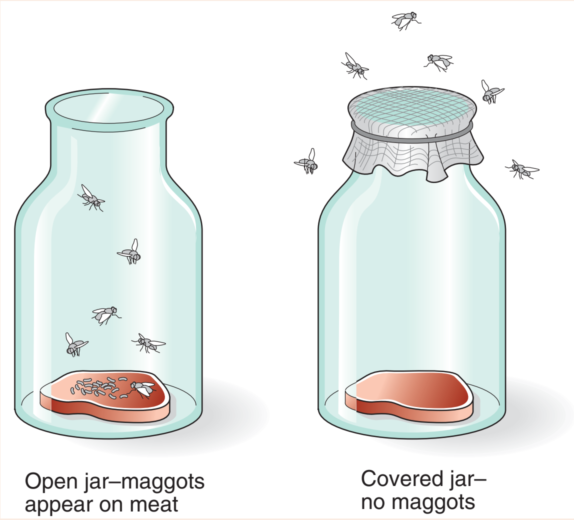
A number of seventeenth and eighteenth century experimentalists showed that spontaneous generation of insects does not occur.

In 1668, the Italian physician, Francesco Redi (1621–1697), who is credited with introducing controlled experiments to the study of spontaneous generation, demonstrated that maggots (larvae) arise only from eggs laid by flies, and that flies arise only from maggots.[a] Maggots and flies appeared within a few days after Redi placed meat in a glass jaw open to the air. If the jar was covered with gauze, adult flies did not enter the jar and lay their eggs, and maggots and flies did not appear (**FIGURE B1.1a, b**). A year later, the Dutch microscopist Jan Swammerdam (1637–1680) showed that the insect larvae found in the abnormal swellings (galls; **FIGURE B1.2**) of plants and trees arise from eggs laid by adult insects (**FIGURE B1.1c, d**).

Within a century, further experiments demonstrated that even the appearance of the microscopic "beasties" in decaying or fermenting solutions and broth observed by Antony van Leeuwenhoek (1632–1723)—another Dutch microscopist and the discoverer of microbes—could be explained as originating

Courtesy of National Library of Medicine

(a)



(b)

(c)

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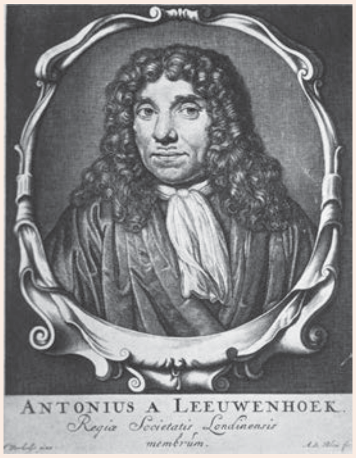
(d)

FIGURE B1.1 Spontaneous generation in the late seventeenth century. Francesco Redi **(a)** showed that maggots did not arise in jars covered with gauze **(b)**. Jan Swammerdam demonstrated that insect larvae in galls **(c)** arise from eggs laid by adult insect **(d)**. Antony van Leeuwenhoek **(e)** used his invention of a microscope **(f)** to demonstrate that microscopic organisms that appeared in broth originated from previously existing particles.

[(c) Courtesy of Dr. Tommi Nyman, Department of Biology, University of Eastern Finland.]

[a]F. Redi (1668). *Esperienze Intorno alla Generazione degl'Insetti (Experiments on the Generation of Insects)*, Florence.

BOX 1.1 Early Experiments Disproving Spontaneous Generation of Insects (Cont...)



Courtesy of National Library of Medicine

(e)

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(f)

from previously existing particles (**FIGURE B1.1e, f**). An Italian physiologist, Lazzaro Spallanzani (Abbé Spallanzani, 1729–1799) heated various types of broth in sealed containers and observed no growth of tiny organisms. Only when the containers were open to airborne particles did organisms appear and grow. Spontaneous generation as a hypothesis for the origin or transformation of life was on the way out, although it was not abandoned until the crucial nineteenth century experiments of the French chemist and microbiologist Louis Pasteur (1822–1895) and the English physician and man of science John Tyndall (1820–1893). As with many discoveries in science, Pasteur's evidence came incidentally, in his case, from experiments to understand the fermentation process used in making beer and wine. Nothing grew when Pasteur sealed broths of beer in airtight glass vessels, further disproving the idea of spontaneous generation.[b]

[b]See J. Farley, J., 1977. *The Spontaneous Generation Controversy from Descartes to Oparin.* The Johns Hopkins University Press, Baltimore, MD, for the definitive treatment of spontaneous generation.

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FIGURE B1.2 Image of a gall produced in response to an insect by a eucalyptus tree.

CHARLES DARWIN AND ALFRED RUSSEL WALLACE

The theory of evolution by natural selection transformed our understanding of the origins of and relationships between organisms into a single tree of life. The theory was developed independently by Charles Darwin and Alfred Russel Wallace, then revealed in a joint report to the Linnaean Society of London in July 1858, and published in a book length treatment, *On the Origin of Species by Means of Natural Selection,* by Darwin in 1859. With this 1859 publication of Darwin's, evolution became the study of:

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

The full title of Darwin's book is **ON THE ORIGIN OF SPECIES BY MEANS OF NATURAL SELECTION OR THE PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.**

Acceptance that organisms could change over time and that new types of organisms could arise revolutionized our understanding of the origin of the natural world: As organisms interact with their environments, species adapt to those environments. The combination of limited resources and the production of more offspring than those resources can sustain results in competition. Individuals who possess heritable traits that make them better adapted to their environment are more likely to survive to produce more offspring (with the same beneficial heritable traits) than individuals who are less adapted to the environment. Because selection works in this way, allowing the better adapted to survive and reproduce, over time, species change. The combination of changing environments, the presence of hereditary variation, and differential reproduction results in the modification of existing characters, or the origin of new characters, that can spread throughout a population or species.

MENDEL AND MUTATIONS

In 1900, evolution entered a new phase of understanding following the rediscovery of Gregor Mendel's (1822–1884) breeding experiments with pea plants, and the ensuing rapid development of **Mendelian genetics**. Geneticists began to work with inbred lines of organisms with animals maintained in laboratories or plants in green houses, and with strains or cultivars that would have a hard time surviving in nature. The genes of these organisms could be manipulated in order to understand the genetics of inheritance.

The discovery of **mutations**—mostly those of large effect, resulting in changes in morphology that could be recognized and quantified—led to notions of large-scale evolution by jumps (saltations), rather than by gradual changes as proposed by Darwin. Evolution by jumps pitted geneticists against Darwinists, many of whom labeled geneticists as anti-Darwinian, as indeed many were. Two conceptual advances led to the reconciliation of Mendelism with Darwinism into what became known as **neo-Darwinism**: (1) The discovery in 1908 of what became known as the Hardy-Weinberg law for calculating gene frequencies in populations under natural selection; (2) the publication in 1918 by the English mathematician R. A. Fisher (1890–1962) of his paper, "The correlation between relatives on the supposition of Mendelian inheritance" (Fisher, 1918). The former showed that changes in a population's genetic structure (such as mutations or selection) can be used to study evolution. The latter proposes a genetic model in which variation in characters was based on Mendelian inheritance.

THE MODERN SYNTHESIS OF EVOLUTION

NEO-DARWINISM *is the theory that evolution occurs by natural selection and not through inheritance of acquired characters. The* **MODERN SYNTHESIS** *(also synthetic theory, evolutionary synthesis) is the integration of neo-Darwinism with Mendelian genetics.*

During the 1930s, the approaches put forth in the Hardy-Weinberg equation and by R. A. Fisher led to the rise of population genetics, the study of changes in gene frequency within a population under the influence of selection, mutation, genetic drift, and gene flow. In the 1940s, the synthesis of population genetics, systematics (the study of the diversification of life and the relationships of species, both past and present) and adaptive change forged what is known as the **Modern Synthesis of Evolution**. An overview of the evolutionary process that emerged from the Modern Synthesis and from the study of genetics and population biology is provided in **TABLE 1.1**.

Population genetics does not provide a complete theory of evolution, however. Why? Because evolution is **hierarchical**, operating on at least three levels:

- the *genetic level*, seen as changes in the genetic composition of individual organisms;
- the *organismal level*, seen as individual variation and differential survival through adaptation[5] (**FIGURE 1.5**) and the evolution of new structures, functions and/or behaviors; and

[5] For adaptation as a property of the phenotype that relates organisms to their environment through selection, see Bock (1980) and Morris and Lundberg (2011).

TABLE 1.1 Major Elements of the Modern Synthesis of Evolution

Organisms exist as individuals. Individual multicellular organisms develop, grow, mature, reproduce, and die.
Natural selection acts on individuals but individuals do not evolve. Individuals pass on their genes to individuals of the next generation.
Individuals exist in populations. Populations usually include different age classes of a single generation and individuals from other generations ('grandparents, grandchildren').
Populations of a sexually reproducing organism consist of individuals that are not identical to one another; they are not clones. Populations of asexually reproducing individuals may be clones.
Populations do not reproduce, individuals reproduce.
Resources are often limited.
Not all individuals in a population will **survive to reproduce** and contribute offspring to the next generation.
Variation is an essential prerequisite for evolution to act. **Natural selection** allows some variants to survive and others not.
Differential reproduction results in survival to the next generation of those individuals best suited to the conditions of their existence.
Because the **genetic background of individual sexually reproducing organisms differs**, those that are selected are more likely to pass their genes to the next generation.
Because of differential reproduction, mutations, and exchange of genes between populations, the **genetic composition of a population** will change gradually from generation to generation.
Populations may subdivide into smaller groups and so reinforce genetic differences that can provide the basis for **speciation**.
Populations or subsets or populations may "crash" or become extinct following environmental catastrophes.

[*Note*: Dates derived mostly from Gradstein et al. A Geological Time Scale. Cambridge University Press, 2004 and Geologic Time Scale, available from http://www.stratigraphy.org, Accessed January 2010.]

- changes in *populations* of organisms, seen as changes in gene flow between populations and the subsequent origin, radiation and adaptation of species (Table 1.1; Hall, 1999; Jablonski, 2007).[6]

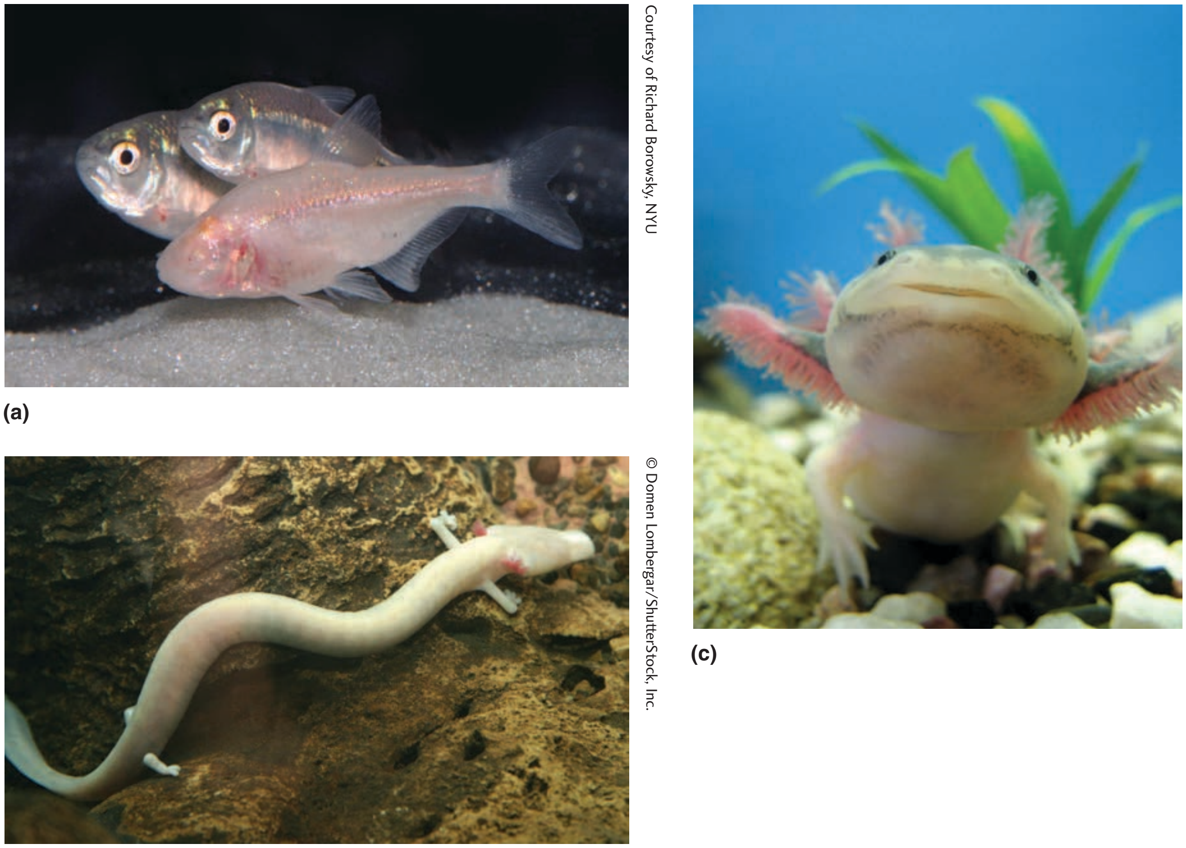
Features that are heritable are evident because they reappear from generation to generation (Figure 1.5). Accumulation of heritable responses to selection of the phenotype, generation after generation, leads to evolution. Importantly, as an individual exists for only one generation, individuals do not evolve. Individuals within each generation, however, respond to **natural selection**, which is the sum of the survival and fertility mechanisms that affect reproductive success. **Genes** exist within individuals and are passed down from generation to generation in those individuals that reproduce. When natural selection on individuals is coupled with changes in the genotype in subsequent generations, populations of individuals evolve, evident in changes in the features shared by a group of organisms (Chanock et al., 2007).

GENOTYPE *is the term for all the genes of an individual. The* **PHENOTYPE** *is all the structural, functional, and behavioral characters of an organism.*

ONLY A THEORY AND NOT SCIENCE?

How our understanding of evolution originated and changed, and how evolution operates at the three levels of genes, organisms, and populations are the major topics of this text. All three levels have to be understood and integrated to paint a complete picture of evolution. That said, it is often claimed that because we cannot see evolution happening, evolution will always be a theory and not a proven body of knowledge.

[6] Authoritative essays on these three levels may be found in Pagel (2002) and in Ruse and Travis (2009).



(a) Courtesy of Richard Borowsky, NYU

(b) © Domen Lombergar/ShutterStock, Inc.

(c) © Misulka/Dreamstime.com.

FIGURE 1.5 Heritable adaptations to life in the dark. **(a)** Surface-dwelling (eyed, pigmented) and cave-dwelling (blind, non-pigmented) forms of Mexican cave fish. Blind and non-pigmented (albino) cave-dwelling axolotls, *Proteus anguinus*, discovered in 1768, shown from the top **(b)** and from the front **(c)** to show the prominent gills.

The foundational theories of the physical sciences—the atomic theory, the theory of relativity, and 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 explains chemical reactions, even though the atoms responsible for the reactions are not visible to the naked eye.[7] The universal theory of gravitation explains why objects remain "tethered" to Earth even though we cannot see the gravitational waves underlying the effect.

The facts of evolution are 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 connect them. The theory of evolution accounts for the historical sequence of organisms through time. It explains their existence through processes that cause changes in their genetic inheritance over time. The theory of evolution is a coherent explanation of the historical course of biology (facts) resulting from natural processes such as mutation, selection, genetic drift, migration, and alterations in how genes function. These explanations are consistent with all observations made so far.[8] For these reasons, evolution is a science.

[7] A scanning transmission electron microscope (STEM) unveiled in 2008 focuses a beam of electrons on a spot smaller than a single atom, scans the atoms, and photographs them in color.

[8] For further reading, see Bock (2007) and Committee on Defining and Advancing the Conceptual Basis of Biological Sciences in the 21st Century (2007).

EVOLUTION AND THE SCIENTIFIC METHOD

It has been claimed that evolution is not a science that can be studied and understood using the **scientific method**, which allows us to gather information that supports or rejects a hypothesis (**BOX 1.2**). The argument is that evolutionary hypotheses cannot be tested and supported (or falsified) in the same way that hypotheses in physics and chemistry are tested. One version of this argument states that because evolution deals with events that occurred in the past (**TABLE 1.2**)—events that are often impossible to repeat in a laboratory—evolutionary biology can never reach the status of the sciences of physics and chemistry. But we can explain historical events in evolution as rationally as we explain other past events, including the origin of Earth and the origin of continents through plate tectonics, both of which are discussed in other chapters. Indeed, just as data can be gathered to demonstrate the movement of continents across the globe over hundreds of millions of years (continental drift) and a theory developed to explain such movements (plate tectonics), so evolution that occurred in the past can be documented, studied, and tested.[9]

The fact of past evolutionary events can be tested scientifically and theories constructed. Note these important facts:

- evidence to test evolutionary hypotheses exists in the fossil record,
- evolution can be tested by comparing organisms and by constructing trees of life (phylogenetic trees), and
- evolution can be tested experimentally.

The sequence of primate-like hominin (humans and their closest relatives) fossils supports the hypothesis that humans have a primate origin. 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 the two proteins. Because either hypothesis could be disproved by finding 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.

Furthermore, evolution can be demonstrated both in nature and experimentally. Indeed, early experimental tests of evolution were carried out during Darwin's lifetime, among the most convincing of which were studies undertaken by British scientist William Dallinger and published in 1878.[10] Dallinger cultivated flagellates (unicellular protozoa, each of which has a locomotory flagellum) in water in which the temperature was gradually increased. After several thousand generations the flagellates had evolved to survive and reproduce at much higher temperatures than those experienced by the initial population. Dallinger communicated with Darwin about his research and Darwin thought Dallinger's results explained how such organisms existed in hot springs.

A recent dramatic example of experimental evolution, documenting mutations, natural selection, and the effect of a beneficial mutation on the rate of evolution in bacterial populations, is outlined in **BOX 1.3**. The ability to undertake such experiments presupposes that we can identify and separate organisms into categories such as species.[11] How this is done, is the topic of another chapter.

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[9] See Rice and Hostert (1993) for an overview of 40 years of laboratory experiments on the mechanisms of speciation, and see Colegrave and Collins (2008) for an overview of experimental studies on the evolution of mutation and genetic exchange.

[10] Rev. Dr. William Henry Dallinger (1839–1909), a Wesleyan Methodist minister, was among the first to undertake microscopic study of the life cycles of unicellular organisms.

[11] Further examples of the demonstration of evolution in experiments using microorganisms are discussed in a paper with the intriguing title "The *Beagle* in a bottle" (A. Buckling et al., 2009. The *Beagle* in a bottle. *Nature,* **457**, 824–829).

BOX 1.2 The Scientific Method

The essential nature of science is discovery using a method—the **scientific method**—that allows discoveries to be made. The discovery may be of a previously unknown object—tubeworms from deep-sea hydrothermal vents (**FIGURE B2.1**)—or a new explanation—how organisms survive and evolved at depth.

The scientific method as we know it developed in Europe in the late seventeenth century. With the publication of *De Motu Cordis* (On the Motion of the Heart and Blood) in 1628, the English physician William Harvey (1578–1657) demonstrated with a brilliant synthesis of theory, observation and experimentation that the circulation of the blood could be explained in terms of pumps and valves. In the words of another famous physician Sir William Osler (1849–1919) two hundred and fifty years after Harvey's death:

> . . . *De Motu Cordis* marks the break of the modern spirit with the old traditions. No longer were men to rest content with careful observation and with accurate description; no longer were men to be content with finely spun theories and dreams, which "serve as a common subterfuge of ignorance"; but here for the first time a great physiological problem was approached from the experimental side by a man with a modern scientific mind, who could weigh evidence and not go beyond it, and who had the sense to let the conclusions emerge naturally but firmly from the observations.*

Applying the scientific method involves four steps:

1. Thinking up a hypothesis.
2. Designing and performing controlled experiments or making observations that allow information (data) relevant to the hypothesis to be collected.
3. Analyzing the data in an objective way against the background of existing knowledge.
4. Drawing conclusions that support or refute the hypothesis (**FIGURE B2.2**).

Courtesy of Monika Bright - University of Vienna, Austria/NOAA

FIGURE B2.1 Deep-sea red tube worms.

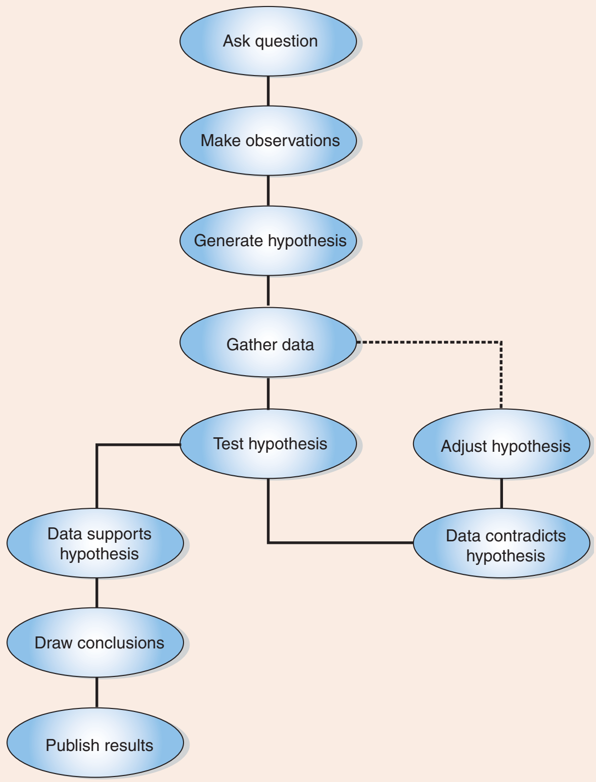


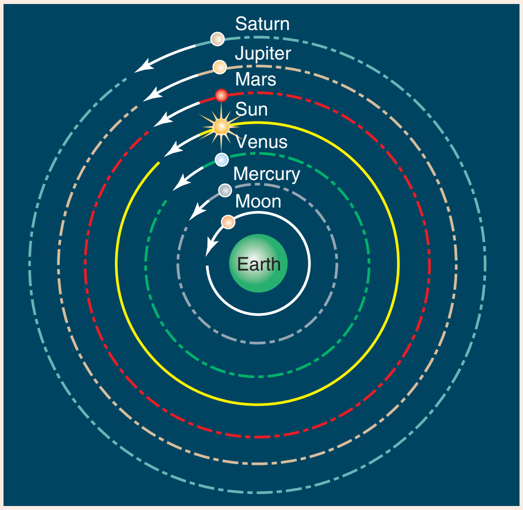
FIGURE B2.2 Diagrammatic representation of the steps in the scientific method.

Through the repeated application of this method, science progresses by accumulating evidence consistent with one interpretation of an event or process 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. Consequently, the scientific method can be applied to astronomy, geology, and past evolutionary events; the scientific method is sufficiently precise to allow explanations of past events. If the explanations contradict present events, new hypotheses are generated and new data obtained.

Systems that are alike in many respects but differ in others can be investigated using the scientific method. Ants and termites can be studied as two types of social insects. Chimpanzees and modern humans can be studied as closely related primates. Here, the hypotheses relate to evolution within related organisms. The scientific method can take us further, however. We can compare ants and humans as two groups of social organisms. Here the hypotheses are that the evolution of social

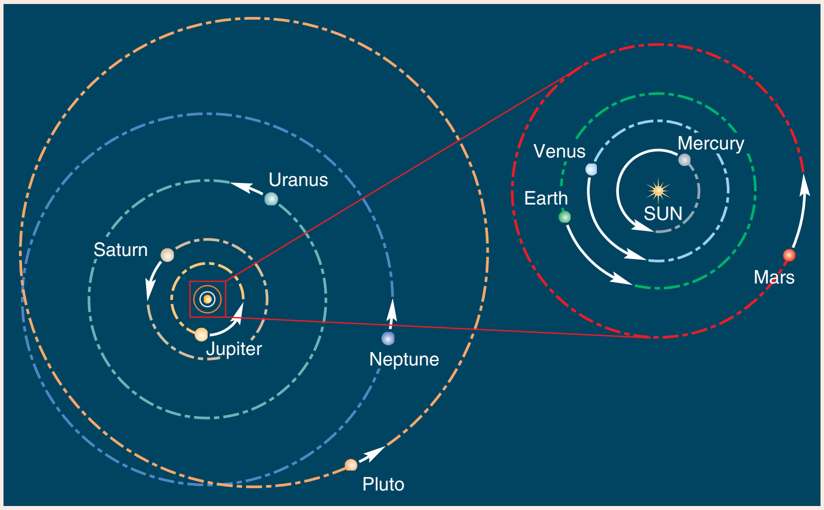
*From the Harveian oration delivered by William Osler at the Royal College of Physicians London, 18 October 1906 and reprinted in the *Brit. Med. J,* 1957, **8**, 1257–1263.

BOX 1.2 **The Scientific Method (Cont...)**



(a)

FIGURE B2.3 Two hypotheses of the orbits of the planets, one in which the planets orbit Earth **(a)**, the other in which the planets orbit the Sun **(b)**.



(b)

organization has elements in common throughout the animal kingdom.

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 and the Sun (FIGURE B2.3), and for the discovery of deoxyribonucleic acid (DNA) as the molecule of inheritance that carries the genetic code from generation to generation. Other discoveries may be, or appear to be, instantaneous: The rising level of the water as he stepped into his bath led Archimedes to shout "Eureka" as he "saw" the principle of buoyancy. Even such "Eureka moments," however, cannot be isolated from past knowledge or current ways of thinking. 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 inter-convertible, expressed in the formula $E = mc^2$ (energy equals mass times the speed of light squared). Even though the formula revolutionized our thinking, earlier theories of matter and energy existed, just as earlier theories of evolution existed before Darwin and Wallace revolutionized our thinking. Similarly, as you progress through this text you will see that evolutionary biology has a history in which earlier hypotheses, types of data, and conclusions have been replaced with later hypotheses, different types of data, and different conclusions. This is why evolution is a science that is understood and explained through the application of the scientific method.

TABLE 1.2 Major Events in Organismal Evolution in Relation to the Geological Time Scale

Time Scale				Millions of Years Before Present (approx.)	Duration in Millions of Years (approx.)	Some Major Organic Events
Eon	**Era**	**Period**	**Epoch**			
Phanerozoic	Cenozoic	Quaternary	Recent (last 5,000 years)	0.01	1.8	Appearance of humans
			Pleistocene	1.8		
		Tertiary	Pliocene	5.3	3.5	Dominance of mammals and birds
			Miocene	23.8	18.5	Proliferation of bony fishes (teleosts)
			Oligocene	34	10.2	Rise of modern groups of mammals and invertebrates
			Eocene	55	21	Dominance of flowering plants
			Paleocene	65	10	Radiation of primitive mammals
	Mesozoic	Cretaceous		142	77	First flowering plants Extinction of dinosaurs
		Jurassic		206	64	Rise of giant dinosaurs Appearance of first birds
		Triassic		248	42	Development of conifer plants
	Paleozoic	Permian		290	42	Proliferation of reptiles Extinction of many early forms (invertebrates)
		Carboniferous	Pennsylvanian	320	30	Appearance of early reptiles
			Mississippian	354	34	Development of amphibians and insects
		Devonian		417	63	Rise of fishes First land vertebrates
		Silurian		443	26	First land plants and land invertebrates
		Ordovician		495	52	Dominance of invertebrates First vertebrates
		Cambrian		545	40	Sharp increase in fossils of invertebrate phyla
Precambrian	Proterozoic	Upper		900	355	Appearance of multicellular organisms
		Middle		1,600	700	Appearance of eukaryotic cells
		Lower		2,500	900	Appearance of planktonic prokaryotes
	Archean			4,000–4,400	1,400	Appearance of sedimentary rocks, stromatolites, and benthic prokaryotes
	Hadean			4,560	160–560	From the formation of Earth until first appearance of sedimentary rocks; no observable fossil organisms

[*Note*: Dates derived mostly from Gradstein et al. *A Geological Time Scale.* Cambridge University Press, 2004, and from *Geologic Time Scale,* available from http://www.stratigraphy.org, accessed August 2012.]

BOX 1.3 **Experimental Evidence for Evolution**

A dramatic illustration of our ability to follow evolution as it occurs—to conduct an experiment in evolution—is provided by a study using the bacterium *Escherichia coli*, which, as of February 2010, had been running for nearly 25 years and had more than 50,000 generations (Lenski and Travisano, 1994 and Lenski, 2010). The design of the study is deceptively simple, considering the wealth of knowledge it gives us. The novelty comes from the tenacity to measure mutation rates and assess the magnitude of their effects in generation after generation, for over two decades.

In February 1988, 12 genetically identical populations of *E. coli* were established in colonies under a selection pressure (glucose in the environment was limited) and were monitored after 2, 5, 10, 15, 20, 40, and 50 generations. Any change (evolution) at the nucleotide level was detected by determining the complete nucleotide sequence of the bacteria at each of these six times and comparing the sequence with earlier time periods and with the genome of the initial population. The **rate of evolution** after 20,000 generations, measured by the accumulation of mutations in nucleotide sequences, was 2 nucleotide changes/1,000 generations. Reproductive success, which was used as a measure of **adaptation,** (Bock, 1980) was 1.5 times higher at 20,000 generations than in the starting populations and continued to rise at a slower rate in subsequent populations. The authors concluded that beneficial mutations were arising and accumulating in the populations. This simple metric provides evidence for the operation of natural selection in these populations.

Interestingly, the trends of rate of evolution, accumulation of mutations, and increased reproductive success seen in the first 20,000 generations did not continue in subsequent generations. Why? Because evolution is not predictable and because some mutations have much greater effects than others. Sometime between generations 20,000 and 40,000 a mutation arose in the gene *mutT* that codes for an enzyme involved in repairing damaged DNA, making the process much more efficient. Because damaged DNA was now being repaired more efficiently, the rate of accumulation of mutations increased from 45 mutations in the first 20,000 generations to 600 mutations between generations 20,000 and 40,000. The rate of evolution of nucleotide sequences changed because a single mutation enabled subsequent mutations to accumulate.

KEY TERMS

adaptation
genes
genotype
hierarchical
Mendelian genetics
modern synthesis
mutations
natural selection
neo-Darwinism
phenotype
preformation
scientific method
spontaneous generation

EVOLUTION ON THE WEB

Explore evolution on the Internet! Visit the accompanying website for *Strickberger's Evolution, Fifth Edition,* at **go.jblearning.com/Evolution5eCW** for exercises and links relating to topics covered in this chapter.

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