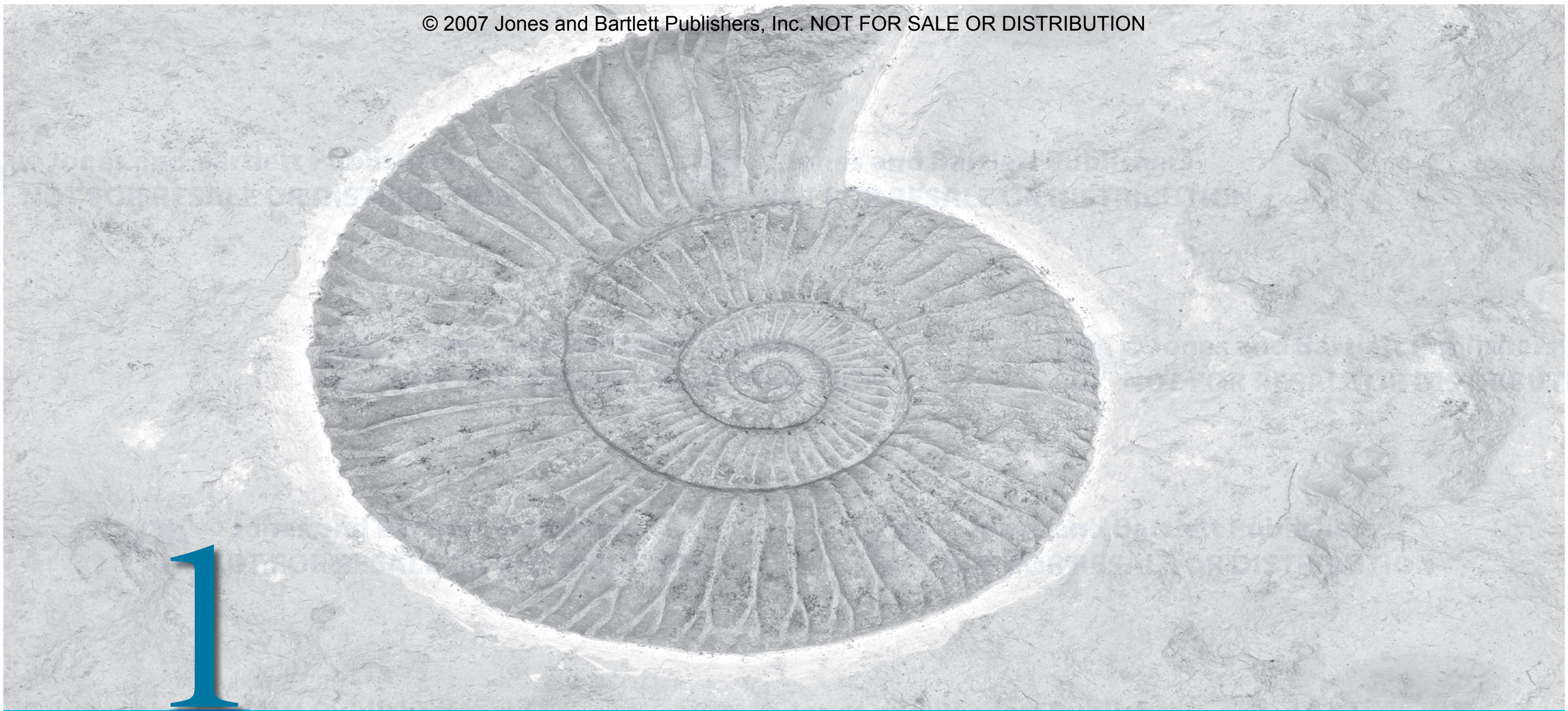


1 Before Darwin

Chapter Summary

Many intellectual threads led to the modern theory of evolution, a theory that requires recognition that Earth is ancient, that there is a common inheritance within a biological group, and that natural events can be explained by discoverable natural laws. But it took a long time before these threads were woven into an evolutionary tapestry.

Plato's idealistic concept, that all natural phenomena are imperfect representations of the true essence of an ideal unseen world, was for centuries the prevailing philosophy in Western Europe. Following Platonic ideas, Aristotle suggested that not only were species immutable but that there was a hierarchical order of species from most imperfect to most perfect, a concept refined over the centuries as the "Great Chain of Being." In hindsight, this philosophy profoundly inhibited the development of evolutionary ideas because it maintained that the world of essences is perfect and all change is illusory. This unchanging order remained unquestioned until inexplicable gaps in the chain of nature prompted philosophers such as Gottfried Leibniz to propose that the universe was not perfect, only that it might go through successive intermediate stages on the way to perfection.

By the seventeenth and eighteenth centuries, new attention to animals and plants as well as far-flung explorations led to an increasing interest in classifying organisms within the natural chain. The Swedish founder of taxonomy, Carolus Linnaeus, revolutionized systematics by using the species as the basic unit and building a hierarchical system from species upward to larger taxonomic categories. The naturalist Buffon (Georges-Louis Leclerc, Comte Buffon) went farther, implying that the species is not just a category in classification, but rather the only natural grouping of historical and interbreeding entities. Buffon maintained that a species was a "real" but static unit. Jean-Baptiste Lamarck evaded this problem by proposing that species are arbitrary (not "real") and that there must be forms intermediate between species. So, Lamarck's view of a species was very different from Charles Darwin's. If species were arbitrary (Lamarck), then species never went extinct but instead evolved into other "species."

The ideas that organisms could arise from nonliving materials by spontaneous generation or that they did not change during their embryonic development but were "preformed" in their ancestors, provided perfectly rational explanations to questions posed at the time. Not until late in the nineteenth century was spontaneous generation finally disproved (many of the first Darwinians believed in it) and the idea established that organisms develop epigenetically, that is, by differentiating from undifferentiated tissues. At last, biological phenomena became amenable to rational explanation.

Discovery of a fossil record of life became a rich source of data for individuals trying to understand relationships between organisms. The discovery of (1) fossils of unknown types of organisms, (2) organisms similar to but not the same as organisms living in that locality, and (3) the apparently inappropriate location of some fossils, suggested that Earth's surface and the organisms on it had existed for a long time, and that organisms succeeded one another through time. These ideas conflicted, however, with the Judeo-Christian view of a recent origin, according to which fossil data were interpreted to accord with biblical catastrophes such as the Noachian flood or as "jokes of nature." Geologists asserted that fossil evidence was only explicable if Earth was indeed old and if forces of nature had shaped its surface. Changes on Earth's surface would have led to alterations in the organisms that lived on it, and these changes would be reflected in their fossil remains. Charles Lyell, a contemporary of Darwin, invalidated the idea that capricious catastrophic and miraculous events had influenced Earth's geological structure. Lyell developed the earlier principle of uniformitarianism, in which the same geological forces acted in the past as in the present. Extrapolating processes back in time helped establish the validity of a world that was both comprehensible and rational.

Biological evolution is concerned with on inherited changes in populations of organisms over time leading to differences among them. **Individuals do not evolve,** in the sense that an individual exists only for one generation. Individuals within each generation, however, do respond to **natural selection.**[1] **Genes** within individuals (**genotypes**) in a population, which are passed down from generation to generation, and the features (**phenotypes**) of individuals in successive generations of organisms do evolve. Accumulation of heritable responses to selection of the phenotype, generation after generation, leads to evolution: Darwin's descent with modification (**Box 1-1**).

All organisms, no matter how we name, classify or arrange them on **The Tree of Life,** are bound together by four essential facts:

1. They share a common inheritance.
2. Their past has been long enough for inherited changes to accumulate.
3. The discoverable taxonomic relationships among organisms are the result of evolution.
4. Discoverable biological processes explain both how organisms arose and how they were modified through time by the process of evolution.

Although each of these aspects has been studied and discussed at various times in human history, only after Charles Darwin developed and published his theory in the mid-nineteenth century did biological evolution become an acceptable scientific (naturalistic) alternative to earlier explanations. Darwin's proposed mechanism, **natural selection,** however, was regarded by many to be of secondary importance to evolution. The acceptance that organisms could change over time brought about enormous shifts in the way we view the world and explain natural phenomena. We begin our exploration by looking at some of the earliest attempts to understand the world around us.

[1] **Selection** is the sum of the survival and fertility mechanisms that affect the reproductive success of genotypes (see Chapter 22).

BOX 1-1 Evolution: An Overview of the Term and the Concept(s)

"Evolution. Development (of organism, design, argument, etc.); Theory of E. (that the embryo is not created by fecundation, but developed from a pre-existing form); origination of species by development from earliest forms" (*Concise Oxford Dictionary*, 5th ed., 1969).

The Word *Evolution*

As the definition above indicates, the word *evolution* has different meanings and the concept of evolution applies to a wide variety of human activity: the evolution of an argument; the evolution of the computer; the evolution of heart valves; evolutionary medicine.

The first definition — evolution as organismal development — reflects the original seventeenth century definition of the word, when evolution (from the Latin *evolutio,* unrolling) was defined as and used for the unfolding of the parts and organs of an embryo to reveal a preformed body plan. An example would be a caterpillar unfolding into a butterfly. Only in the nineteenth century did evolution come to mean transformation of a species or transformation of the features of organisms.[a]

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 theory of evolution proposed by Swammerdam and Malpighi prevails almost everywhere . . . Most of these men teach that there is in fact included in the egg a germ or perfect little human machine . . . And not a few of them say that 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*). He 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.[b]

Just nine years before Darwin published *On the Origin of Species*,[c] evolution was still being used for individual development. Here is a question from an examination held at Cambridge University in 1851, a question that presumes that species have not evolved: "Reviewing the whole fossil evidence, shew that it does not lead to a theory of natural development through a natural transmutation of species" (cited in Hall, 1999a). Even Darwin, who proposed a theory of evolution as descent with modification from generation to generation, only used the word evolution once, as the last word of his 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*.

It appears that Darwin had two concerns over the word evolution. One was its established use for the unfolding of development according to some preset plan. Another, but more difficult to establish, was Darwin's concern that he not be viewed as promoting the idea of **progress** (see Chapter 2 and Box 19-1).

Concept of Evolution as a Process

Perhaps not surprisingly in hindsight, and given the nature of the evidence they discovered, geologists were among the first to use the term *evolution* for the transformation of species and progressive change through geological time.

Robert Grant (1793–1874), who gave the name Porifera to the sponges, used the term evolution in 1826 for the gradual origin of

[a] See the essays in Hall and Olson (2003) for evaluations of the major concepts in evolution and development.

[b] Various topics (*emboîtment*, preformation, transformation, population genetics) and some of the individuals (Bonnet, Darwin and Lyell) introduced in this box are discussed in greater detail in the text.

[c] What is the appropriate (proper?) way to abbreviate the title of Darwin's book, the full title of which is, *On the Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life?* Some abbreviate it to *On the Origin of Species*, others to *On the Origin*, yet others to *the Origin*. We use either *On the Origin of Species*, the mode preferred by Darwinian scholars and historians, or *The Origin*.

Idealism, Species and the Species Concept

Attempts to understand the world in a rational way — that is, by methods of thought and logic — began about the fifth century BC in Greece.

Plato (428–348 BC), the philosopher who along with Aristotle (384–322 BC) had the greatest impact on Western thought, suggested that the observable world (our experience) is no more than a shadowy reflection of underlying "ideals" that are true and eternal for all time. Most things, according to Plato, were originally in the form of such eternal ideals, a philosophy we now know as **idealism.** Plato and his successors assumed that only ideal generalizations are real; all else was merely a shadowy illusion. In Plato's famous parable in his dialogue, *The Republic*, humans deprived of philosophy are depicted as cave-confined prisoners facing a wall upon which are displayed their own shifting, distorted shadows as well as shadows of objects situated behind them that they cannot see directly. Their chains prevent them from turning their heads toward the light. As a result, the prisoners interpret the observed deformed, shadowy aberrations invertebrate groups. Charles Lyell (1797–1875) used evolution in 1832 for gradual improvement associated with the transformation of aquatic to land-dwelling organisms: "the testacea of the ocean existed first, until some of them, by gradual evolution, were *improved* into those inhabiting the land." Even so, an argument can be made that both Grant and Lyell were using evolution in the sense of change during development. Not so for the engineer, journalist and writer Herbert Spencer (1820–1903), whom we associate with the origin of the term 'struggle for existence' and with Social Darwinism (the application of evolutionary theory to society). He used evolution in 1852 to mean **progression towards greater complexity,** heralding a century and a half-long controversy over whether evolution leads to progress, as Lyell, Spencer, and perhaps Thomas Huxley thought it did (Ruse, 1996; Shanahan, 2004). Julian Huxley penned one of the clearest statements of biological progress in 1947, a statement to which Darwin would not have objected: "Biological progress exists as a fact of nature external to man, and . . . consists basically of three factors — increase in control over the environment, increase in independence of the environment, and the capacity to continue further evolution in the same progressive direction."

Although many did not accept natural selection as the most important mechanism of evolution, most naturalists/biologists accepted that evolution had occurred. From the publication of *On the Origin of Species* in 1859 until 1900, evolution was the study of:

- **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 → tetrapods); and
- **the transformation of features** such as jaws, limbs, kidneys, nervous systems **within lineages of organisms.**

A new approach to evolution followed the rediscovery in 1900 of Gregor Mendel's experiments and the development of Mendelian genetics. Geneticists began to work with pure 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 discovery of mutations — mostly of large effect, as only these were readily manifest in morphology and could be recognized and quantified — led to notions of large-scale evolution by saltation. This pitted geneticists against Darwinists, many of whom labeled geneticists as anti-Darwinian, as indeed many were. Not until the origination in 1908 of what became known as the Hardy-Weinberg law for calculating gene frequencies in populations under natural selection (see Chapter 21) and 1918 when R. A. Fisher published his paper, "The correlation between relatives on the supposition of Mendelian inheritance" (see Chapter 22), were doors opened that could reconcile Mendelism with Darwinism. During the 1930s, it led to the rise of population genetics, in which speciation was seen as resulting from genetic changes within a lineage as reflected in changes in gene frequency (Chapter 22). In the 1940s, the synthesis of population genetics, systematics and adaptive change forged what we know as the **Modern Synthesis of Evolution** or **neo-Darwinism.**

Although some thought otherwise, population genetics does not provide a complete theory of evolution. Now evolution is seen as **hierarchical,** operating on organisms on at least three levels:

- the *genetic level*, seen as substitution of alleles, changes in gene regulation and changes in gene networks;
- the *organismal level*, seen as individual variation and differential survival through adaptation and the evolution of new structures, functions and/or behaviors; and
- changes in *populations* of organisms, seen as the curtailment of gene flow between populations and the subsequent origin, radiation and adaptation of species (see Box 11-1, Hierarchy).

Natural selection acts because of the differential survival of individual organisms with particular features. The response to selection lies in the information content of the genome, information that can change because of mutation.

Because evolution acts at genetic, organismal and population levels, a definition ideally should reflect evolution at all three levels. In many respects, Darwin's concept of **descent with modification** remains an inclusive definition of (biological) evolution. Evolution is descent with modification, encompassing evolutionary change at genetic, organismal and/or population levels. How our views of evolution originated and have changed, and how evolution operates at the three levels of genes, organisms and populations are the major topics of this book. Rather, we should say, *is the major topic of this book* — an understanding and integration of all three levels are required to paint a complete picture of evolution.

as reality, while the actual unchanging humans and objects are the true "essences" or "forms." Any change would cause disharmony and so disrupt eternal ideals.

The Platonic goal for human society was to analyze experience in order to understand and strive for ideal perfection. Plato's writing had a goal that was founded in his belief in the centrality of beauty, truth and justice and the need to shape a society in which all could attain those goals. The concepts of perfect circles to explain the motions of the heavenly bodies (**Fig. 1-1**), perfect numbers such as 6 (1 + 2 + 3) and 10 (1 + 2 + 3 + 4), and the four "elements" (earth, water, fire, and air) to which all matter could be reduced were among the results of their search for perfection.[2]

To a large extent, idealism originates from the practice of abstracting concepts from experience. For example, to

[2] Variations on this theme were common. To the four elements Empedoceles (c. 490–430 BC) added two active principles: *love*, which binds elements together, and *hate*, which separates them. In respect to mystical numbers, Lorenz Oken (1779–1851), one of the German Natural Philosophers, proposed that the highest mathematical idea is zero, and God, or the "primal idea," is, therefore, zero.

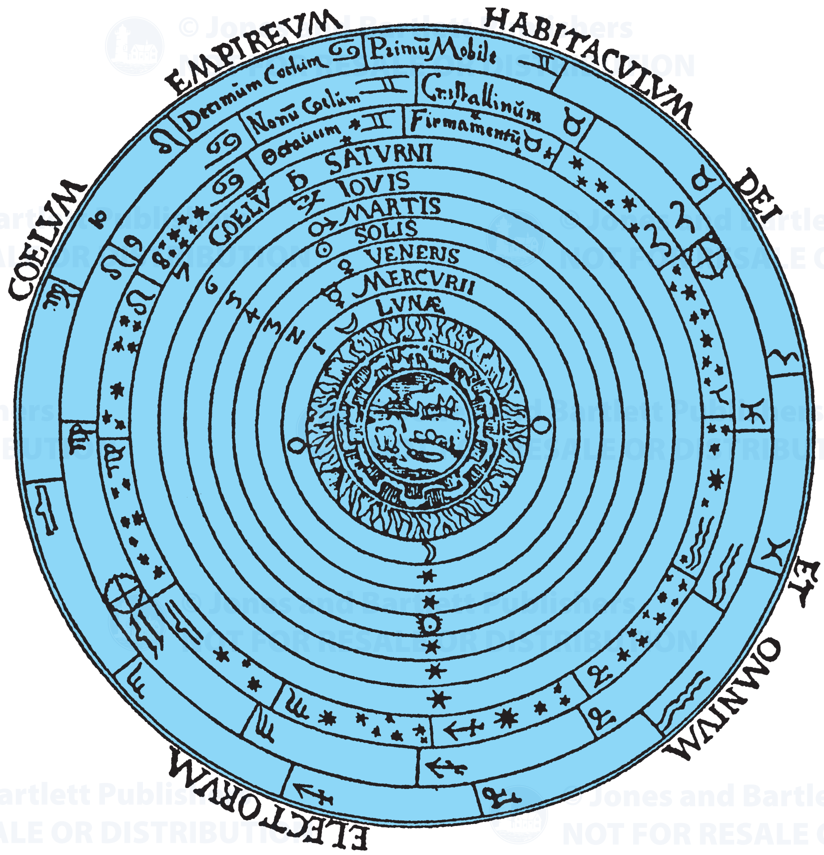


FIGURE 1-1 A medieval concept of the ten spheres of the universe with Earth and its four elements (earth, air, fire, water) at the center, according to Apian's *Cosmographia* (published 1539 in Antwerp). Surrounding Earth are transparent crystal spheres containing in succession the moon, Mercury, Venus, the sun, Mars, Jupiter, Saturn, the fixed stars, and spheres involved in the motion of the stars and of the entire universe ("Primu Mobile"). Beyond these spheres lies Heaven ("The Empire and Habitation of God and All the Elect").

think of "cat" in a way that includes all cats, rather than one particular animal of specific size and head shape, with claws, tail, fur, and so on. Abstraction allows us to generalize our experience, to differentiate between cat and tiger, to pet the cat and run from the tiger and to communicate these general concepts or universals to others through symbolic language. Despite these advantages, however, generalizations are not always reliable. Experiences can modify the generalizations; for example, not all cats or tigers are the same. The dilemma for **natural scientists**[3] has always been to recognize the reality of differences among members of a group and yet to recognize the reality of the group itself. Idealism offered practically no means of reconciling these two aspects of reality. No sooner do we conceive of some new generality than we discover further instances that may force us to modify our original concept.

Experience stresses continual change; generalization stresses stability. With the notable exception of Heraclitus (540–475 BC), few Greek thinkers tried to incorporate change into their philosophies. Heraclitus' philosophy disturbed that equilibrium, and we think, rightly so. Heraclitus maintained that all things are made of fire and so all things are constantly in motion or changing. The adages, "you cannot step into the same river twice" and "there is nothing permanent except change," capture his philosophy, as you will realize if you think about these two phrases for a moment or two. Biology is change, even when appearances are to the contrary. Maintaining a constant body temperature involves an enormous amount of change on second-by-second, minute-by-minute time scales; maintaining physiological stability *(homeostasis)* is really all about maintaining constancy in the face of change.

To Plato, the form of a structure could be understood from its function because function dictated form; the form of the universe derives from its function of goodness and harmony imposed by an external creator. Aristotle, whom

[3] We use the terms *natural scientist* and *natural historian* when referring to individuals working before the twentieth century, the term *scientist* having been introduced in 1830. The term *biology* was first used in 1800, independently by Lamarck and by the German naturalist, Gottfried Treviranus (1776–1837). The term *biologist*, which was introduced in the nineteenth century by William Whewell (1794–1866), did not come into general usage until the twentieth century. Although some studied zoology, others morphology and yet others botany or physiology, these specialized terms were not in general use. Nowadays, biology has become so specialized and fragmented that (1) one of the functions of a book such as this, (2) the integration of evolution and development as evolutionary developmental biology ("evo-devo"; Hall, 1999a; Hall and Olson, 2003), and (3) the call for an integrative biology, is to provide an integrative biology of the twenty-first century, an integration that was second nature to natural scientists in the nineteenth century.

many regard as the founder of biology (among other sciences), modified this notion to accommodate the embryonic development of organisms,[4] pointing out that the last stage of development — the adult form — explains the changes that occur in the immature forms. This type of explanation is called teleological (goal-oriented), where the adult represents the "telos," or final goal, of the embryo.

To many later thinkers, **teleology** became associated with Platonic processes by which advanced stages influenced and affected earlier stages. Because ideals implied conscious creation, it seemed as though organs and organisms were designed for some special purpose and that each species was created as an ideal in anticipation of its future use. Pliny the Elder (23–79 AD) carried this notion to the point of claiming that all species were created for the benefit of man, a concept laid out in the Jewish Testament. Some two hundred years later, Lucius Lactantius (c. 260–340 AD) wrote, "Why should anyone suppose that, in the contrivance of animals, God did not foresee what things were living, before giving life itself?" This view helped cast the teleological origin of species more permanently into the religious form it took in Christian Europe from the Middle Ages until Darwin, during which time natural science was inseparable from religion. Thus, the prominent thirteenth century Christian theologian Thomas Aquinas (c. 1225–1274) wrote in his *Summa Theologica*:

> Whatever lacks knowledge cannot move towards an end, unless it be directed by some being endowed with knowledge and intelligence; as the arrow is directed by the archer. *Therefore some intelligent being exists by whom all natural things are directed to their end*; and this being we call God (emphasis added).

Five centuries later, Linnaeus extended teleology even to science:

> If the Maker has furnished this globe, like a museum, with the most admirable proofs of his wisdom and power; if this splendid theater would be adorned in vain without a spectator; and if man the most perfect of all his works is alone capable of considering the wonderful economy of the whole; it follows that man is made for the purpose of studying the Creator's work that he may observe in them the evident marks of divine wisdom (Linnaeus, 1754, *Reflections on the Study of Nature*).

The Great Chain of Being

The idealistic concept of a species became strongly tied to its use in explaining the divine origin and design of nature. Plato had defined the species as representing the initial mold for all later replicates of that species: "The Deity wishing to make this world like the fairest and most perfect of intelligible beings, framed one visible living being containing within itself all other living beings of like nature." Aristotle expanded this view to a chain-like series of forms called the **Scale of Nature**, with each form representing a link in the progression from least perfect to most perfect (**Fig. 1-2**). This concept continued long into the history of European thought, merging with other ideas into the **Ladder of Nature** and the **Great Chain of Being** (Lovejoy, 1936).

Philosophically satisfying as it was, the concept of the Great Chain of Being did not necessarily put humans on the highest, or even near the highest, rung of the Ladder of Nature. Many who contemplated the innumerable steps between humans and perfection (God) felt the despair of occupying a relatively lowly position and only consoled themselves with the thought that there were even more lowly organisms. We insult someone if we call them a worm. Yet, despite its discomforts, the Great Chain of Being was accepted well into the eighteenth century.

In Germany, this notion was fostered by Johann Gottfried von Herder (1744–1803, a Protestant minister, philosopher and author), Johann von Goethe (1749–1832, the polymath who coined the term morphology), and others of the Natural Philosophy (*Naturphilosophie*) school, who tied the Great Chain of Being to an idealistic concept of biological forms. According to Goethe, the creation of each level of organisms was based on a fundamental plan: an **archetype** or ***Bauplan*** (pl. *Baupläne*). Goethe conceived the morphology of plants, for example, as founded on an *Urpflanze* (ancestral plant) that had only one main organ, the leaf, from which the stem, root and flower parts derived as variations (**Fig. 1-3a**). Similarly, the bones of the skull were modifications of the vertebrae of an *Urskeleton* (animal archetype) composed only of vertebrae. Ribs were modifications of vertebral processes (**Fig. 1-3b**).[5]

To most of its exponents, the Ladder of Nature had the comforting quality of stressing a precisely ordered regularity of relationships among organisms and could also be used to support and justify the prevailing social and political orders. As expressed by the literary Christian apologist Soame Jenyns (1757):

[4] *Embryology* was the term used for the study of embryonic development until the mid-twentieth century. In the early twentieth century, embryology was divided into descriptive and experimental and often taught as such in separate classes. In the mid 1950s, embryology was renamed *developmental biology*.

[5] *Archetypes* were taken up in a big way in the nineteenth century by Richard Owen; see Amundson (2007) for a reprinting of a classic paper by Owen on the essential nature of limbs. Hall (1994) and Bowler (2003) treat these topics further.

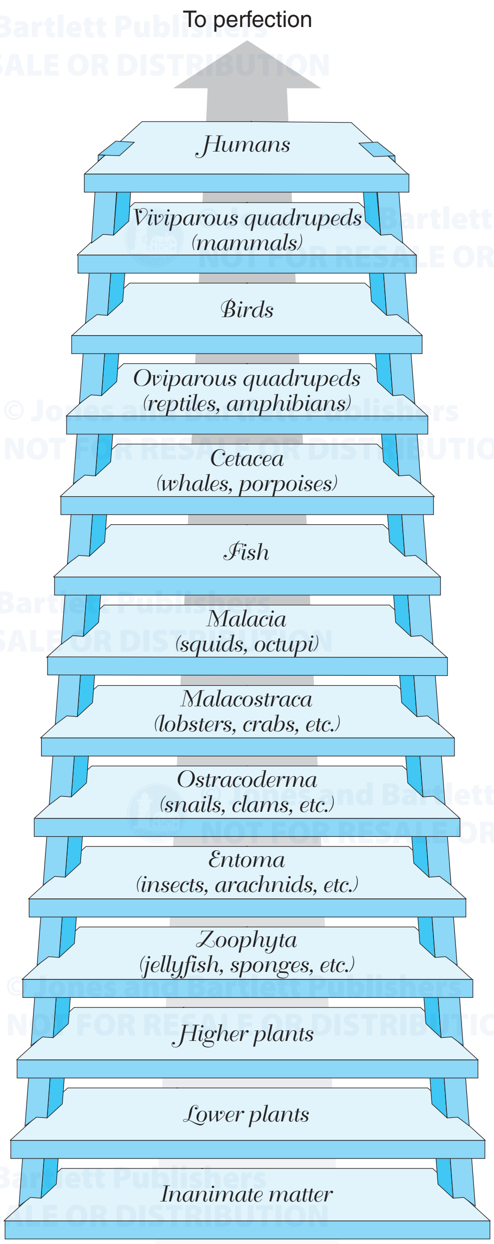


FIGURE 1-2 Aristotle's Scale of Nature (Adapted from descriptions in Guyénot, E., 1941. *Les Sciences de la Vie: L'Idee d'Evolution.* Albin Michel, Paris).

> The universe resembles a large and well-regulated family, in which all the officers and servants, and even the domestic animals, are subservient to each other in a proper subordination; each enjoys the privileges and perquisites peculiar to his place, and at the same time contributes, by that just subordination, to the magnificence and happiness of the whole.

Among the relatively few who disputed this concept was Voltaire (François-Marie Arouet; 1694–1778), who addressed the question of the many observed gaps between species, an observation that did not seem to be in accord with the expected innumerable steps in the continuous progression from imperfect to perfect. Voltaire proposed that although there were no living species to fill these gaps, such gaps were real, perhaps caused by the extinction of species, the concepts of adaptation and extinction having been developed by Lucretius as early as 55 BC. In this respect, Voltaire essentially echoed the writings of the philosophers René Descartes (1596–1650) and Leibniz (1646–1716).

Progress to Perfection

To Leibniz, the evolution of species was part of the perfection toward which the universe continually progressed. His philosophy represented a *major shift* from a perfectly created universe to one in the process of becoming perfect. Progress toward the perfection of species was expressed by natural historians such as Charles Bonnet (1720–1793), who maintained that the development[6] of any organism from its "seed" was an unfolding of a preconceived plan inherent in the seeds of previous generations. The notion of progress therefore fitted into a teleological framework: that it was "necessary" and directed toward some particular end.

As with so many changes in thought during the eighteenth century, these evolutionary rumblings were associated with major changes occurring in society following the Reformation that included the Enlightenment, the rise of empiricism and challenges to Papal authority (Chapter 3). The progressive weakening of feudalism, which had begun in the fourteenth century with the rise of commerce and the new power of the merchant classes, was accelerating because of rapid advances in technology and the Industrial Revolution. The old, rigid, land-based class structures were breaking up. Social institutions and the ideas expressed by many thinkers reflected these changes and became more mobile and flexible.

The Oxford historian John Roberts captured the essence of the Enlightenment as, "thousands of Europeans . . . felt, that they need no longer distrust the spread of knowledge; indeed, the idea that new knowledge was, in its social tendency, fundamentally progressive was another characteristic of 'Enlightenment'." He saw four changes as being particularly important in changing minds and attitudes, all of which had an impact on the reception of evolution:

- A new emphasis on and encouragement towards science and the manipulation of the natural world;
- A new skepticism that began to sap religious belief;
- A desire to want to be more humane, and "most important of all";
- "The growth of the idea that Progress was normal" (1985, p. 236).

The Great Chain of Being had important effects on plant and animal classification, which derived partly from the search

[6] Bonnet used the term evolution (*evolutio*, Latin) in its original meaning of unfolding during development (see Box 1-1).

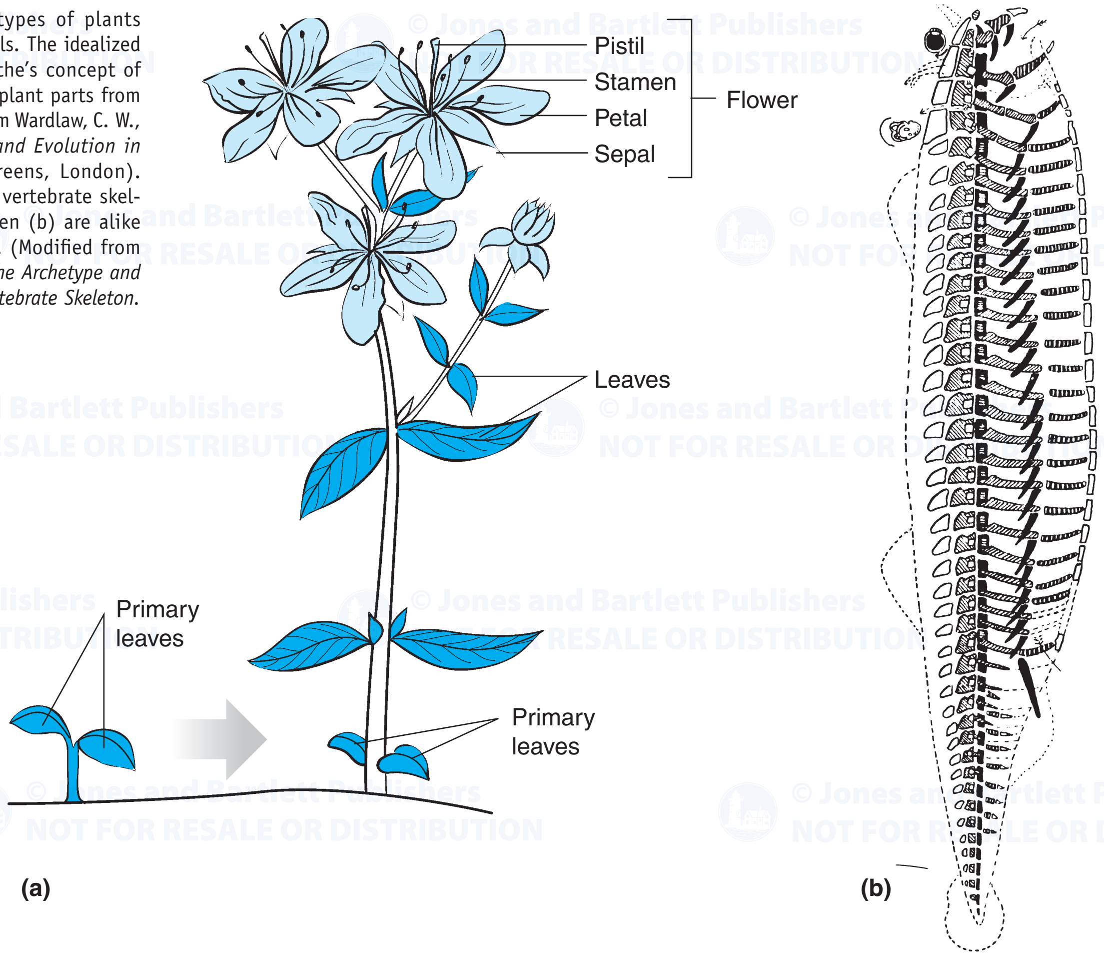


FIGURE 1-3 Archetypes of plants and vertebrate animals. The idealized plant (a) shows Goethe's concept of the derivation of all plant parts from the leaf. (Adapted from Wardlaw, C. W., 1965. *Organization and Evolution in Plants*. Longmans Greens, London). The segments in the vertebrate skeleton pictured by Owen (b) are alike from cranium to tail. (Modified from Owen, R., 1848. *On the Archetype and Homologies of the Vertebrate Skeleton*. Voorst, London).

for the multitude of organisms that many believed occupied all the rungs of the Ladder of Nature. There were proposals that even humans could be linked to other species through the "wildman of the woods" (the orangutan; **Fig. 1-4**). Other anthropologists thought the link between humans and animals was via a South African tribe, the Hottentots, whom Europeans believed to be almost indistinguishable in reasoning power from apes and monkeys. Despite the observed gaps between many species, all had been linked by a principle of continuity, expressed by Leibniz as, "Nature makes no leaps." Although not espousing the evolution of species as such, Emanuel Kant expressed this same idea as "the principle of affinity of all concepts, which requires continuous transition from every species to every other species by a gradual increase of diversity."

Thus, despite its idealistic nature, the Great Chain of Being led almost directly to the idea that the perfection of organisms may demand multiple intermediate stages. By the eighteenth century, the basic concept of **evolution** — the transformation of one species into another — required only the philosophical acceptance of actual change between the innumerable steps in the Great Chain of Being.

Classification and the Reality of Species

From the biological viewpoint, however, considerable difficulties remained concerning how species were to be defined, classified, distinguished one from the other and placed into groups that reflected their most significant features. Without a rational system of classification, evolutionary relationships between most species would have been impossible to establish (see Chapter 11). But recognition of the **biological importance** of species took considerable time.

In Europe during the Middle Ages, species were collected and described on the basis of their culinary or medical properties. The discovery of many new lands, floras, faunas and species of plants and animals, as a result of the expansion of worldwide exploration and trade in the sixteenth and seventeenth centuries, greatly increased the problems of classification and began to raise questions about relationships. Thomas Moufet (1553–1604), a prominent sixteenth century English entomologist, described grasshoppers and locusts:

FIGURE 1-4 Presumed "missing links" between apes and humans in the Ladder of Nature. These individuals received binomial species designations, and Linnaeus tried to place them in his *Systema Naturae*. This figure is reproduced from an eighteenth century work by Linnaeus's student, C. E. Hoppius, who also noted the close similarity between humans and apes, "So near are some among the genera of Men and Apes as to structure of body: face, ears, mouth, teeth, hands, breasts; food imitation, gestures, especially in those species which walk erect and are properly called Anthropomorpha, so that marks sufficient for the genera are found with great difficulty." Social institutions, however, often greeted such proposed relationships with horror or derision: the 1770 suggestion by DeLisle de Sales that the orangutan was the human ancestor led to a prison sentence. (Reproduced from the original held by the Department of Special Collections of the University Libraries of Notre Dame.)

> Some are green, some black, some blue. Some fly with one pair of wings, others with more; those that have no wings they leap, those that cannot either fly or leap, they walk; some have longer shanks, some shorter. Some there are that sing, others are silent. And as there are many kinds of them in nature, so their names were almost infinite, which through the neglect of naturalists are grown out of use.

Nor were plants exempt from difficulties in classification. For example, Al-Dinawari's (820–895) *Book of Plants*, which was consulted through the Middle Ages, grouped plants according to at least two different systems: overwintering and growth.

> Plants are divided into three groups: in one, root and stem survive the winter; in the second the winter kills the stem, but the root survives and the plant develops anew from this surviving rootstock; in the third group both root and stem are killed by the winter, and the new plant develops from seeds scattered in the earth. All plants may also be arranged in three other groups: some rise without help in one stem, others rise also but need the help of some object to climb, whilst the plants of the third group do not rise above the soil, but creep along its surface and spread upon it.

Early attempts at classification usually followed Aristotle in postulating a broad category (for example, "substance"), and then creating subsidiary categories, each with its distinguishing elements (for example, body, animal), until an individual species could be placed into a particular subdivision. The method of classification devised by Carl Linnaeus (1707–1778)[7], the founder of systematics, represented a major advance. Beginning with a precise description of each species, Linnaeus grouped species closely related by their morphology into a category called a **genus** (plural genera). He then grouped related genera into **orders,** orders into classes, and established a system of **binomial nomenclature** in which each **species** name defines its membership in a genus and provides it with a unique species name and identity, for example, *Homo sapiens* (humans).

Designating the species as the basic unit of classification enabled Linnaeus to arrive at groupings far more "natural" in their interrelationships than many of the previously proposed artificial groups. In his scheme, species were separated or united into groups on the basis of fundamental structural and morphological features. To use a somewhat simplified

[7] Carl von Linné, usually known by the Latinized form of his name, Carolus Linnaeus, inherited his love of plants and their names from his father, Nils Ingemarsson Linnaeus, a Lutheran pastor.

example, one pre-Linnaean classification separated animals into those that can fly and those that cannot. Consequently, flying fish were considered to be hybrids between birds and fish. By ignoring categories based on lifestyle and confining his attention to a detailed description of the species itself, Linnaeus showed that a basic relationship of flying fish to other fish underlay the change in its fins that enables it to glide.[8] Therefore, except for those features shared by all vertebrate groups, there are no special birdlike structures in flying fish at all. Even though his system was idealistic — it treated species as ideal forms — Linnaeus's contribution to classification was an important step in allowing natural evolutionary relationships between organisms to be revealed.

Although late in life Linnaeus toyed with the concept of transitions between species, for much of his career he conceived of the species as a fixed entity. His concept was derived from the natural historian John Ray (1627–1705), who defined a species on the basis of its common descent. "The specific identity of the bull and the cow, of the man and the woman, originate from the fact that they are born of the same parents," wrote Ray. He attempted to separate different species on the basis of whether they could be traced to different ancestors. "A species is never born from the seed of another species." Thus, a species, with only rare exceptions, could never change, and its ultimate ancestor could only be divinely created. Linnaeus adopted this view but with the proviso that varieties within a species may show considerable non-heritable differences among themselves. Two examples from his work are his subdivision in 1758 of humans (*Homo sapiens*) into four races (Asiatic, American, European, African) and his designation in 1753 of the species *Beta vulgaris* for beets, whose cultivated varieties (spinach beet, chard, beetroot, fodder beet and sugar beet) were given varietal names, for example, *Beta vulgaris perennis* for sea beet. Linnaeus had second thoughts and in 1763 assigned the sea beet as a separate species, *Beta maritima*. Taxonomists now designate the sea beet as a subspecies *Beta vulgaris* subsp. *maritima* (L.). Why? Because it interbreeds with cultivated varieties of *Beta vulgaris*, from which it can be almost impossible to distinguish morphologically; variation within a single species can be considerable. Again, we see the idealism in Linnaeus' conception of species.

Under Linnaeus, the art of systematics developed rapidly as many species were described, mainly on the basis of their reproductive parts, and classified into groupings that are still valid today, despite the mix of artificial and natural categories.[9] Generally, however, classification was almost always based on appearance and not on observations of ancestry, because the classifiers (taxonomists) usually described preserved specimens whose natural behavior and origins were often unknown. In accord with idealist concepts, each species was believed to possess a unique "essence" that determined all its specific characters. This **"essentialist"** or **"typological"** view of species[10] was reinforced by taxonomists who deposited "type" specimens in museums or herbaria to be used as the standards (types) for classifying further specimens.

TABLE 1-1 A few of the major figures whose contributions in the nineteenth century or earlier influenced evolutionary concepts

Author	Contribution
Linnaeus 1707–1778	*System Naturae* (1735–1758)
Buffon 1707–1788	*Natural History* (1749–1767)
Malthus 1766–1834	*An Essay on the Principle of Population* (1798)
Cuvier 1769–1832	*Lessons of Comparative Anatomy* (1805)
Lamarck 1774–1829	*Zoological Philosophy* (1809)
Lyell 1797–1875	*Principles of Geology* (1830–1833)
Darwin 1809–1882	*Voyage of the Beagle* (1837) *On the Origin of Species* (1859)
Gray 1810–1888	*Darwiniana* (1876)
Mendel 1822–1884	*Experiments in Plant Hybridization* (1866)
Wallace 1823–1913	Joint essays with Darwin (1858)
Huxley 1825–1895	*Collected Essays* (1893–1894)
Weismann 1834–1914	*Studies in the Theory of Descent* (1882)
Haeckel 1834–1919	*General Morphology of Organisms* (1866)
Bateson 1861–1926	*Materials for the Study of Variation* (1894)

Although Linnaeus placed special emphasis on the species as the practical unit of classification, Buffon (1707–1788; **Table 1-1**) codified the notion that species are the only biological units that have a natural existence ("*Les espéces sont les seuls êtres de la nature*"). Buffon introduced the idea that species distinctions should be made on the basis of whether there were reproductive barriers to crossbreeding between groups ("reproductive isolation"), evidenced by whether fertile or sterile hybrids were produced:

> We should regard two animals as belonging to the same species if, by means of copulation, they can perpetuate themselves and preserve the likeness of the species; and we should regard them as belonging to different species if they are incapable of producing progeny by the same means.

To Buffon, considerable variation could occur between individuals of a species, perhaps eventually even produc-

[8] See the chapters in Hall (2007a) for the development, transformation and evolution of fins and limbs.

[9] Less well known, Linnaeus spent much of his life attempting to organize the economy of Sweden according to scientific principles, to adapt crops such as rice and tea to grow in the Arctic tundra and to domesticate elk, buffalo and guinea pigs as farm animals.

[10] A number of historians of systematics (P. F. Stevens, 1994; Winsor, 2003, 2006; and Müller-Wille, 2003) make the case that Linnaeus and most other pre-Darwinian systematists were not essentialists.

ing completely new varieties, for example, different kinds of dogs. Despite such variation, a species itself remained permanently distinguished from other species, although at times Buffon seemed to indicate the possibility that a species could change significantly (and through degeneration[11]), as the last lines of the quotation below show):

> Not only the ass and the horse, but also man, the apes, the quadruped, and all the animals, might be regarded as constituting but a single family. . . . If it were admitted that the ass is of the family of the horse, and differs from the horse only because it has varied from the original form, one could equally well say that the ape is of the family of man, that he is degenerate man, that man and ape have a common origin; that, in fact, all the families, among plants as well as animals, have come from a single stock, and that all animals are descended from a single animal, from which have sprung in the course of time, as a result of progress or of degeneration, all the other races of animals (*Natural History*, 4th volume, 1753).

Despite this clear statement of an evolutionary view, however, Buffon rejected transformation in part because it was contrary to religion ("all animals have participated equally in the grace of direct creation").

Strangely enough, the eighteenth-century barrier to the acceptance of evolution seemed to rest mostly on the reality of species. If species were indeed real, they seemed inevitably fixed. How could new species arise? Buffon, who had proposed evolutionary events on cosmological and geological scales, established three basic arguments *against* biological evolution, arguments that were used by antievolutionists well into the nineteenth century:

- New species have not appeared during recorded history.
- Although mating between different species fails to produce offspring or results only in sterile hybrids, this mechanism could certainly not apply to mating between individuals of the same species. How could individuals of a single species be separated from others of the same kind and become transformed into a new species?
- Where are all the missing links between existing species if transformation from one to the other has taken place? Numerous missing links had been imagined (Fig. 1-4) but Buffon claimed that none had been found, despite Tyson's (1699) dissection and comparison of monkeys, orangutans, apes and humans as variations on a single type.

Because these arguments were not refuted until after Darwin, it is no surprise that one of the first serious pre-Darwinian proponents of biological evolution, Jean-Baptiste de Lamarck (1744–1829), proposed that one must do away with the concept of the fixity of species (species distinctions as artificial and arbitrary, although they may be helpful in classification) to establish the possibility of evolution. The observable gaps between species, genera, families, and so on were only apparent, not real; all intermediate forms existed someplace on Earth, although they were not necessarily easy to discover.

Thus, although Lamarck shared the concept of the Great Chain of Being that species do not become extinct, because of his conception of a species, he did not believe that species were separately created, proposing rather that they had evolved from each other. His branching classification of animals (**Fig. 1-5**) introduced a direct challenge to the venerable doctrine of a Scale of Nature, which goes in only one direction, from imperfect to perfect. "In my opinion, the animal scale begins with at least two separate branches and . . . along its course, several ramifications seem to bring it to an end in specific places."

As discussed in Chapter 2, the mechanisms Lamarck offered to account for these evolutionary changes were inadequate. However, even if Lamarck's explanations had seemed reasonable, a more serious impediment to evolutionary thought concerned the questions of life itself: Is continuity between the generations of a species necessary at all? What if species arise anew every generation?

Spontaneous Generation

Until perhaps the middle of the nineteenth century, the common belief was that although most large organisms reproduce by sexual means, smaller organisms could arise spontaneously from mud or organic matter. Some folklore suggested that, when they died, larger organisms decomposed into smaller ones. There were even legends that magical transitions could change an individual of one species into another, a human into a werewolf, for example. About 400 years ago the physician and chemist Johann van Helmont (1577–1644) offered a classic expression 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 almost simultaneously. The Linnaean contribution

[11] See Box 19-1 for further discussion of degeneration in parasites with respect to progress.

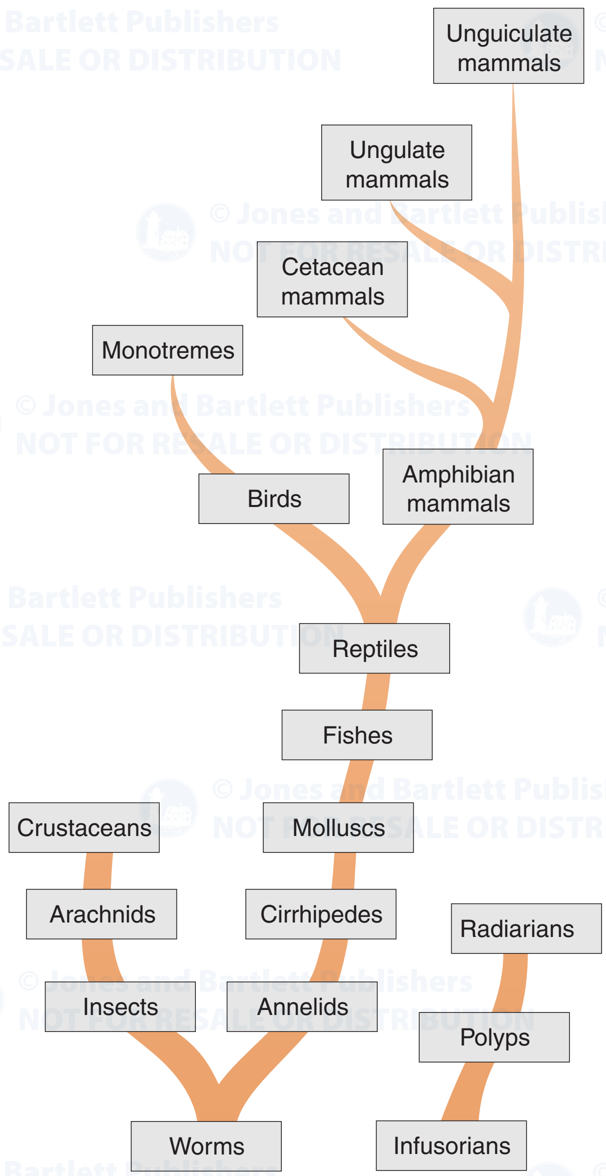


FIGURE 1-5 Evolutionary relationships among animals according to Lamarck.

of *species constancy* helped raise the question of the origin of species, but by insisting on *species fixity*, prevented consideration of any evolutionary transformations. Belief in **spontaneous generation,** in contrast, seemed contrary to species fixity, but at the same time 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 their origin or the sequence of their appearance?

By the late seventeenth century, use of the experimental method had begun, and a number of experimentalists showed that, at least for insects, spontaneous generation does not occur. In 1668, Francesco Redi (1621–1697) demonstrated that maggots (larvae) arise only from eggs laid by flies, and flies arise only from maggots. If meat is protected so that adult flies cannot lay their eggs, maggots and flies are not produced. A year later, Jan Swammerdam (1637–1680) showed that the insect larvae found in plant galls arise from eggs laid by adult insects. Within a century, further experiments demonstrated that even the appearance of the microscopic "beasties" observed by Antony van Leeuwenhoek (1632–1723) in decaying or fermenting solutions and broth could be explained as originating from previously existing particles. The 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 grow.

Preformation

Although the theory of spontaneous generation was not abandoned until the crucial experiments of the chemist Louis Pasteur (1822–1895) and the physician John Tyndall (1820–1893) in the nineteenth century, serious attempts to replace it with a theory of **preformationism** had begun much earlier (Farley, 1977). In the words of Swammerdam, preformation embodied the idea that "there is never generation in nature, only an increase in parts." That is, at conception, each embryonic organism is preformed as a perfect replica of the adult structure, which gradually enlarges through the nourishment provided by the egg and the environment. Some preformationists, now known as *ovists,* proposed that the miniature adult was contained within the maternal egg. Others (now known as *spermists* or animalculists) imagined that the adult in miniature was contained within the paternal seminal fluid (**Fig. 1-6**).

In its most extreme form, preformationism led to the ***emboîtment*** (encasement) theory, espoused by Bonnet and others, in which the initial member of a species encapsulates within it the preformed "germs" of all future generations; Eve's ovaries contained the entire preformed human species nested within like an infinite set of Russian dolls. Although preformation had the satisfying quality of explaining the many different plans of organismal growth and discounting the idea of spontaneous generation, it led once again to the fixity of species and brought the question of the origin of species back to an unknowable creation and/or creator.

Epigenesis

By the nineteenth century, improved experimental techniques and microscopic observations resulted in the replacement of preformationism[12] with the theory of **epigenesis,** according to which an embryo develops by gradually dif-

[12] The preformation story is much more complex than presented here. Today, we do not consider preformation versus epigenesis or that one side won out over the other. Each animal starts life as a preformed egg, so in this sense, preformation is alive and well. The egg nucleus, membranes and genes all are preformed. The way that these inherited structures are deployed and elaborated in development is epigenetic, as discussed further in Chapter 13.

FIGURE 1-6 A fully formed human (homunculus) encased within the head of a sperm as imagined by Nicholas Hartsoeker (1694).

ferentiating undifferentiated tissues into organs that were not present at conception. At first, this was believed to occur because of nonphysical forces, such as the contribution of "form" by the seminal fluid (Aristotle), an "*aura seminalis*" (William Harvey, 1578–1657) or "*vis essentialis*" (Kaspar Wolff, 1733–1794).

Such explanations are **vitalistic**: They ascribe to living beings a vital force that cannot be explained by any physical or chemical principles. By the mid-third of the nineteenth century — coinciding with the studies of the comparative embryologist Karl von Baer (1792–1876) — the prevailing view of epigenesis had changed and biologists could accept differentiation and growth as being as natural and explainable a set of processes as any others. In addition, Friedrich Wohler's (1800–1882) 1828 biochemical synthesis of an organic compound (urea), the first such extraorganismal synthesis, showed there was no mystical essence in organic molecules that could not be explained by the laws of chemistry. Such ideas of rational biology helped cultivate the climate in which evolutionary concepts could develop further. A sample of some of those who contributed to evolving evolutionary concepts in the eighteenth and nineteenth centuries is outlined in Table 1-1.

Fossils

An essential basis for understanding evolutionary relationships between organisms of the past, and for appreciating their lengthy history, was the study of their **fossil** remains.

It had long been known that the fossilized bones of animals do not resemble extant species, and that strange seashells can be found in the most unlikely places, such as mountaintops. The ancient Greeks were aware of such fossils, and a number of ancient writers, including Herodotus (484–425 BC), suggested that they could be explained by changes in the positions of sea and land. To Aristotle, there was no question that these changes occurred over considerable periods of time:

> The whole vital process of the earth takes place so gradually and in periods of time which are so immense compared with the length of our life, that these changes are not observed; and before their course can be recorded from the beginning to end, whole nations perish and are destroyed (Aristotle, Treatise on *Meteorology*).

But as Christianity gained ascendancy in Europe, influential church authorities began to estimate Earth's age by the number of generations since Adam in the biblical book of Genesis, calculating Earth's origin as no earlier than perhaps 4000 to 7000 BC. Limited to such a relatively short period, fossils could hardly be ascribed to a long historical process. During the sixteenth and seventeenth centuries, although regarded as being "naturally formed," these *stones* (now known as fossils) were regarded as images of God's creation, placed on Earth for man's admiration and use but naturally formed by God (**Fig. 1-7**.)

The discovery of fossils in exposed riverbanks, mines, and on eroded surfaces posed a challenge to the concept of the Great Chain of Being. For example, Thomas Jefferson (1743–1826; agriculturalist, botanist, fossil hunter and third president of the United States) discovered the extinct clawed giant sloth *Megalonix jeffersoni* (**Fig. 1-8**), which he mistakenly thought was a giant lion that perhaps still existed in the unexplored areas of North America (Rudwick, 2005).

Did fossils indicate possible errors in the plan of nature, causing some species to become extinct? They were commonly called *lusi naturae*, or "jokes of nature." Were there gaps in the Ladder of Nature caused by the loss of

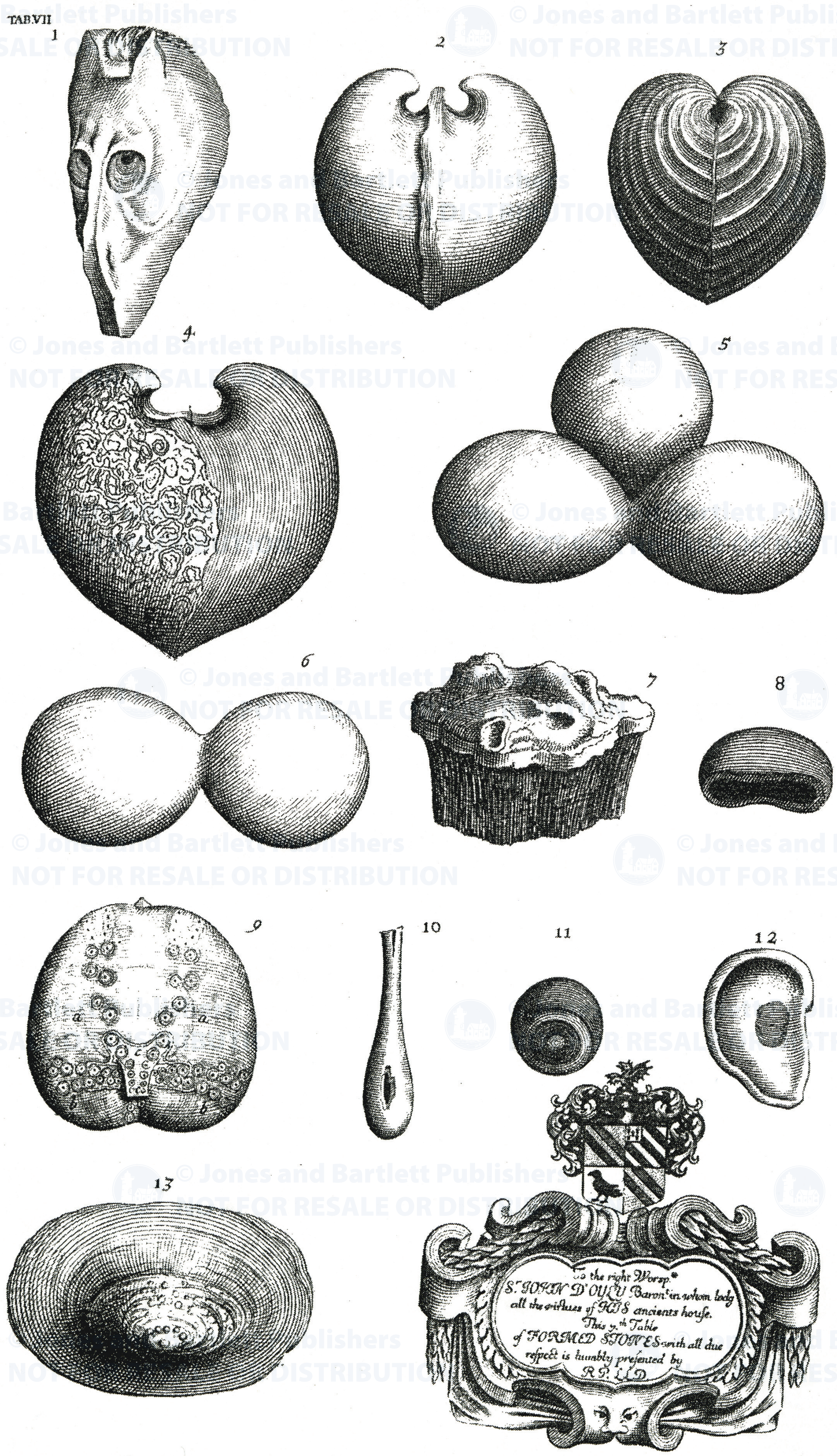


FIGURE 1-7 Plate 7 from *The Natural History of Oxfordshire* by Robert Plot (1676) illustrating naturally formed stones interpreted as representing parts of the human body, including: the heart (1-4) the holes in 1 being interpreted as the major artery taking blood away from the ventricles; the brain (9, showing the cerebellum and medulla oblongata); nerves (10, the olfactory nerve); the eye obscured by a cataract (11); and the external ear or pinna (12).

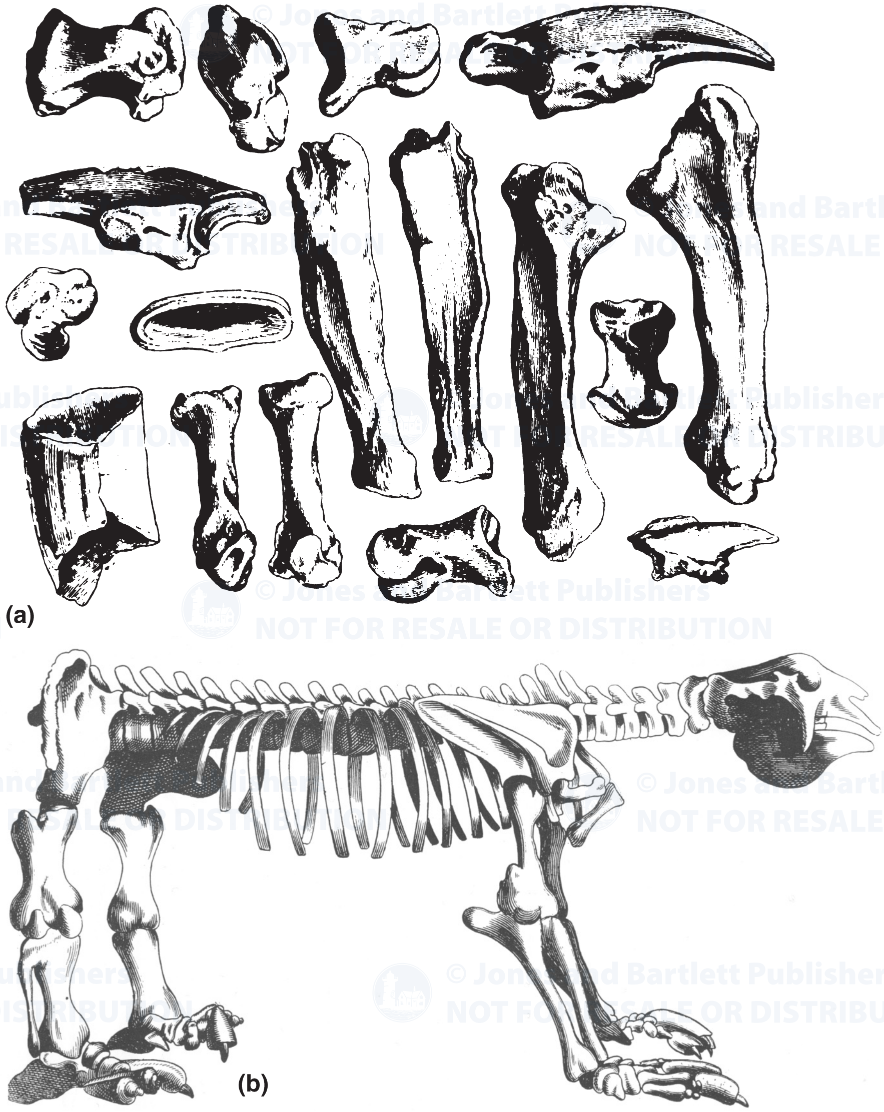


FIGURE 1-8 (a) Some of the bones of the extinct giant sloth, *Megalonix jeffersoni*, discovered in western Virginia in 1796. (b) Reconstruction by Cuvier of the skeleton of a similar extinct South American giant sloth, *Megatherium*. Both sloths were edentates, clawed mammals without cutting teeth (From Greene, J. C., 1959. *The Death of Adam*. Iowa State University Press, Ames.)

these extinct species? Like many others who addressed these questions, Jefferson proposed that these species were not really extinct, only rare: "Such is the economy of nature, that no instance can be produced of her having permitted any one race of her animals to become extinct; of her having formed any link in her great works so weak to be broken." Other theories sought to explain fossils as caused by the Noachian flood described in Genesis or having purposely been implanted into Earth at the time of creation in order to test humanity's faith in religion.

Contrary arguments such as those proposing the reality of fossil species by the physician and naturalist Robert Hooke (1635–1703) and by the anatomist and geologist Nicolaus Steno (1638–1686) led to more naturalistic attempts to understand fossil origins. Such views helped place fossils in a historical sequence. When arranged by stratigraphic age, with deeper strata signifying older age than superimposed strata, older fossils showed greater differences from extant species than did later fossils (see Fig. 5-5), indicating changes over time (**Box 1-2** — Classification of Geological Strata).

Once the reality of fossils and of extinction was accepted, it was possible to conceive of a "law of succession" in which one form replaced another.

One of the commonly held theories during the late 1700s and early 1800s was **catastrophism,** popularized largely by followers of Georges Cuvier (1769–1832), one of the most gifted French comparative anatomists and the founder of paleontology (Table 1-1).[13] According to catastrophism, the sharp discontinuities in the geological record — stratifications of rocks, layering of fossils and transition from marine

[13] Weishampel and White (2003) provided the wonderful service of translating and reprinting important papers in the discovery of dinosaur fossils, including seven articles by Cuvier on crocodile fossils.

BOX 1-2 Classification of Geological Strata

The system of geological classification adopted in the eighteenth and early nineteenth centuries, which was initially suggested by the mining specialist and "Father of Italian Geology," Giovanni Arduino (1714–1795), followed the practice of designating **primary rocks** as those without fossils. These were believed to date from the origin of Earth's crust and appeared as typical nonstratified, ore-bearing outcroppings in mountainous areas.

Geologists called stratified fossiliferous rocks, such as sandstone and limestone, **secondary.** Secondary strata contained ancient molluscan fossils such as ammonites and belemnites (see Chapter 15) as well as early fish and reptiles that differed considerably from present forms (see Chapters 17 and 18). Geologists believed **tertiary sedimentary rocks** to be derived from secondary strata by flooding, erosion, volcanic action and so on, and to contain ancient representatives of more recent forms such as mammals.

Quaternary rocks represented the glacial and alluvial deposits of relatively recent times. Because neither all mountains nor all strata are of the same age, these divisions were difficult to apply universally. All except tertiary and quaternary were abandoned. *Tertiary* came to mean the period of preglacial deposits corresponding to most of the Cenozoic period. *Quaternary* means the period dating from the Pleistocene ice age deposits to the present.

fossils to freshwater fossils — indicated sudden upheavals caused by catastrophes, glaciations, floods, and so on. Fossils were recognized as extinct species "whose place those which exist today have filled, perhaps to be themselves destroyed and replaced by others." To some upholders of the biblical account, catastrophism had the advantage of explaining at least some catastrophes as obvious departures from "natural" laws that could be ascribed to divine intervention. Some, such as the Swiss paleontologist, geologist, naturalist and founder of the Museum of Comparative Zoology at Harvard University Louis Agassiz (1807–1873), proposed that there may have been as many as 50 to 100 successive special divine creations. This approach justified the prior existence of fossil species *and* the biblical flood, and made it possible to conceive that all extant organisms arose within the time span the Judeo-Christian Bible provided, although preceded by many geological ages.

In contrast to Cuvier's catastrophist position, Lamarck proposed that geological discontinuities represented gradual changes in the environment and climate to which species were exposed. Through effects on organisms these changes led to species transformation. This **uniformitarian** concept, that the steady, uniform action of the forces of nature could account for Earth's features, had been foreshadowed by Buffon and others and was strongly developed in the work of the geologist James Hutton (1726–1797).[14] Later, Charles Lyell (1797–1875), a geologist and contemporary of Charles Darwin, offered the *uniformitarian reply to catastrophism* through the following arguments:

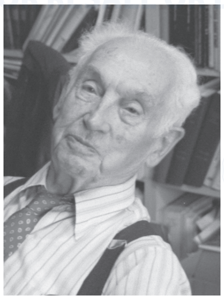
1. Sharp, catastrophic discontinuities are absent if geological strata are examined over widespread geographical areas. Any widely distributed stratum often shows considerable regularity in its structure and composition (see Box 1-2). Only in specific localities do rapid shifts seem to appear and then because of local changes.
2. Changes in the geological record arise from the action of erosive natural forces such as rain and wind as well as from volcanic up thrusts and flood deposits (Box 1-2). The laws of motion and gravity that govern natural events are constant through time. Therefore, past events are caused by the same forces that produce phenomena today although the extent of phenomena, such as volcanism, might have fluctuated in the past. This means that all natural causes for phenomena should be investigated before supernatural causes are used to explain them.
3. Earth must be very old for its many geological changes to have taken place by such gradual processes.

The frontispiece of Lyell's 1830 *Principles of Geology* is a portrait of the three remaining columns of the ruined "Temple of Serapis" in Pozzuoli, Italy, showing that they had been historically subjected to rise and fall in sea level. A 3-m section of these columns contains holes bored by molluscan bivalves, indicating that these columns were once partially submerged. Lyell used this portrait through 12 editions of his book as an example of gradual geological change. Thus, although uniformitarianism did not exclude sudden geological changes such as floods, volcanic eruptions and meteorite impacts — events that were of common or recorded knowledge — it led to the view that even such "catastrophes" could be naturally caused and rationally explained.

The transition from catastrophism to uniformitarianism had profound effects because it helped liberate scientific thinking from the concept of a static universe powered by capricious, unexplainable changes to one that is perpetually dynamic and more historically understandable. Charles

[14] In physics, Isaac Newton pointed out that, "we are to admit no more causes of natural things than such as are both true and sufficient to explain their appearance." The case has been made that evolution was (is) to biology as energy was (is) to physics, as each synthesizes previously separate domains to find deeper common principles. However, because the laws of physics pertaining to the physical interactions of matter relate to the transfer of energy, while biology deals with transform of information, biology cannot be reduced to physics.

Ernst Mayr



Birthday: July 5, 1904
Birthplace: Germany
Died: February 5, 2005[15]
"Late Professor Emeritus
Harvard University
Cambridge, Massachusetts."

What prompted your initial interest in evolution?

I was a born naturalist, roaming the fields and woods ever since I was a small boy. What most attracted me was the immense diversity of life. Why are there so many different kinds of species? Later on I asked how they originated. I looked for the solution on expeditions to New Guinea and the Solomon Islands in the 1920s.

What do you think has been most valuable or interesting among the discoveries you have made in science?

Science advances by discoveries and by the introduction of new concepts. It is to the latter that I made most of my contributions:

- The biological species concept
- The concept of sibling species
- The importance of geographic speciation
- Speciation through founder populations
- The origin of evolutionary novelties
- Species turnover on islands
- The relation between population size and evolution
- The holistic concept of the genotype
- Individuals and social groups are the targets of selection, not genes

My most interesting discovery was the great speedup of evolutionary rate in small populations isolated beyond the previous species borders.

What areas of research are you (or your laboratory) presently engaged in?

I am now exploring the philosophical consequences of the discovery of new evolutionary principles.

In which directions do you think future work in your field needs to be done?

The internal structure of the genotype, the workings of the central nervous system, and the interaction of species in the ecosystem are now the most exciting frontiers of biology.

What advice would you offer to students who are interested in a career in your field of evolution?

My advice to beginners is to become thoroughly familiar with one particular group of organisms in order to be able to test any new ideas or theories against the background of that set of solid facts. Pure speculation and model building without a solid factual basis rarely leads to sound advances.

[15] Ernst Mayr, one of the most influential evolutionary biologists of the twentieth century, was a staunch defender of the Modern Synthesis, a synthesis that he played a major role in creating. His last book entitled, *What Evolution Is*, published in 2001, is a thorough and thoughtful exploration of evolutionary biology. His contributions are celebrated in *Systematics and the Origin of Species: On Ernst Mayr's 100th Birthday*, which you can read on the Internet at *http://newton.nap.edu/catalog/11310.html#toc*.

EVOLUTION ON THE WEB biology.jbpub.com/book/evolution

Darwin first offered an acceptable explanation for historical changes among organisms and thereby helped tie all organisms together by a community of descent: **evolution.**

KEY TERMS

archetype	idealism
binomial nomenclature	Ladder of Nature
Bauplan	preformationism
catastrophism	species
emboitment	spontaneous generation
epigenesis	teleological
fossil	uniformitarian
Great Chain of Being	vitalistic

DISCUSSION QUESTIONS

1. What is Platonic idealism?
2. Why did idealism become such an important approach to nature?
3. What is the connection between idealism and the description and classification of organisms?
4. Is the concept of the Great Chain of Being (Ladder of Nature) idealistic? Why or why not?
5. Can the concept of biological evolution be held by those who believe in idealism?
6. Why has freedom from cultural constraints and prejudices been more difficult for evolutionary studies than for physics or chemistry?

7. Discuss how the concept of the spontaneous generation of species contradicts the concept that each species is created individually.
8. What obstacles made it difficult for individuals to consider the reality of fossil species?
9. What differences exist between the concepts of catastrophism and uniformitarianism in their explanations for evolutionary changes?
10. Can uniformitarianism be defined to include occasional catastrophic changes?

EVOLUTION ON THE WEB

Explore evolution on the Internet! Visit the accompanying Web site for *Strickberger's Evolution*, Fourth Edition, at http://www.biology.jbpub.com/book/evolution for exercises and links relating to topics covered in this chapter.

RECOMMENDED READING Historical Aspects of Evolution

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