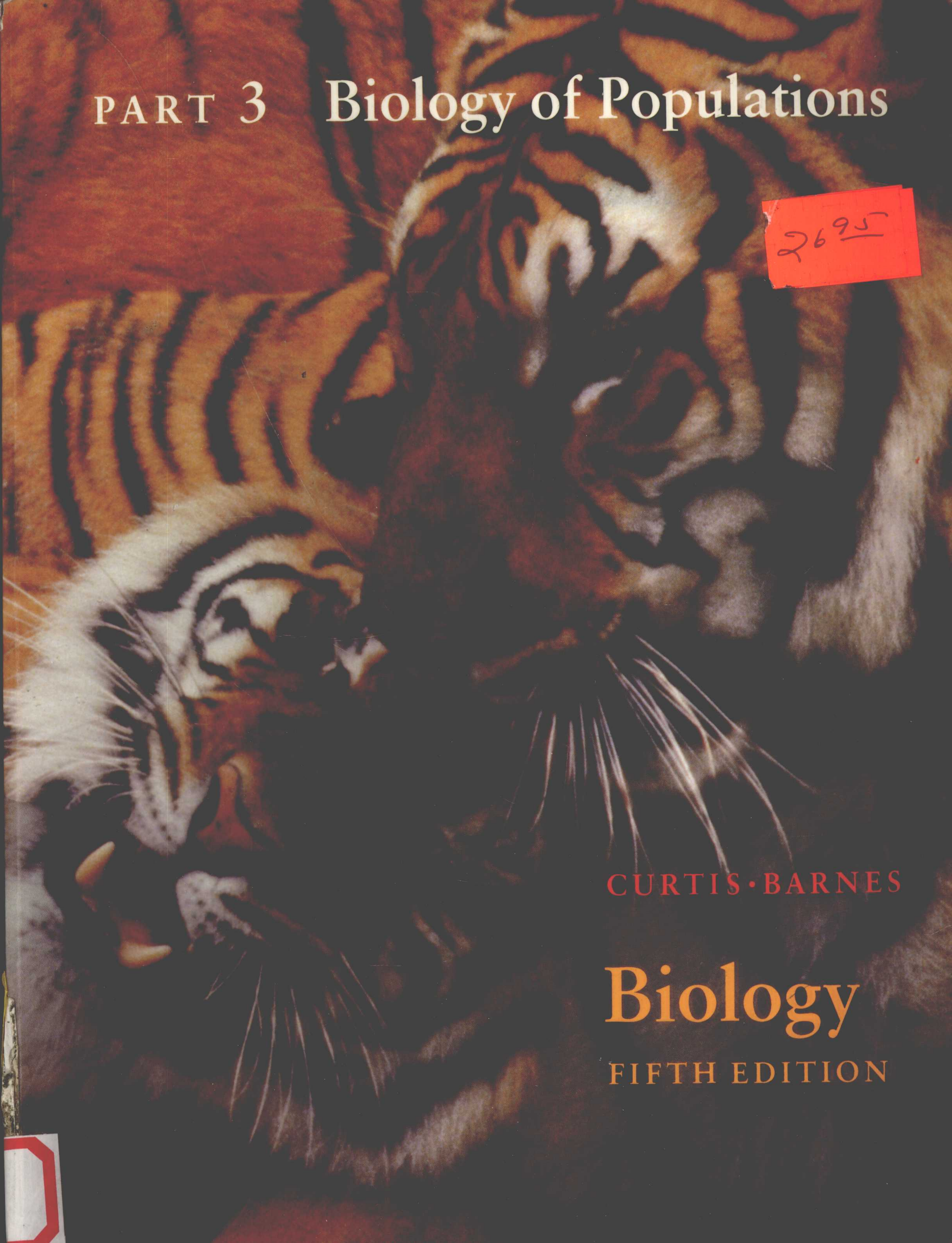

PART 3 Biology of Populations

CURTIS · BARNES

Biology

FIFTH EDITION

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PART 3 Biology of Populations

HELENA CURTIS

N. SUE BARNES

WORTH PUBLISHERS, INC.

Young Bengal tigers (Panthera tigris). *Tigers originated in Siberia and spread south to India and adjoining countries. Intolerant of the heat of their tropical habitat, Bengal tigers cool off by immersing themselves in water and, in fact, are excellent swimmers. They hunt in the cool of the evening, relying on their sharp eyes and ears and their especially well-developed sense of smell. Although social when young, tigers become solitary as adults. Human destruction of the forest habitat of the Bengal tiger has caused it to become severely endangered. (© Kjell Sandved)*

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33 IRVING PLACE

NEW YORK, NEW YORK 10003

This book is dedicated to those whose creative and painstaking studies have contributed to our understanding of biology.

Preface

Preface

In the twenty years since the first edition of *Biology* appeared, the science of biology has been characterized by ever accelerating change, including not only a flood of new information but also new ideas and unifying concepts. Some areas of biology have undergone metamorphoses before our very eyes, while others have attained a new maturity. This has presented us—now at our word processors—and you—in the classroom and laboratory—with new challenges and opportunities as we work together to provide students with a solid foundation in the principles of biology while simultaneously sharing with them the excitement of the contemporary science.

With this, the Fifth Edition, *Biology* becomes both one of the oldest and one of the newest introductory biology textbooks. One of our principal goals in preparing this edition has been to maintain a balance between the old and the new. This has required not only a willingness to discard material, but also considerable care that we not eliminate or slight material that, although not new, is essential if students are to be adequately prepared to understand current and future developments in biology. Simultaneously, we have, of course, wanted to be as up to the minute as possible, without becoming merely trendy. At a time when important discoveries are published almost continuously, there is a temptation to become so engrossed in the new that we lose sight of the fact that the majority of today's students are, like their predecessors, coming to the formal study of contemporary biology for the first time. The clear explication of the basic principles of biology, with pertinent and readily understood examples, has become increasingly important with each passing year. Thus, specific topics for detailed treatment have been selected on the basis of their centrality to modern biology, their utility in illuminating basic principles, their importance as part of the requisite store of knowledge of an educated adult as we approach a new century, and their inherent interest and appeal to students. Throughout, we have tried to provide the underlying framework and arouse student curiosity so that a foundation is laid for those areas—very diverse—in which you may wish to give more extensive coverage in the classroom or laboratory than is possible in any introductory textbook, regardless of its length.

The central, essential foundation of biology is, of course, evolution, the major organizing theme of this text as of all modern biology texts. As in previous editions, the stage is set in the Introduction, which focuses on the development of the Darwinian theory. New to the Introduction is a section previewing the other major unifying principles of modern biology that are also recurring themes throughout the text; also new is a brief overview of the diversity of life. Both are designed to provide students with a broad framework before they begin their study of the details on which modern biology is built. In this edition, we have also strengthened the introductory discussion of the nature of science, and, throughout the text, we have included more information about how biologists know what they know and how scientists in general go about their business.

After the Introduction, this edition, like previous editions, follows the levels-of-organization approach. Part 1 deals with life at the subcellular and cellular levels, Part 2 with organisms, and Part 3 with populations, ending with a survey of the distribution of life on earth. Each part is divided into two or three sections. A significant amount of restructuring has occurred in the sequence of chapters within certain sections and within the chapters themselves.

One of the most striking aspects of the enormous burst of new discoveries in molecular and cell biology since the Fourth Edition is the power of these discoveries to explain processes that previously could only be described—and in the most general terms. The immune response, olfaction and color vision, events at the synapse, the summing of information by individual neurons, and differentiation and morphogenesis in animal development are just a few of the many phenomena whose secrets are being revealed by studies at the molecular and cellular level. These revelations depend, in large part, on what is now a flood tide of reports identifying specific membrane proteins, their amino acid sequences, their three-dimensional structures, and, in many cases, the nucleotide sequences of the genes coding for the proteins and the location of these genes within the genome. Because these discoveries, although fascinating in and of themselves, are of such value in explaining organismal phenomena, we have generally chosen to defer their discussion to later sections of the text, where their significance will be most readily grasped by students. Molecular and cell biology have, in many ways, come of age, and it seems to us that the essential task in these early sections of the book has become the clear communication of the underlying principles on which so much is now being built—rather than a catalog of the latest new discoveries, which will soon be superseded by even more exciting ones.

The extraordinary pace of discovery in genetics, principally as a result of recombinant DNA technology, requires, with each new edition, a major rethinking of Section 3. Responses to our surveys indicate that, however tempting it might be to begin the section with molecular genetics and to reduce the coverage of classical genetics, doing so could make this most exciting area of modern biology less accessible to students. Thus, as in previous editions, we begin our consideration of genetics with Mendel and take an essentially historical approach to the development of the powerful science we know today. Within that overall framework, however, there has been the addition of a significant amount of new material, coupled with a number of internal reorganizations that we believe provide greater clarity and a smoother conceptual development in our coverage of molecular genetics.

Part 2, Biology of Organisms, has also undergone many changes, particularly in the early chapters of Section 4 and in Sections 5 and 6. In the previous edition, Section 4, The Diversity of Life, was significantly expanded. The enthusiasm with which the revised section was received—plus our own continuing awe at the incredible variety of living organisms—led to our decision to retain the expanded section intact. We have, however, made major revisions in the first chapter of the section, dealing with the classification of organisms, and minor revisions throughout the section.

The organization of Section 5, the Biology of Plants, has long been problematic. It has been difficult to find a sequence that would flow logically, coordinate well with laboratory programs, and—most important—captivate students with the beauty and biological accomplishments of plants without overwhelming them with the vocabulary necessary for an accurate description of the living plant. In this edition we have chosen to begin the section with the familiar—the flower—and with the dynamic process of plant reproduction, a sequence that flows directly from the discussion of plant evolution and diversity in Section 4. In the following chapter, the anatomy of the plant body is considered in conjunction with another dynamic process, the development of the embryo into the mature sporophyte. The two chapters on plant hormones and plant responses in the Fourth Edition have now been merged into one integrated chapter; new understandings of the physiological processes of plants have made such a separation increasingly artificial.

In Section 6, the Biology of Animals, we have retained the overall organizational scheme and problem-solving approach of the Fourth Edition, while significantly revising many chapters. As noted previously, animal physiology is one of the principal areas in which enormous and rapid progress is being made as a result of new discoveries at the molecular and cellular level, and we have tried to capture and share with students as much of the current excitement as possible. Although we have continued to use the human animal—inherently fascinating to most students—as our representative organism in these chapters, we have strengthened the comparative thread and made explicit much comparative material that was previously implicit.

Part 3, the Biology of Populations, covers what G. E. Hutchinson aptly described as "the ecological theater and the evolutionary play." Modern evolutionary theory and ecology are so intertwined that any separation of the two is arbitrary. We believe, however, that the student's understanding of modern ecology is deepened and enriched if it is preceded by a knowledge of the mechanisms of evolution.

In Section 7, Evolution, the five chapters of the previous edition have been reworked into four. As in the Fourth Edition, the section begins with a chapter that reviews the key points of Darwin's theory, examines the types of evidence that support evolution, and considers the changes that have occurred in evolutionary theory since Darwin's original formulation. This is followed by extensively revised chapters on the genetic basis of evolution, natural selection, and the origin of species. Then follow two chapters, also heavily revised, on the evolution of the hominids and on animal behavior and its evolution. Many of you have told us that you prefer to cover human evolution while the discussion of evolutionary mechanisms is still fresh in students' minds, and we have accordingly shifted that chapter to this section from the end of the book. Behavior is a topic for which little, if any, time is available in many courses, but it holds great interest for students, professors, and these authors alike. We have tried to provide students with a solid introduction to the contemporary study of behavior and then to focus on topics that we think are most likely to be of immediate interest and appeal to them.

Section 8, Ecology, has also been extensively revised, as we attempt to track the continual shifts, rethinkings, and controversies that characterize this most vibrant science. As in the Fourth Edition, the section moves from population dynamics, through the interactions of populations in communities and ecosystems, to the overall organization and distribution of life on earth. The text ends with a consideration of the tropical forests—the most complex and most seriously threatened of all ecological systems.

Each section ends with suggestions for further reading. Scientifically speaking, the selections are arbitrary. They were chosen not as documentation for statements in the book or as fuller presentations of difficult subjects, but rather because of their accessibility to students. Our hope is that at least some students will continue reading on their own, preferably reports not yet published about discoveries just now being dreamed of.

A number of new supplements accompany this edition of *Biology.* Of particular interest is *More Biology in the Laboratory,* by Doris R. Helms of Clemson University, an expanded version of *Biology in the Laboratory,* which accompanies the Fourth Edition of *Invitation to Biology.* A detailed Preparator's Guide accompanies the lab manual. Other supplements include *BioBytes,* a series of computer simulations by Robert Kosinski of Clemson University, a Study Guide and a Test

Bank by David J. Fox of the University of Tennessee, a new computerized test-generation system, a new and greatly expanded Instructor's Resource Manual by Debora Mann of Clemson University, and an extensive set of acetate transparencies, most of them in color.

As with previous editions, we have been deeply dependent on the advice of consultants and reviewers. In addition to her work on the new laboratory manual, Dori Helms played a major role in the revisions of the genetics section, the plant section, and the development chapter in animal physiology. She has generously shared with us her extensive knowledge, her wealth of experience in the classroom and laboratory, and her enthusiasm—all of which have been marvelous resources that we have greatly appreciated.

We are also deeply indebted to Rita Calvo of Cornell University, who reviewed a series of revisions of the genetics section; to Jacques Chiller of the Lilly Research Laboratories, who has been an invaluable source on contemporary immunology; to Mark W. Dubin of the University of Colorado, who guided us through our revision of the integration and control chapters of animal physiology; and to Manuel C. Molles, Jr., of the University of New Mexico, and Andrew Blaustein of Oregon State University, both of whom made major contributions to our revision of the evolution and ecology sections.

In addition, we have been greatly assisted by advice and counsel from the following reviewers:

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As always, the preparation of a new edition is a staggering and complex task, and its successful completion has depended on the efforts of many highly talented individuals. In particular, we wish to thank Shirley Baty, who, in addition to preparing many new illustrations for this edition, has reworked virtually all of the Fourth Edition art as we converted the book to full color throughout; David Hinchman, Anne Feldman, and Elaine Bernstein, who have located an enormous number of marvelous new photographs and micrographs; John Timpane, who prepared the comprehensive index; George Touloumes and the members of his staff who are responsible for the design and layout of each page of the book; Sarah Segal, who has managed the production process and somehow kept us all on course; and Sally Anderson, our extraordinary editor, and her capable assistant, Lindsey Bowman. Sally's editorial expertise, her thorough knowledge of biology in general and of this text in particular, and her long experience in working with us both have played an incalculable role in the successful completion of this revision. And, a special thank you to Bob Worth, whose vision and constant support have made it all possible.

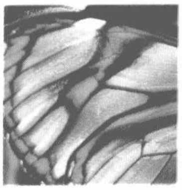
Finally, we want to thank all of the professors and students who have written to us, some with criticisms, some with suggestions, some with questions, and some simply because they enjoyed the book. These letters serve to remind us of how privileged we are to be writing for young people. We continue to appreciate their curiosity, their energy, their imaginativeness, and their dislike of the pompous and pedantic. We hope we serve them well.

New York — Helena Curtis

December, 1988 — N. Sue Barnes

An added note: As you may have noticed, with this edition of *Biology*, N. Sue Barnes is listed as coauthor. This is a recognition long overdue. Sue has been a member of the team for eleven years now. Over this period of time, she has assumed increasing responsibility for the revisions of both *Biology* and *Invitation to Biology* (on which she has been listed as coauthor for the last two editions). The Fifth Edition of *Biology* would have been impossible without her. In addition, I wish to express my personal gratitude for her integrity, patience, fortitude, and good spirits—and for the fact that she always comes through.

H.C.



Introduction

In 1831, the young Charles Darwin set sail from England on what was to prove the most consequential voyage in the history of biology. Not yet 23, Darwin had already abandoned a proposed career in medicine—he described himself as fleeing a surgical theater in which an operation was being performed on an unanesthetized child—and was a reluctant candidate for the clergy, a profession deemed suitable for the younger son of an English gentleman. An indifferent student, Darwin was an ardent hunter and horseman, a collector of beetles, mollusks, and shells, and an amateur botanist and geologist. When the captain of the surveying ship H.M.S. *Beagle,* himself only a little older than Darwin, offered passage for a young gentleman who would volunteer to go without pay, Darwin eagerly seized this opportunity to pursue his interest in natural history. The voyage, which lasted five years, shaped the course of Darwin's future work. He returned to an inherited fortune, an estate in the English countryside, and a lifetime of independent work and study that radically changed our view of life and of our place in the living world.

THE ROAD TO EVOLUTIONARY THEORY

That Darwin was the founder of the modern theory of evolution is well known. Although he was not the first to propose that organisms **evolve**—or change—through time, he was the first to amass a large body of supporting evidence and the first to propose a valid mechanism by which evolution might occur. In order to understand the meaning and significance of Darwin's theory, it is useful to look at the intellectual climate in which it was formulated.

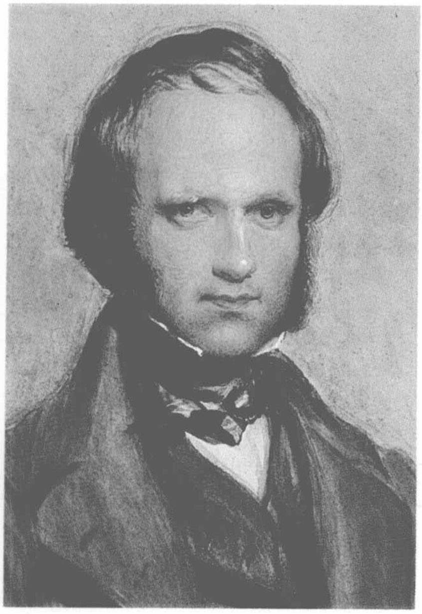
Aristotle (384–322 B.C.), the first great biologist, believed that all living things could be arranged in a hierarchy. This hierarchy became known as the *Scala Naturae,* or ladder of nature, in which the simplest creatures had a humble position on the bottommost rung, man occupied the top rung, and all other organisms had their proper places in between. Until the late nineteenth century, many biologists believed in such a natural hierarchy. But whereas to Aristotle living organisms had always existed, the later biologists (at least those of the Occidental world) believed, in harmony with the teachings of the Old Testament, that all living things were the products of a divine creation. They believed, moreover, that most were created for the service or pleasure of mankind.

That each type of living thing came into existence in its present form—specially and specifically created—was a compelling idea. How else could one explain the astonishing extent to which every living thing was adapted to its environment and to its role in nature? It was not only the authority of the Church but also, so it seemed, the evidence before one's own eyes that gave such strength to the concept of special creation.

I-1 *When Charles Darwin visited the Galapagos archipelago, he found that each major island had its own variety of tortoise, so distinct from the others that it was easily recognized by local sailors and fishermen. This was one of the clues that led him to the formulation of the theory of evolution.*

The Galapagos consists of 13 volcanic islands that pushed up from the sea more than a million years ago. The major vegetation is thornbush and cactus, and the original black basaltic lava is often visible, as it is beneath the lumbering feet of this tortoise on Hood Island—"what we might imagine the cultivated parts of the Infernal regions to be," young Darwin wrote in his diary.

Among those who believed in divine creation was Carolus Linnaeus (1707–1778), the great Swedish naturalist who devised our present system of nomenclature for species, or kinds, of organisms. In 1753, Linnaeus published *Species Plantarum,* which described, in two encyclopedic volumes, every species of plant known at the time. Even as Linnaeus was at work on this massive project, explorers were returning to Europe from Africa and the New World with previously undescribed plants and animals and even, apparently, new kinds of human beings. Linnaeus revised edition after edition to accommodate these findings, but he did not change his opinion that all species now in existence were created by the sixth day of God's labor and have remained fixed ever since. During Linnaeus's time, however, it became clear that the pattern of creation was far more complex than had been originally envisioned.



I–2 *Charles Darwin in 1840, four years after he returned from his five-year voyage on H.M.S.* Beagle. *In his later book,* The Voyage of the *Beagle, Darwin made the following comments about his selection for the voyage: "Afterwards, on becoming very intimate with Fitz Roy [the captain of the* Beagle*], I heard that I had run a very narrow risk of being rejected on account of the shape of my nose! He . . . was convinced that he could judge of a man's character by the outline of his features; and he doubted whether anyone with my nose could possess sufficient energy and determination for the voyage. But I think he was afterwards well satisfied that my nose had spoken falsely."*

Evolution before Darwin

The idea that organisms might evolve through time, with one type of organism giving rise to another type of organism, is an ancient one, predating Aristotle. A school of Greek philosophy, founded by Anaximander (611–547 B.C.) and culminating in the writings of the Roman Lucretius (99–55 B.C.), developed not only an atomic theory but also an evolutionary theory, both of which are strikingly similar to modern conceptions. The work of this school, however, was largely unknown in Europe at the time that the science of biology, as we know it today, began to take form.

In the eighteenth century, the French scientist Georges-Louis Leclerc de Buffon (1707–1788) was among the first to propose that species might undergo changes in the course of time. He suggested that, in addition to the numerous creatures that were produced by divine creation at the beginning of the world, "there are lesser families conceived by Nature and produced by Time." Buffon believed that these changes took place by a process of degeneration. In fact, as he summed it up, ". . . improvement and degeneration are the same thing, for both imply an alteration of the original constitution." Buffon's hypothesis, although vague as to the way in which changes might occur, did attempt to explain the bewildering variety of creatures in the modern world.

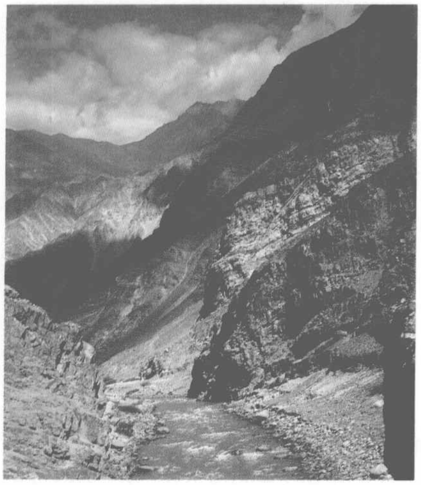
Another doubter of fixed and unchanging species was Erasmus Darwin (1731–1802), Charles Darwin's grandfather. Erasmus Darwin was a physician, a gentleman naturalist, and a prolific writer, often in verse, on both botany and zoology. He suggested, largely in asides and footnotes, that species have historical connections with one another, that animals may change in response to their environment, and that their offspring may inherit these changes. He maintained, for instance, that a polar bear is an "ordinary" bear that, by living in the Arctic, became modified and passed the modifications along to its cubs. These ideas were never clearly formulated but are interesting because of their possible effects on Charles Darwin, although the latter, born after his grandfather died, did not profess to hold his grandfather's views in high esteem.

The Age of the Earth

It was geologists, more than biologists, who paved the way for modern evolutionary theory. One of the most influential of these was James Hutton (1726–1797). Hutton proposed that the earth had been molded not by sudden, violent events but by slow and gradual processes—wind, weather, and the flow of water—the same processes that can be seen at work in the world today. This theory of Hutton's, which was known as uniformitarianism, was important for three reasons. First, it implied that the earth has a long history, which was a new idea to eighteenth-century Europeans. Christian theologians, by counting the successive generations since Adam (as recorded in the Bible), had calculated the maximum

4004 BC

age of the earth at about 6,000 years. As far as we know, no one since the followers of Anaximander (whose school maintained that the earth was infinitely old) had thought in terms of a longer period. Yet 6,000 years is far too short for major evolutionary changes to take place, by any theory. Second, the theory of uniformitarianism stated that change is itself the *normal* course of events, as opposed to a static system interrupted by an occasional unusual event, such as an earthquake. Third, although this was never explicit, uniformitarianism suggested that there might be alternatives to the literal interpretation of the Bible.



I–3 *While the* Beagle *sailed up the west coast of South America, Darwin explored the Andes on foot and horseback. He saw geological strata such as these, discovered fossil sea shells at about 3,700 meters (12,000 feet), and was witness to the upheaval of the earth produced by a major earthquake that occurred while he was there. In 1846, he published a book on his geological observations in South America. Strata are now seen as pages in evolutionary history.*

The Fossil Record

During the latter part of the eighteenth century, there was a revival of interest in fossils, which are the preserved remains of organisms long since deceased. In previous centuries, fossils had been collected as curiosities, but they had generally been regarded either as accidents of nature—stones that somehow looked like shells—or as evidence of great catastrophes, such as the Flood described in the Old Testament. The English surveyor William Smith (1769–1839) was among the first to study the distribution of fossils scientifically. Whenever his work took him down into a mine or along canals or cross-country, he carefully noted the order of the different layers of rock, known as geological strata, and collected the fossils from each layer. He eventually established that each stratum, no matter where he came across it in England, contained characteristic kinds of fossils and that these fossils were actually the best way to identify a particular stratum in a number of different geographic locations. (The use of fossils to identify strata is still widely practiced, for instance, by geologists looking for oil.) Smith did not interpret his findings, but the implication that the present surface of the earth had been formed layer by layer over the course of time was an unavoidable one.

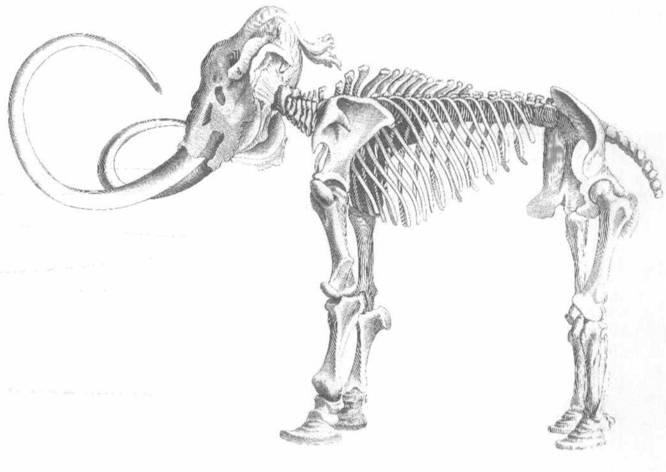
Like Hutton's world, the world seen and described by William Smith was clearly a very ancient one. A revolution in geology was beginning; earth science was becoming a study of time and change rather than a mere cataloging of types of rocks. As a consequence, the history of the earth became inseparable from the history of living organisms, as revealed in the fossil record.

Catastrophism

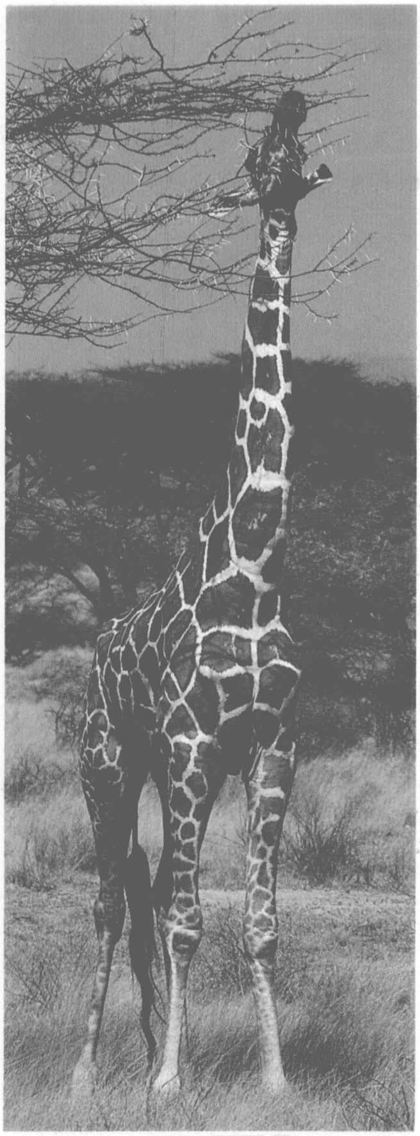
Although the way was being prepared by the revolution in geology, the time was not yet ripe for a parallel revolution in biology. The dominating force in European science in the early nineteenth century was Georges Cuvier (1769–1832). Cuvier was the founder of vertebrate paleontology, the scientific study of the fossil record of vertebrates (animals with backbones). An expert in anatomy and zoology, he applied his knowledge of the way in which animals are constructed to the study of fossil animals, and he was able to make brilliant deductions about the

I–4 *Particular strata, even though widely separated geographically, have characteristic assemblages of fossils. These fossil trilobites from the Devonian period (360 to 408 million years ago) were found in strata in* (a) *Ohio,* (b) *Oklahoma, and* (c) *upstate New York.*

(a) (b) (c)



I–5 *A drawing by Georges Cuvier of a mastodon. Although Cuvier was one of the world's experts in reconstructing extinct animals from their fossil remains, he was a powerful opponent of evolutionary theories.*



I–6 *According to Lamarck's hypothesis —now known to be in error—as giraffes stretched to reach the high branches, their necks lengthened, and this acquired characteristic was transmitted to their offspring.*

form of an entire animal from a few fragments of bone. Today we think of paleontology and evolution as so closely connected that it is surprising to learn that Cuvier was a staunch and powerful opponent of evolutionary theories. He recognized the fact that many species that had once existed no longer did. (In fact, according to modern estimates, considerably less than one percent of all species that have ever lived are represented on the earth today.) Cuvier explained the extinction of species by postulating a series of catastrophes. After each catastrophe, the most recent of which was the Flood, new species filled the vacancies.

Cuvier hedged somewhat on the source of the new animals and plants that appeared after the extinction of older forms; he was inclined to believe they moved in from parts unknown. Another major opponent of evolution, Louis Agassiz (1807–1873), America's leading nineteenth-century biologist, was more straightforward. According to Agassiz, the fossil record revealed 50 to 80 total extinctions of life, followed by an equal number of new, separate creations.

The Concepts of Lamarck

The first modern scientist to work out a systematic concept of evolution was Jean Baptiste Lamarck (1744–1829). "This justly celebrated naturalist," as Darwin himself referred to him, boldly proposed in 1801 that all species, including *Homo sapiens*, are descended from other species. Lamarck, unlike most of the other zoologists of his time, was particularly interested in one-celled organisms and invertebrates (animals without backbones). Undoubtedly it was his long study of these forms of life that led him to think of living things in terms of constantly increasing complexity, each species derived from an earlier, less complex one.

Like Cuvier and others, Lamarck noted that older rocks generally contained fossils of simpler forms of life. Unlike Cuvier, however, Lamarck interpreted this as meaning that the more complex forms had arisen from the simpler forms by a kind of progression. According to his hypothesis, this progression, or evolution, to use the modern term, is dependent on two main forces. The first is the inheritance of acquired characteristics. Organs in animals become stronger or weaker, more or less important, through use or disuse, and these changes, according to Lamarck's proposal, are transmitted from the parents to the progeny. His most famous example was the evolution of the giraffe. According to Lamarck, the modern giraffe evolved from ancestors that stretched their necks to reach leaves on high branches. These ancestors transmitted the longer necks—acquired by stretching—to their offspring, which stretched their necks even longer, and so on.

The second, equally important force in Lamarck's concept of evolution was a universal creative principle, an unconscious striving upward on the *Scala Naturae* that moved every living creature toward greater complexity. Every amoeba was on its way to man. Some might get waylaid—the orangutan, for instance, had been diverted from its course by being caught in an unfavorable environment—but the will was always present. Life in its simplest forms was constantly emerging by spontaneous generation to fill the void left at the bottom of the ladder. In Lamarck's formulation, Aristotle's ladder of nature had been transformed into a steadily ascending escalator powered by a universal will.

Lamarck's contemporaries did not object to his ideas about the inheritance of acquired characteristics, which we, with our present knowledge of genetics, know to be false. Nor did they criticize his belief in a metaphysical force, which was actually a common element in many of the concepts of the time. But these vague, untestable postulates provided a very shaky foundation for the radical proposal that more complex forms evolved from simpler forms. Moreover, Lamarck personally was no match for the brilliant and witty Cuvier, who relentlessly attacked his ideas. As a result, Lamarck's career was ruined, and both scientists and the public became even less prepared to accept any evolutionary doctrine.

DEVELOPMENT OF DARWIN'S THEORY

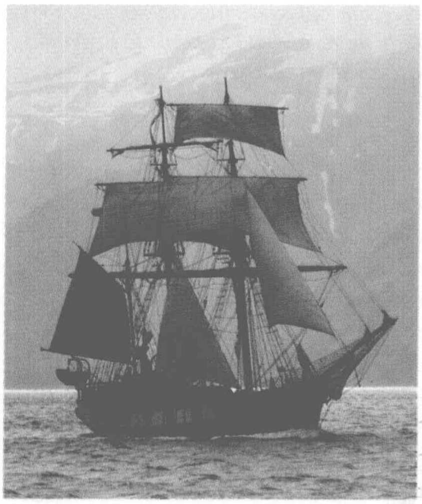
The Earth Has a History

The person who most influenced Darwin, it is generally agreed, was Charles Lyell (1797–1875), a geologist who was Darwin's senior by 12 years. One of the books that Darwin took with him on his voyage was the first volume of Lyell's newly published *Principles of Geology*, and the second volume was sent to him while he was on the *Beagle*. On the basis of his own observations and those of his predecessors, Lyell opposed the theory of catastrophes. Instead, he produced new evidence in support of Hutton's earlier theory of uniformitarianism. According to Lyell, the slow, steady, and cumulative effect of natural forces had produced continuous change in the course of the earth's history. Since this process is demonstrably slow, its results being barely visible in a single lifetime, it must have been going on for a very long time. What Darwin's theory needed was time, and it was time that Lyell gave him. In the words of Ernst Mayr of Harvard University, the discovery that the earth was ancient "was the snowball that started the whole avalanche."

The Voyage of the *Beagle*

This, then, was the intellectual climate in which Charles Darwin set sail from England. As the *Beagle* moved down the Atlantic coast of South America, through the Strait of Magellan, and up the Pacific coast, Darwin traveled the interior. He explored the rich fossil beds of South America (with the theories of Lyell fresh in his mind) and collected specimens of the many new kinds of plant and animal life

I–7 (**a**) *A reproduction of the* Beagle, *sailing off the coast of South America.* (**b**) *Cutaway view of the ship. Only 28 meters in length, this "good little vessel" set sail on its five-year voyage with 74 people aboard. Darwin shared the poop cabin with a midshipman and 22 chronometers belonging to Captain Fitz Roy, who had a passion for exactness. Darwin's sleeping space was so confined that he had to remove a drawer from a locker to make room for his feet.*



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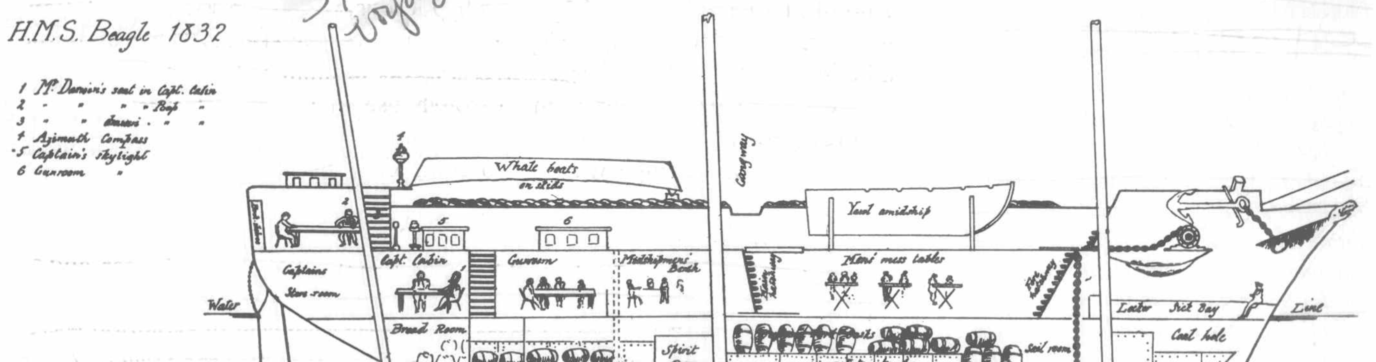

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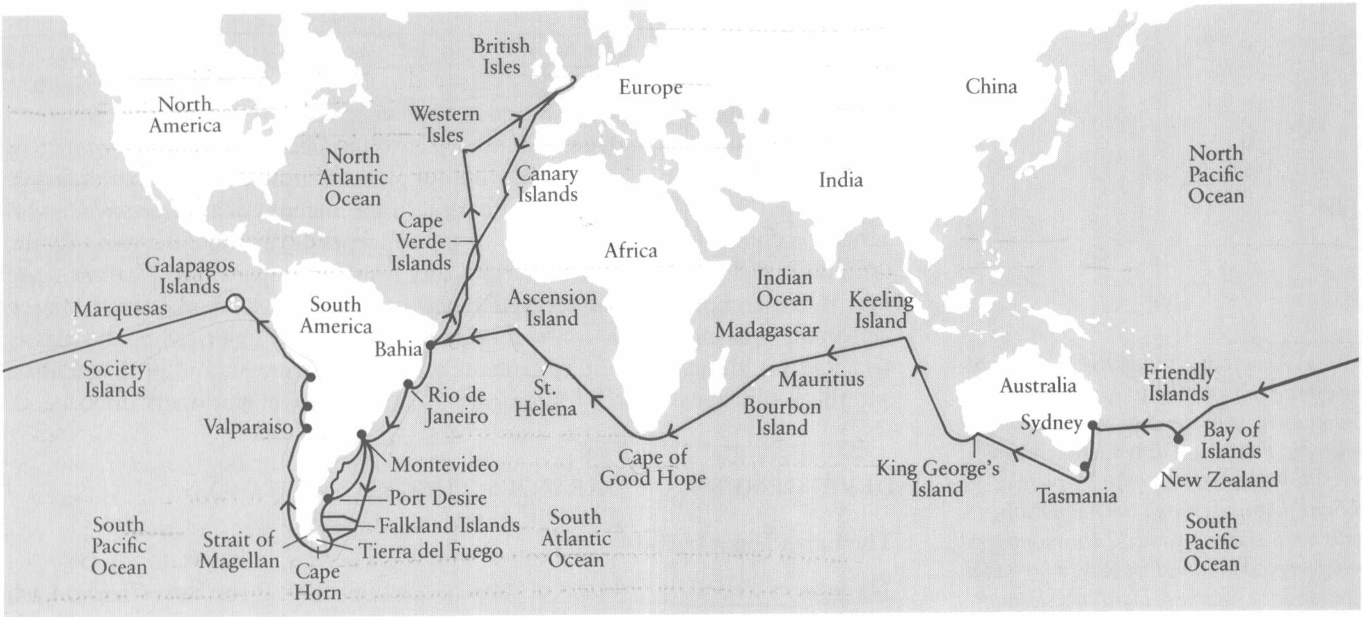
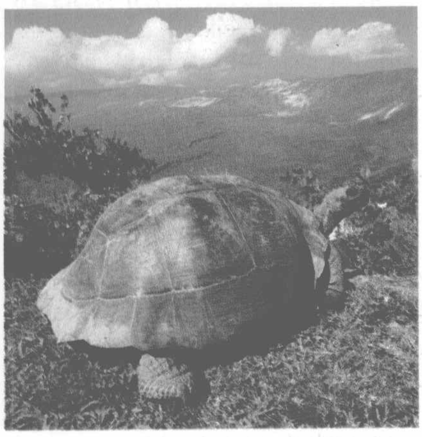


I–8 *The* Beagle's *voyage. The ship left England in December of 1831 and arrived at Bahia, Brazil, in late February of 1832. About 3½ years were spent along the coast of South America, surveying and making inland explorations. The stop at the Galapagos Islands was for slightly more than a month, and, during that brief time, Darwin made the wealth of observations that were to change the course of the science of biology. The remainder of the voyage, across the Pacific to New Zealand and Australia, across the Indian Ocean to the Cape of Good Hope, back to Bahia once more, and at last home to England, occupied another year.*



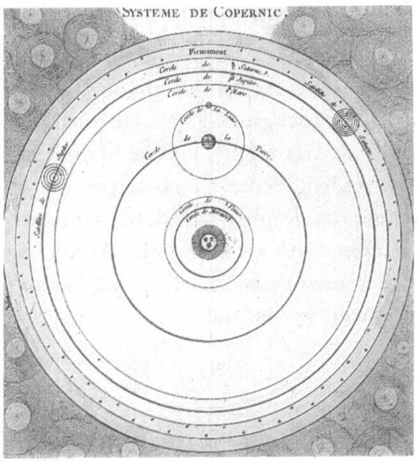
I–9 *A distinguishing feature of the Galapagos tortoise is the shape of its carapace, or shell, which varies according to its island of origin. The tortoises found on the islands with comparatively lush vegetation are characterized by a domed shell, shown here, which affords protection of the tortoise's soft parts as it makes its way through the thick undergrowth. The high arch at the front of the saddleback shell (see Figure I–1) enables the tortoise to reach upward in search of food; such shells are typical of tortoises living on arid islands where food may be scarce.*

he encountered. He was impressed most strongly during his long, slow trip down one coast and up the other by the constantly changing varieties of organisms he saw. The birds and other animals on the west coast, for example, were very different from those on the east coast, and even as he moved slowly up the western coast, one species would give way to another.

Most interesting to Darwin were the animals and plants that inhabited a small, barren group of islands, the Galapagos, which lie some 950 kilometers off the coast of Ecuador. The Galapagos were named after the islands' most striking inhabitants, the tortoises (*galápagos* in Spanish), some of which weigh 100 kilograms or more. Each island has its own type of tortoise; sailors who took these tortoises on board and kept them as convenient sources of fresh meat on their sea voyages could readily tell which island any particular tortoise had come from. Then there was a group of finchlike birds, 13 species in all, that differed from one another in the sizes and shapes of their bodies and beaks, and particularly in the type of food they ate. In fact, although clearly finches, they had many characteristics seen only in completely different types of birds on the mainland. One finch, for example, feeds by routing insects out of the bark of trees. It is not fully equipped for this, however, lacking the long tongue with which the true woodpecker flicks out insects from under the bark. Instead, the woodpecker finch uses a small stick or cactus spine to pry the insects loose.

From his knowledge of geology, Darwin knew that these islands, clearly of volcanic origin, were much younger than the mainland. Yet the plants and animals of the islands were different from those of the mainland, and in fact the inhabitants of different islands in the archipelago differed from one another. Were the living things on each island the product of a separate special creation? "One might really fancy," Darwin mused at a later date, "that from an original paucity of birds in this archipelago one species had been taken and modified for different ends." This problem continued, in his own word, to "haunt" him.

(a)



(b)

I-10 (**a**) *A view of the universe first proposed by the early Greeks and accepted throughout the Middle Ages. In this colored woodcut from Martin Luther's* Bible, *dated 1534, earth is in the center of the universe, surrounded by a layer of air containing clouds, stars, planets, the sun, and the moon. Beyond this is an outer layer of fire.* (**b**) *The solar system, as proposed by Nicholas Copernicus. In 1543, Copernicus set forth in* De Revolutionibus *the new concept that the sun, not the earth, is the center of the solar system. His theory was supported by the German astronomer Johannes Kepler (1571–1630), who discovered the laws of planetary motion, and by the Italian Galileo Galilei (1564–1642). The latter spent the last 10 years of his life confined to his home for heresy because of his advocacy of Copernican beliefs.*

The Darwinian Theory

Darwin was an assiduous and voracious reader. Not long after his return, he came across a short but much talked about sociological treatise by the Reverend Thomas Malthus that had first appeared in 1798. In this essay, Malthus warned, as economists have warned ever since, that the human population was increasing so rapidly that it would soon be impossible to feed all the earth's inhabitants. Darwin saw that Malthus's conclusion—that food supply and other factors hold populations in check—is true for all species, not just the human one. For example, Darwin calculated that a single breeding pair of elephants, which are among the slowest reproducers of all animals, would, if all their progeny lived and reproduced the normal number of offspring over a normal life span, produce a standing population of 19 million elephants in 750 years, yet the average number of elephants generally remains the same over the years. So, although a single breeding pair could have, in theory, produced 19 million descendants, it did, in fact, produce an average of only two. But why these particular two? The process by which the two survivors are "chosen" Darwin called **natural selection.**

Natural selection, according to Darwin, was a process analogous to the type of selection exercised by breeders of cattle, horses, or dogs. In artificial selection, we humans choose individual specimens of plants or animals for breeding on the basis of characteristics that seem to us desirable. In natural selection, the environment takes the place of human choice. As individuals with certain hereditary characteristics survive and reproduce and individuals with other hereditary characteristics are eliminated, the population will slowly change. If some horses were swifter than others, for example, these individuals would be more likely to escape predators and survive, and their progeny, in turn, might be swifter, and so on.

According to Darwin, inherited variations among individuals, which occur in every natural population, are a matter of chance. They are not produced by the environment, by a "creative force," or by the unconscious striving of the organism. In themselves, they have no goal or direction, but they often have positive or negative adaptive values; that is, they may be more or less useful to an organism as measured by its survival and reproduction. It is the operation of natural selection—the interaction of individual organisms with their environment—over a series of generations that gives direction to evolution. A variation that gives an organism even a slight advantage makes that organism more likely to leave surviving offspring. Thus, to return to Lamarck's giraffe, an animal with a slightly longer neck may have an advantage in feeding and thus be likely to leave more offspring than one with a shorter neck. If the longer neck is an inherited characteristic, some of these offspring will also have long necks, and if the long-necked animals in this generation have an advantage, the next generation will include more long-necked individuals. Finally, the population of short-necked giraffes will have become a population of longer-necked ones (although there will still be variations in neck length).

As you can see, the essential difference between Darwin's formulation and that of any of his predecessors is the central role he gave to variation. Others had thought of variations as mere disturbances in the overall design, whereas Darwin saw that variations among individuals are the real fabric of the evolutionary process. Species arise, he proposed, when differences among individuals within a group are gradually converted into differences between groups as the groups become separated in space and time.

The Origin of Species, which Darwin pondered for more than 20 years after his return to England, is, in his own words, "one long argument." Fact after fact, observation after observation, culled from the most remote Pacific island to a neighbor's pasture, is recorded, analyzed, and commented upon. Every objection is weighed, anticipated, and countered. *The Origin of Species* was published on November 24, 1859, and the Western world has not been the same since.