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CHAPTER 6

THE DARWINIAN REVOLUTION

THE POPULARITY OF THE TERM "DARWINIAN REVOLUTION" (Himmelfarb 1959; Ruse 1979) suggests that we are dealing with a scientific theory with major consequences. If Darwin's naturalistic theory of evolution were accepted, then a host of beliefs and values that had been integral to Christian culture would have to be rejected or renegotiated. Living things, including the human species, could no longer be regarded as divine creations. At best God might be supposed to play some indirect role in the process of evolution, but even that was difficult to imagine if it worked through as harsh a mechanism as natural selection. Equally seriously, the status of the human soul was threatened. If we are just improved animals, then it is hard to believe that we have an immortal soul if the lower animals do not. And to abandon the concept of a spiritual dimension to human existence would undermine traditional concepts of morality and threaten the stability of the social order.

What lines of evidence could have been so persuasive that they required scientists such as Darwin to take so bold a step? On the model of history preferred by scientists such as Gavin De Beer (1963) it is possible to see how Darwin was led to his theory by an accumulation of new information from areas as diverse as the fossil record and the study of animal breeding. If there were problematic consequences of the theory, then people simply had to cope with them if they wanted to live in the real world. But even today there is no shortage of critics who maintain that the Darwinian theory is not good science, so Darwin and his followers must be driven by something more than the desire to study nature. To modern creationists, Darwinism is the agent of a materialist philosophy that wants to destroy traditional values and beliefs and plunge the world into anarchy. They argue that the materialists manipulate dubious scientific evidence to support a theory whose real purpose is much more ambitious and much more dangerous.

There is another line of argument, however, that has also been used in an effort to undermine Darwinism's scientific credibility. Socialist critics from Marx and Engels onward have noted the analogy between Darwin's "struggle for existence" and the competitive free-market economy in which individuals struggle to gain a living. Can it be a coincidence, argue the critics, that such a theory was proposed in the heyday of Victorian capitalism? Darwin simply projected the ideology of the class to which he belonged onto nature so that he and his followers could maintain that a competitive society was "only natural." This is a very different argument questioning the theory's scientific credentials. Cautious observers may, however, reflect on the fact that the creationists who decry Darwinian materialism are among the most vociferous supporters of the free-enterprise system—so can they, too, be unwitting social Darwinists?

These rival perceptions of modern Darwinism are reflected in the vast range of historical literature on the theory's origins. De Beer's interpretation of Darwin as the courageous scientist is followed by that of other scientist-historians such as Michael Ghiselin (1969) and Ernst Mayr (1982). The values of those who dislike the implications of Darwinism can be seen in the far less flattering portraits created by Jacques Barzun (1958) and Gertrude Himmelfarb (1959). The sociological interpretation of the origins of Darwinism is explored in the writings of the Marxist historian Robert Young (1985) and in a biography of Darwin by Adrian Desmond and James Moore (1991). Other historians have tried to balance the conflicting pressures. Few would now deny that Darwin was influenced—perhaps creatively—by the ideology of his time, but there is a widespread suspicion that we cannot make sense of his contribution unless we see those creative insights through the medium of his scientific work (for surveys, see Bowler [1983b, 1990]; Eiseley [1958]; and Greene [1959]). The historians' task is made more complicated by the vast archival record of Darwin's activity that is being edited for publication (e.g. Darwin 1984–, 1987).

The temptation for both supporters and critics to focus on the work of Darwin himself may have distorted our image of the Darwinian revolution. It is all too easy to assume that there must have been a sudden transition from a more-or-less stable creationism to a rabidly materialistic Darwinism that has continued undaunted (if not unchallenged) to today. This perception feeds off a peculiar combination in Darwin's achievements: he converted the world to evolutionism, and he was also the discoverer of what most modern biologists take to be the correct explanation of how evolution works, natural selection. There is an obvious temptation to believe that he must have successful because his contemporaries realized that he had got the mechanism right. On this model, only a limited "tidying up" of the theory was needed to generate modern Darwinism. Yet an increasing number of studies suggest that natural selection was not accepted by Darwin's fellow scientists. Rival mechanisms of evolution flourished through into the early twentieth century. We need to see the emergence of modern Darwinism as a much more protracted process requiring major transformations long after the basic idea of evolution was accepted (Bowler 1988).

These points feed into the work of historians who are developing a more complex model of how the first generation of Darwinians succeeded in dominating the scientific community. Darwin was not the first to initiate widespread discussion of evolutionism. Long before he published the *Origin of Species* in 1859, radical writers were promoting the theory as a foundation for a political philosophy that demanded social progress. By undermining the traditional beliefs that sustained the Church, evolution opened up the prospect that nature itself was founded on a law of progress—which then made human progress seem inevitable. Such ideas made little impression on the scientific elite, but they paved the way for the reception of Darwin's theory and may have shaped the popular assumption that it, too, was the basis for a philosophy of universal progress. If this is so, many of the philosophical, theological, and ideological consequences normally attributed to Darwinism may be a reflection of this wider cultural movement.

At the same time, we need to look more carefully at what made scientists take Darwin more seriously than they did earlier writers. They certainly saw his book as a new initiative that would transform many areas of science, especially in morphology (the comparative study of animal structures) and paleontology. And even though most of them did not accept natural selection as the main mechanism of evolution, they thought it was a plausible and scientifically testable theory that went far beyond the earlier speculations. It has been suggested that younger professional scientists, such as T. H. Huxley (who became known as "Darwin's bulldog"), were attracted to the theory because it helped their campaign to convince the public that science rather than the Church was the best source of expertise in a modern economy. All this suggests that the impact of Darwinism must be evaluated both in terms of its scientific advantages (which were real enough even to those who had doubts about the detailed theory of selection) and its appeal to the values and prejudices of potential supporters both inside and outside science.

Design in the Natural World

The worldview still accepted by modern creationists does not date back to the foundations of Christianity. As noted in chapter 5, "The Age of the Earth," a literal reading of the Genesis creation story first became widely accepted in the seventeenth century. If the earth was only a few thousand years old, any gradual process of development became unthinkable. The only explanation for the origin of plants, animals, and human beings was that their first ancestors were created directly by God. The naturalists of the period were only too happy to exploit this insight to provide a justification for science's exploration of the natural world. After all, there were critics who warned against the materialism of the new science being promoted by Galileo, Descartes, and Newton. If the whole world was to be treated as a giant machine, then the only way to preserve a role for the Creator was to insist that the machine needed a wise and intelligent Designer. Even if they did not believe in the Garden of Eden, seventeenth-century naturalists could appeal to a "natural theology" in which the study of living things would reveal God's handiwork. The "argument from design" sought to convince the skeptics that the best explanation for the existence of such complex structures as living things was a God who had, in the analogy used later by William Paley, designed them just as a watchmaker designs a watch (see chap. 15, "Science and Religion.").

A leading advocate of this view was the English naturalist John Ray, whose *Wisdom of God Manifested in the Works of Creation* appeared in 1691 (Greene 1959). Ray appealed to the structure of the human body, especially the eye and the hand, to argue that here were complex mechanisms exquisitely designed so as to provide us with the instruments we need to conduct our lives. But Ray did not believe that the whole world was created for our benefit alone. Each animal species has its own structures designed to allow the individuals to gain a livelihood and enjoy their lives in a particular environment. The argument from design thus focused attention onto the adaptation of structure to function. God is not only wise, he is also benevolent because he gives each species exactly what it needs to live in the place where he created it. The argument presupposes a static creation, in which species and their environments remain just as they were when first created. It has often been said that Darwin would turn the argument from design on its head by showing that adaptation is a process by which species are adjusted to changing environments.

Ray's vision of a designed world was not without its applications in the scientific world of the time. It encouraged the detailed study of species and their relationship to the environment. But it was also the basis for the first efforts to provide a biological taxonomy, a system for classifying the animals and plants so that we can try to make sense of the bewildering diversity of species. Each individual species has its own special adaptations, but there are relationships between species that surely imply that there must be some rational pattern in God's creation. The lion and the tiger are both "big cats"—we can see the relationship between them, and a more distant resemblance to the domestic cat. If these and other degrees of similarity can be ordered and related together, we might be able to see the whole plan of creation displayed in our natural history museums or textbooks. There will also be an immense benefit for scientists who need to refer unambiguously to any one of the vast number of living species, a problem made the more acute as European naturalists confronted the vast array of new species discovered in remote parts of the world.

Ray made important contributions toward establishing such a system, but it was the Swedish naturalist Carl von Linné, better-known by the Latinized form of his name, Linnaeus, who laid down the foundations of the modern system of biological taxonomy (Farber 2000). His *System of Nature* (1735) eventually expanded into a multivolume work that attempted to classify every plant and animals species into a rational system. Linnaeus also founded the system for naming species still in use today, the binomial nomenclature. The most closely related species are linked into a genus (plural "genera") and each is given two Latin names, always italicized: the first is the name of the genus, the second of the individual species. Thus the lion was *Panthera leo,* the tiger *Panthera tigris.* The big-cat genus *Panthera* was then included within the family Felidae (the cat family), which in turn belongs to the order Carnivora (the flesh eaters) of the class Mammalia (the mammals). Although much has changed in how we assess the relationships and in the details of some of the groupings, this is still how scientists classify species. Darwin's theory of evolution explains the grouping of species as a result of common ancestry: in the branching "tree of life," the more recently two species share a common ancestor, the more closely they are related. It is worth remembering, however, that when Linnaeus set up the system he believed it represented the divine plan of creation—the relationships existed only in the mind of God. He thought that most species were created exactly as we see them today.

The pattern of relationships that Ray and Linnaeus sought to represent consists of groups nesting within larger groups, which is why it is consistent with Darwin's model of branching evolution. The system undermined a much older vision of natural order known as the "chain of being," founded on the commonsense notion that some animals are higher or more advanced than others. Most of us think that humans are superior to the other animals, and we tend to see mammals as being superior to fish, and fish to invertebrates. From the ancient Greeks onward, this natural hierarchy had been visualized as a linear chain in which the species were the links, stretching down from humans to the lowest form of life. A spiritual hierarchy also stretched up through the angels to God, so that humans occupied the crucial boundary between the animal and spiritual realms. The chain of being was still exploited by eighteenth-century poets such as Alexander Pope (see Lovejoy 1936), but Linnaeus and the naturalists had now shown that as a practical system of classification it did not work. However, the broader notion of an animal hierarchy was too deeply rooted for it to be abandoned, and the theory of evolution would be shaped by a widespread assumption that the history of life must represent the ascent of life toward higher forms (Ruse 1996). The tree of life retained a main trunk, equivalent to the chain of being, but with a host of minor side branches (see fig. 6.5 below).

Forerunners of Darwin?

The naturalists who believed that the universe was a divine creation did not find this a very precise guide, given the detailed nature of their work, and such ambiguities would get worse as the life sciences became more sophisticated. But by the mid-eighteenth century there was a growing movement to reject the whole idea of design and look for more materialistic explanations of how things came to be in their present state. Some of the resulting theories do include an element of transformism, or what we would today call evolution, and the naturalists who proposed them have sometimes been hailed as the "forerunners of Darwin" (Glass, Temkin, and Straus 1959). Later historians have become suspicious of this search for the precursors of the modern theory, because it fails to take into account the very different context within which these early ideas were articulated. It is easy to find isolated passages that give the impression that eighteenth-century thinkers were coming close to Darwinism, but a more careful reading suggests that they were usually thinking of something quite different from the modern theory. There are many different ways of imagining how the universe might change through time, and Darwinism is only one of them. The so-called forerunners were actually exploring very different models of how new forms of life might appear. We should be aware of the growing willingness to challenge the idea of a static creation, but to twist these early ideas to fit our modern theories can only distort them beyond recognition.

The motivation behind many of these speculations lay in the philosophy of the Enlightenment, which celebrated the power of human reason to understand the world and dismissed all traditional religions as superstition. The Church was seen as a barrier to social reform, so undermining the credibility of the Genesis creation story had an ideological as well as an intellectual purpose. Some of the Enlightenment philosophers became outright atheists and materialists, and they sought an explanation of the origin of life that did not depend on the supernatural (Roger 1998). For Denis Diderot, the world was a ceaseless round of material transformations that formed and reformed material structures without any predesigned plan or purpose. He challenged the assumption that species are constant and emphasized the unplanned nature of natural change by speculating that monstrosities might sometimes be born with new characters that by chance enabled the creature to survive and establish a new species. But materialists like Diderot developed no detailed theory of transformism because they also thought that inorganic nature could produce even complex living things directly by a process know as "spontaneous generation."

This alternative also occurs in the thought of the most influential naturalist of the Enlightenment, Georges Louis Leclerc, comte de Buffon (Roger 1997). It was Buffon who promoted the new timescale of earth history on which these speculations about the origin of life rested (on developments in geology and paleontology, see chap. 5, "The Age of the Earth"). He proposed a theory that postulated that the earth is not only very old but was also hotter and hence more energetic in the distant past. His multivolume *Natural History,* which began publishing in 1749, also provided an overview of all the known animal species and included several (not altogether consistent) speculations about their origin. Buffon ridiculed Linnaeus's search for the divine plan of creation, although he too accepted the reality of species. But he became increasingly convinced that the species have a good deal of flexibility to adapt to the new conditions they encounter in an ever-changing world. In a 1766 chapter titled "On the Degeneration of Animals," he argued that the species making up a modern genus have all descended from a single ancestor—so the lion and the tiger are not true species, only varieties of a single big cat species. But the ancestral forms have not evolved from anything else, and it is clear from his other writings that Buffon thought they were originally produced by spontaneous generation. In his supplementary volume *The Epochs of Nature* (1778) he suggested two episodes of spontaneous generation in the course of the earth's history, one to produce creatures adapted to the early, very hot conditions and a second to produce the ancestors of the modern forms. This was certainly a bold alternative to Genesis, but it involved only very limited amounts of transmutation.

At the end of the century there were two thinkers whose ideas included a more substantial element of what we might call evolution. One of them, the English physician and poet Erasmus Darwin, has attracted much attention because it was his grandson, Charles Darwin, who proposed the modern theory of evolution. Erasmus endorsed the idea of a gradual development of life through time in his poems (which were quite popular at the time) and in a chapter of his *Zoonomia* of 1794–96. But far more influential was the parallel theory developed by the French naturalist J. B. Lamarck (Burkhardt 1977; Jordanova 1984). Lamarck studied the invertebrate animals at the Museum of Natural History established in Paris by the revolutionary government and made important contributions to invertebrate taxonomy. Around 1800 he abandoned his original commitment to the fixity of species and began to develop the theory he published in his *Zoological Philosophy* (1809). He accepted spontaneous generation, appealing to electricity as a force that could vivify nonliving matter, but assumed that only the simplest forms of life could be produced in this way. The higher animals evolved in the course of time by a progressive trend that made each generation slightly more complex than its parents. Lamarck thought that this progression would in theory generate a linear scale of animal organization—in effect, a chain of being with humans as the last and highest products. Note, however, that this "ladder" model of evolution included no branching—there were many parallel lines ascending the scale starting from different acts of spontaneous generation. Lamarck denied the possibility of extinction and the reality of species. He thought the scale was absolutely continuous, with no gaps marking off distinct species (the gaps we see are due to lack of information—the missing links are all out there somewhere).

This is a model of evolution quite unlike anything we accept today. But Lamarck was an experienced naturalist and he knew that we cannot in fact fit the various forms of life into a linear pattern. He supposed that there was a second evolutionary process at work, which distorted the chain and produced an irregular arrangement. It is this second process for which he is remembered because it was taken seriously by biologists through until the

emergence of modern genetics. Lamarck knew that species were adapted to their environments, but he could not attribute this to design by God. He supposed instead that species are adapted to changes in their surroundings by a process called the "inheritance of acquired characteristics" or "use inheritance." An acquired character is one developed by the organism after birth as a result of it exercising its body in an unusual way. The weightlifter's bulging muscles are an acquired character because they would be much smaller if it were not for all the exercise. Lamarck (and many others) supposed that such acquired characters might have a very slight tendency to be inherited, so that the weightlifter's children would be born with muscles slightly larger as a result of their parents' efforts. This process would produce adaptive evolution if the new habit directing the exercise was adopted to cope with a change in the environment. In the classic example, the giraffe's long neck is a consequence of generations of its ancestors reaching up to feed off the leaves of trees.

Lamarck's theory was the last product of the age of Enlightenment speculation, and historians of science used to think that it had been dismissed as nonsense by a new generation of conservative naturalists working in the Napoleonic era. It was certainly dismissed by some of the elite, but as we shall see in the next section there were still radicals willing to use the idea of evolution to challenge traditional beliefs. For these radicals, there were elements of Lamarck's theory that fit well with their continued calls for social reform.

Interpreting the Fossil Record

The scientific elite of the early nineteenth century was anxious to distance itself from Enlightenment materialism. In Britain, this meant a revival of natural theology. On the Continent there were fewer explicit appeals to religion, but new approaches to the life sciences tended to reinforce belief in the fixity of species and in some cases presented the world of life as an orderly pattern that expressed some rational principle at the heart of nature. But there was a new factor that had to be taken into account by all these theoretical approaches: the history of life as revealed by the fossil record (see, for an outline of the impact of the fossil record, chap. 5). However conservative in outlook, naturalists had to see the modern species as the last stage of a historical process. They had to transform the older traditions to incorporate this element of change without supporting transmutation as the agency by which new species appeared. At one time, it seemed easy for historians to dismiss these efforts as mere stopgaps desperately trying to hold back the emergence of Darwinian evolutionism. But modern studies suggest that in some cases these early theories had important results that helped to create the worldview to which Darwin also contributed. Recent work also confirms the point noted above: the radicals did not go away, and to some extent the antievolutionary philosophies of the scientific establishment were designed to combat the threat from this source.

The work of Georges Cuvier and his followers on vertebrate fossils established that the present order of nature was merely the last in a long series. To reconstruct the fossilized remains of extinct animals, Cuvier drew on his skills in comparative anatomy (see chap. 7, "The New Biology"). He showed that the earth had passed through a number of geological epochs, each with its own distinct population of animals and plants. How was this insight to be accommodated without giving ground to Lamarck and the evolutionists? Cuvier was convinced that geological catastrophes wiped out the populations of whole continents, leaving room for an entirely new population to occupy the area after things had settled down. He went out of his way to ridicule Lamarck's theory, arguing that the structure of each species is so carefully balanced that any significant disturbance would make the organism nonviable. Yet he did not appeal to design, and he evaded the need to postulate successive creations to explain the appearance of new species, suggesting instead that they migrated in from areas not affected by the catastrophe. To his British followers, however, the idea of successive creations was irresistible. The Genesis story would have to be modified to include a series of miraculous creations in the course of the earth's history (Gillispie 1951). They applauded William Paley's *Natural Theology* (1802), which restated the argument from design using the analogy of the watch and the watchmaker, and saw themselves as modifying this traditional view in the light of the new knowledge of the fossil record. William Buckland contributed to a series known as the *Bridgewater Treatises*, commissioned to promote natural theology, using his volume to show how the species comprising each successive population were all adapted to the prevailing conditions. By supposing that the earth was gradually cooling down so that the environment moved step by step toward the one we enjoy today, he could explain why it was necessary for God's creations to be wiped out periodically in order to leave room for newer populations approximating more closely to the creatures we see today.

In Germany there was a more innovative challenge to materialism associated with the Romantic movement in the arts and idealism in philosophy. Idealists believed that the material world is an illusion created by the sense impressions in our minds, and since the world is orderly, the laws of

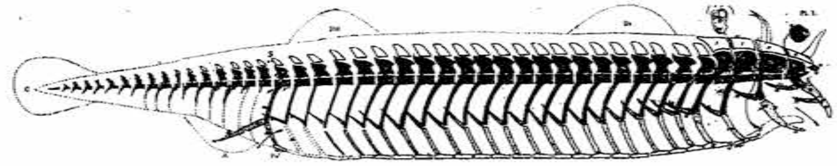

FIGURE 6.1 The vertebrate archetype, from Richard Owen, *On the Archetype and Homologies of the Vertebrate Skeleton* (1848). This is an idealized representation of the simplest imaginable backboned animal, with all the specializations of real species stripped away. It does not correspond to a real animal, although evolutionists would later try to identify the simplest and most primitive vertebrate form from which the whole phylum had developed by divergent evolution.

nature must represent some ordering principle in whatever ultimate reality is the source of those impressions. Whether one calls this ordering principle God, or some more abstract term such as the "Absolute," the implication is that the apparent complexity of nature conceals a deeper underlying pattern. Inspired by such beliefs, a group of *Naturphilosophen* (nature philosophers) sought to explain the orderly groupings among species revealed by taxonomy as just such a pattern. This viewpoint was imported into Britain by Richard Owen, who made creative use of it in his concept of the archetype defining the basic form of each major taxonomic group (Rupke 1993). Owen's vertebrate archetype, proposed in 1848, defined the essence of what it was to be a backboned animal. It was an idealized model of the simplest conceivable vertebrate—all real vertebrate species were more or less complex adaptive modifications of the archetypical form (fig. 6.1). This idealist approach allowed Owen to define the important concept of homology: the fact that the same combination of bones can be modified for different purposes in species adapted to different environments (fig. 6.2). The archetype did not, however, undermine the idea of progress—primitive fish were the simplest modifications, human beings the most complex. To Owen this offered a better form of the argument from design because it implied that underneath the bewildering variety of different species described in the *Bridgewater Treatises* was an ordering principle that could only arise from the mind of the Creator. Owen saw the successive expressions of the archetype as a progressive pattern unfolding through time, something that at times brought him perilously close to transformism, although he always insisted that each species was a distinct unit in the divine plan. Darwin's theory of branching evolution drew on a similar model of development, albeit for Darwin the archetype was replaced by the common

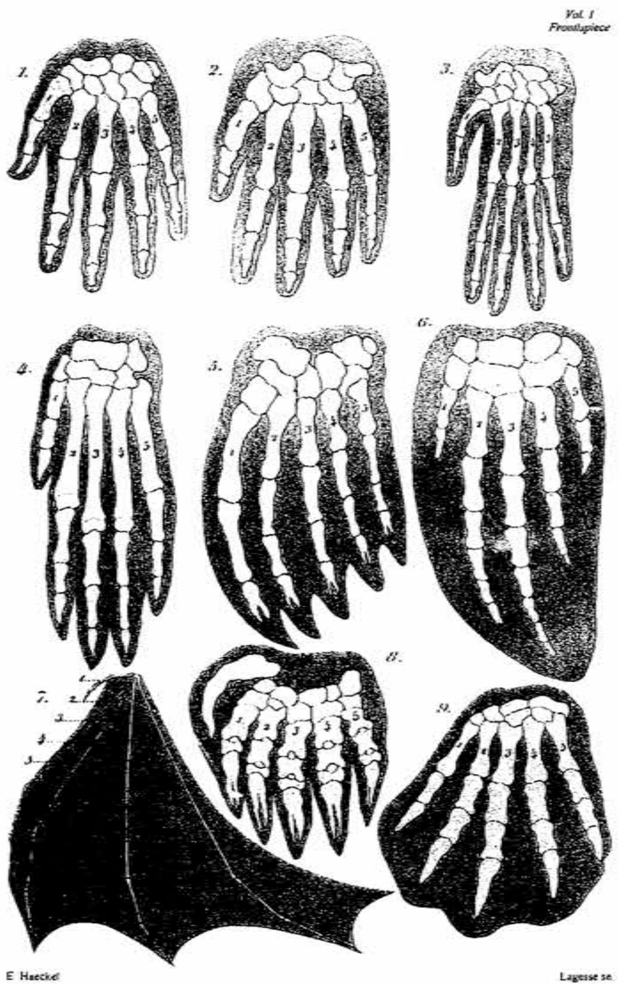

FIGURE 6.2 Homologies of the mammalian "hand" as depicted in Ernst Haeckel's *History of Creation* (New York, 1876), vol, 2, plate 4. The same bones as found in the human hand (*1, top left*) are adapted to different purposes in the forelimbs of the gorilla (*2*), the orangutan (*3*), and the dog (*4*); for swimming in the seal (*5*) and the porpoise (*6*); for flying in the bat (*7*); for digging in the mole (*8*); and again for swimming in a primitive mammal, the duck-billed platypus (*9*). The modification of the same basic structure for different purposes in different animals was described by Richard Owen as an illustration of the rational foundations of the plan of creation, but for Haeckel it was evidence that all the mammals had all descended from a common ancestor.

ancestor from which the various members of the group diverged in the course of evolution.

Other idealists, including the Swiss naturalist Louis Agassiz—who became one of the founding fathers of American biology—focused on the development of the human embryo as an illustration of how the pattern of creation unfolded (Lurie 1960). The embryo was seen to develop from a simple uniform substance in the fertilized egg, gradually acquiring the more complex structures it needed in order to become an adult. It was widely believed at the time that the new structures were added in a way that paralleled the taxonomic hierarchy: the human embryo passed through stages resembling a fish, a reptile, and a simple mammal, before adding on the final characters that defined it as human. But this was also the sequence embodied in the ascent of life revealed by the fossil record, and to Agassiz this parallelism must be God's way of telling us that we humans are the goal of his creation. Here an element of the old chain of being crept back into naturalists' thinking, although Agassiz was well aware that there would have to be many branches off the main line. Like Owen, he also went out of his way to deny an evolutionary interpretation of his model. Every species was a distinct element in the divine plan, supernaturally created at the appropriate point in time.

These models of the history of life have been central to most histories of the period leading up to the publication of the *Origin of Species*. Later studies have shown, however, that they are not the whole story. There were more radical alternatives under discussion, sometimes within the scientific community itself but also among interested laypersons. In France, Cuvier was challenged by Étienne Geoffroy Saint-Hilaire, who proposed a materialist interpretation of the archetype concept (Appel 1987). He envisioned a form of transmutation based on saltations, or sudden leaps, by which one species could be transformed into another instantaneously through the appearance of "monstrosities" that could survive and breed. In Britain, Geoffroy Saint-Hilaire's ideas, along with those of Lamarck, were favored by radicals seeking to discredit the traditional perspective as part of their plan to reform the medical profession (Desmond 1989). The Lamarckian anatomist Robert Grant was discredited by Owen after he moved to London in the 1830s. Although blocked from serious influence in the scientific community, these transformists kept the idea alive and to some extent forced the elite to liberalize its views in order to defend them within a context that increasingly took the idea of progressive development for granted.

Perhaps the most important move in this campaign came from the Edinburgh publisher Robert Chambers, who published his anonymous

Vestiges of the Natural History of Creation in 1844 (Secord 2000). Chambers wanted to sell the idea of progressive evolution to the middle classes because it would offer them an ideology in which their demands for reform would seem part of nature's own development. Social progress would be merely a continuation of the history of life on earth. But to do this he had to sidestep the image of Lamarckism as a dangerously radical idea. His tactic was to argue that the progressive development of life was central to God's plan but was engineered not through a succession of miracles but through laws built into nature by its Creator. The normal law of reproduction (like produces like) was occasionally interrupted by the operation of a higher law that jumped the embryo one stage further up the hierarchy of organization. Here the law of parallelism between embryological development and the history of life on earth was transformed into a law of evolution by progressive saltations. Nor did Chambers shrink from extending the law to the human species: we were merely the highest animals, our superior mental powers the result of an expansion of the brain through successive saltations. He appealed to the science of phrenology in which different parts of the brain were supposed to be responsible for different mental functions—if new parts of the brain were added by evolution, then new mental functions would appear.

The conservative establishment condemned *Vestiges* as dangerous materialism that would undermine moral values and the fabric of society. Outside the scientific community the book was widely read, and it seems that many were prepared to take the basic philosophy of "progress by law" seriously (see chap. 16, "Popular Science"). The book thus prepared the world for Darwin's far more radical ideas and shaped the way that the *Origin of Species* would be read. There was no built-in progressive trend in Darwin's theory, although he did not doubt that natural selection would produce progress in the long run. But people automatically assumed that evolution did mean progress, and this was the legacy of *Vestiges*. Even some members of the scientific elite began to concede that God's purpose might be worked out through predesigned laws rather than a series of miracles. In his analysis of *Vestiges'* impact, James Secord (2000) suggests that the book should be regarded as the real starting point of the public debate about evolution that was resolved by the controversy sparked by Darwin's *Origin*.

The impact of *Vestiges* on scientists was less conclusive, and this left the whole issue still in the air. It is interesting to note the reaction of younger, more radical scientists such as Thomas Henry Huxley, soon to become Darwin's leading advocate (Desmond 1994; Di Gregorio 1984). Huxley condemned *Vestiges* in a review that even he later conceded was unjustly vitriolic. This was partly because Chambers's science was sloppy. He had slurred over real difficulties in the fossil record, which did not support the linear model of progress. But more seriously, Chambers's theory was not radical enough for Huxley. He was a professional scientist anxious to demolish the image of the clergyman-naturalist and he was looking for a theory that would eliminate all trace of the argument from design. Chambers's book left the reader to believe that the only explanation of progress was God's purpose. If Huxley was to accept evolution, it would have to be based on a mechanism driven solely by observable effects, not by mysterious trends designed by God. Fortunately for him, Darwin would soon publish a theory that fulfilled exactly this requirement.

The Development of Darwin's Theory

Darwin had conceived his theory in the late 1830s, but he had not published and only gradually allowed a few close contacts to know what he was doing. Thus the publication of the *Origin of Species* in 1859 came like a bolt from the blue as far as most scientists were concerned. Here was a major new initiative on the cause of evolution, backed up by a wealth of evidence and insight accumulated by Darwin over twenty years. As noted in the introduction to this chapter, historians disagree radically over how to interpret the process by which Darwin put his ideas together. For some he worked as a pure scientist, and if he gained insights from social debates this does not undermine the credibility of his theory (De Beer 1963). Others stress the parallel between natural selection and the competitive ideology of Victorian capitalism and see Darwin as someone who projected the social values of his own class onto nature itself (Desmond and Moore 1991; Young 1985). Many historians seek to balance these two positions, acknowledging the inspiration provided by social theories but recognizing that we can only explain the unique character of Darwin's thinking if we take note of how he applied his insights to a particular set of scientific questions (Bowler 1990; Browne 1995; Kohn 1985).

Darwin was born into a prosperous middle-class family in 1809. He was sent to Edinburgh for medical training, where he met and worked with the Lamarckian anatomist Robert Grant (although he subsequently claimed to have been unimpressed by Grant's evolutionism). He abandoned medicine and went to Cambridge to study for an arts degree, as a prelude to becoming an Anglican clergyman—an ideal career for an amateur naturalist. All his scientific training at Cambridge was thus outside the curriculum, but he impressed the professors of botany and of geology, John Stevens Henslow and Adam Sedgwick, respectively. Henslow then helped to gain him the opportunity that would transform his life: he was accepted as the gentleman-naturalist to travel with the survey vessel H.M.S. *Beagle*, about to sail for South America. The voyage of the *Beagle* lasted five years (1831–36), and while the ship was charting the coastal waters, Darwin had ample opportunities to travel to the interior. Here he made discoveries in geology and natural history that would make his reputation as a scientist and give him the insights that made him an evolutionist.

Sedgwick had trained Darwin as a catastrophist, interpreting the discontinuities in the geological record as evidence of vast upheavals in the past. But Darwin had been given the first volume of Charles Lyell's *Principles of Geology*, and his own observations soon made him a uniformitarian (see chap. 5, "The Age of the Earth"). He saw how the Andes Mountains were still being raised by earthquakes, as well as evidence that the whole range had been elevated gradually over a vast period of time, not in a single catastrophe. From that point on, Darwin felt it necessary to explain the distribution and adaptations of animals and plants in Lyellian terms: the present situation must be the outcome of slow changes driven by natural causes. At Cambridge he had read Paley's *Natural Theology* and been impressed with the claim that adaptation was an indication of God's design. But Paley's argument didn't work in a world of gradual change. As Lyell himself recognized, if geology is constantly modifying the environment by elevating and destroying mountains, species must either migrate to find conditions they can survive in or gradually go extinct. Lyell remained convinced that species are fixed, leaving it for Darwin to raise the possibility that they might be transformed by a process that adapts them to changes in their environment.

In South America, Darwin saw evidence that species competed with one another to occupy territory, a struggle whose outcome might be influenced by changes in the environment. But the most crucial observations came when the *Beagle* called at the Galapagos Islands, a group of volcanic islands lying five hundred miles off the coast in the Pacific. Although he nearly missed the evidence, Darwin was able just in time to appreciate that the animals were different on different islands. The giant tortoises on each island had significantly different shells, while the birds, especially the mocking birds and finches, displayed an immense variety. The finches could be found in a range of forms with entirely different beak structures adapted to different ways of finding food (fig. 6.3). Darwin only noticed the significance of this fact just before he left the islands, but he pondered on its implications while on the way home, and when he was told by the orni-

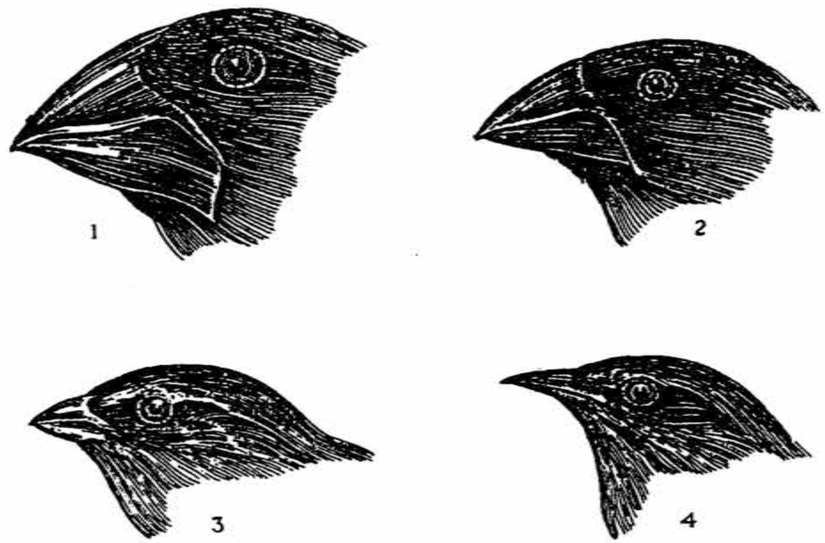

FIGURE 6.3 Heads of four of the Galapagos ground finches, from Darwin's *Journal of Researches into the Geology and Natural History of the Countries Visited during the Voyage of H.M.S. Beagle* (reprint, London 1891), chap. 17. The variation in the beak structures shows adaptation to different ways of obtaining food, such as cracking seeds or picking up insects. Darwin was told that these forms should be classified as distinct species, but he was convinced that they must have evolved from a common ancestor that had adapted to different ways of life on the various Galapagos Islands.

thologist John Gould that the various finches had to be counted as distinct species, he was faced with a dilemma. He could not accept that God had independently created a range of distinct species to occupy each of these tiny islands. It was more reasonable to believe that small populations derived from South America had been able to establish themselves on each island and had there changed to adapt themselves to their new environment. Transmutation, what we call evolution, could create not just new varieties but also new species, and if it could create species, why not—given time—new genera, families, and even classes?

Dissatisfied with the explanations offered by Lamarck and earlier writers (although he did not deny a limited role for the inheritance of acquired characteristics), Darwin set out to discover a plausible mechanism. His ideas were constrained by the Lyellian principle that the mechanism must be based on a combination of observable processes. Evolution is essentially an adaptive process, and it cannot be predetermined because the branching effect seen in the Galapagos implies that when a population is subdivided by geographical barriers, each group is able to adapt in its own way. There is no automatic ladder of progress—although Darwin did not deny that in the long run some branches of the tree of life had advanced to higher levels of organization than others. Many branches have evidently ended in extinction, while others have multiplied by subdivision.

In search of clues, Darwin turned to one area where animals could actually be observed to change: the production of artificial varieties by human breeders. The path of discovery revealed by his notebooks (reprinted as Darwin 1987) is complex, but in the end the breeders taught him certain important principles. All populations exhibit individual differences: no one organism is identical to another (just as no human being is identical to another). And there seems to be no obvious pattern or purpose to this variation (just as there seems no obvious purpose in, for instance, the variation of hair color in humans). How do the breeders use this random variation to create a new variety of dogs or pigeons? The answer, Darwin eventually realized, was selection—they pick out the very few individuals who happen to vary in the direction they want and breed only from them. The rest are rejected and probably killed.

Could there be a natural equivalent of this artificial selection, a process that would pick out only those better adapted variants to breed for the next generation? Darwin realized that there could be a natural form of selection when he read the clergyman Thomas Malthus's *Essay on the Principle of Population*. This work on political economy was intended to challenge Enlightenment optimism by showing that human progress was impossible. All efforts at social reform were doomed because poverty was not a consequence of social inequality—it was natural because the reproductive capacity of any population always exceeds the food supply. The consequence was that in every generation many must starve, and when writing of the wild tribes of central Asia (not, significantly, of his own society), Malthus argued that there must be a "struggle for existence" to determine who would live and who would die. Darwin picked up this idea and realized that the variability of the population would give some individuals an edge in the struggle. Those best adapted to any change in the environment would be most likely to survive and breed, those less well adapted would starve, and the result would be that the next generation would be bred largely from better adapted parents. Repeated over innumerable generations, this process of natural selection would modify organs and habits and, in the end, produce new species. It is the influence of Malthus that is often singled out to argue that natural selection reflects the values of free-enterprise capitalism. There can be little doubt that Darwin did think of the species in individualist terms, as a population not as a type. But he applied this insight in a unique way shaped by his scientific observations—Malthus had not seen his principle as source of change, and it was only after Darwin published his findings that people began to think seriously of struggle as the driving force of progress.

In an essay Darwin wrote in 1844 to outline his theory (intended for publication only in case of his death), he described the effect thus, using the example of a population of dogs forced to chase faster-running prey (hares instead of rabbits):

> Let the organization of a canine animal become slightly plastic, which animal preyed chiefly on rabbits, but sometimes on hares; let these same changes cause the number of rabbits very slowly to decrease and the number of hares to increase; the effect of this would be that the fox or dog would be driven to try to catch more hares, and his numbers would tend to decrease; his organization, however, being slightly plastic, those individuals with the lightest forms, longest limbs and best eyesight (though perhaps with less cunning or scent) would be slightly favored, let the difference be ever so small, and would tend to live longer and to survive during that time of the year when food was shortest; they would also rear more young, which young would tend to inherit these slight peculiarities. The less fleet ones would be rigidly destroyed. I can see no more reason to doubt but that these causes in a thousand generations would produce a marked effect, and adapt the form of the fox to catching hares instead of rabbits, than that greyhounds can be improved by selection and careful breeding. (Darwin and Wallace 1958, 120)

Over the next twenty years this was the theory that Darwin would explore in all its ramifications. He continued to work with animal breeders. He corresponded with a vast range of naturalists, sounding them out on detailed questions without revealing his true purpose. He undertook a massive study of barnacles, then a little-known group, which helped him to understand how branching evolution could be mapped onto the taxonomic hierarchy. This study also showed him that, on many branches of the tree of life, adaptive evolution has led to parasitism and degeneration. Perhaps inevitably, given its source in Malthus's principle, this was not a theory of inevitable progress—better adapted to a particular environment does not mean "fitter" in any absolute sense. Yet in the end Darwin did believe that higher animals, and ultimately the human species itself, had been produced. Struggle did tend to set in motion improvement, at least some of the

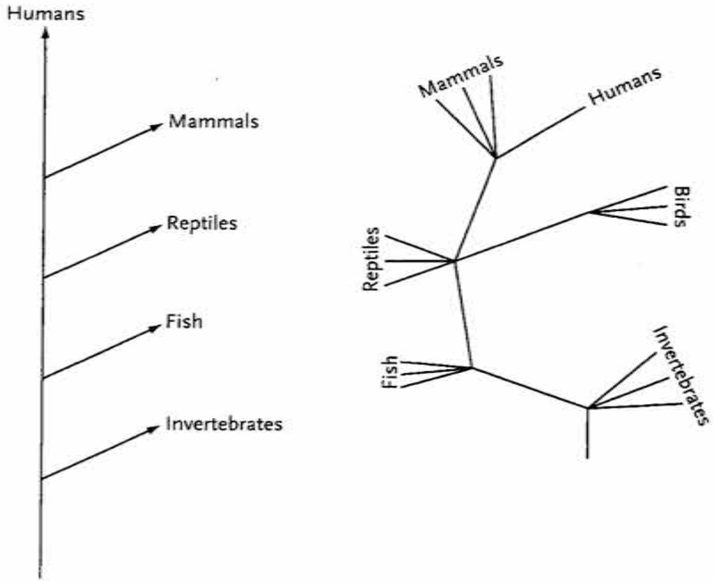

FIGURE 6.4 Diagram illustrating the difference between a linear model of evolution (*left*) and a branching model (*right*). The linear model treats evolution as a progressive advance along a linear hierarchy toward the human species. The "lower" forms of life thus appear as the rungs of a ladder that life has climbed to reach its goal in humanity. This model is easily compatible with the recapitulation theory in which the human embryo passes through stages corresponding to the lower animals. In the branching model, the emphasis is on adaptation and divergence, not progress. Each class splits into a range of different adaptations, and later classes are derived from a single branch of a previous class. Progress has to be defined in terms of distance from the simplest common ancestor, but there are many different lines of advance and no living form can be treated as a stage in the development of another. This diagram focuses on the vertebrates, but note that in fact the invertebrates form a range of phyla fully equivalent to the vertebrates in diversity.

time, and this viewpoint would eventually be incorporated into "social Darwinism." Yet Darwin was very careful not to link his theory to the linear model of progress. There was no main line of evolution, and most adaptive trends have nothing to do with the ascent of life. Darwin also admitted that the imperfection of the fossil record would make it difficult to reconstruct the detailed course of evolution, although the general outline of the record fit a theory of branching, adaptive evolution in which each branch was specializing for a different way of life (fig. 6.4).

By the mid-1850s Darwin had let a few colleagues, including Lyell and

the botanists Joseph Hooker and Asa Gray, know the details of his theory and had begun writing. He was interrupted in 1858 by the arrival of a paper written in the Far East by another naturalist, Alfred Russel Wallace, outlining a theory similar to his own. Historians have disagreed enormously over the significance of Wallace's discovery. Some accept Darwin's initial reaction at face value and treat Wallace as the codiscoverer of the theory, implying that the subsequent events were designed to rob Wallace of his credit. Others have taken a closer look at Wallace's 1858 paper and point out that there are significant differences that Darwin seems to have overlooked. Wallace had no interest in artificial selection, and it is quite possible that his paper was really intended to describe a form of natural selection acting between varieties or subspecies, not between the individuals of the same population (for an overview, see Kottler 1985). This may not be a case of independent discovery at all, but of two naturalists with similar, but not identical, backgrounds exploring different aspects of the same problem. Whatever the differences and similarities, Darwin saw enough of a parallel with his own work to fear the loss of his twenty-year priority. Lyell and Hooker arranged for the publication of two extracts of Darwin's writings along with Wallace's paper (reprinted in Darwin and Wallace 1958). No one paid much attention, but Darwin now rushed to complete the account of his theory, which was published at the end of 1859 as *On the Origin of Species.*

The Reception of Darwin's Theory

The *Origin* sparked a renewed debate over evolution. Darwin was an eminent scientist, and natural selection was an important new initiative backed up by a wealth of new evidence. The debate was rendered all the more emotional because the theory seemed to undermine any hope of seeing evolution as the unfolding of a divine plan. In these circumstances, both scientists and laypersons were forced to assess the theory at various levels: their evaluation of the evidence would almost certainly be influenced by their wider beliefs. Debates raged over the plausibility of both evolution in general and natural selection in particular. Darwin had important new lines of argument, but there were also technical arguments against his theory. Some of these focused on the area of heredity, where his thinking did not anticipate modern genetics and left him vulnerable to arguments that would not be plausible today. In these circumstances, there was little hope of a clear-cut debate that would end decisively with the rejection or acceptance of the new theory. No one was going to be converted by scientific arguments alone, and to some extent the outcome would depend on the politics of the scientific community and the possibility of a wider change in public opinion. In the end, after a few years of uncertainty, the general idea of evolution came to be widely accepted, but natural selection remained controversial.

To younger, radical scientists such as T. H. Huxley, Darwin's theory offered immense opportunities (Desmond [1997]; on the scientific debate, see Hull [1973]). As professional scientists they were anxious to discredit natural theology, which in their eyes left science subservient to religion (see chap. 14, "The Organization of Science"). Darwin's theory certainly did this and, thus, fit well into the philosophy that Huxley called "scientific naturalism"—although to his opponents it was little better than materialism. The whole world, including the human mind, was to be explained in terms of the operations of natural law. Here Huxley could make common cause with the philosopher Herbert Spencer, who presented evolution as the underlying principle of both nature and society. Spencer welcomed the individualism of Darwin's theory, since it fit his view that the general progress of nature was the product of innumerable acts by individuals, each seeking its own wellbeing. This points the way to the social applications of Darwin's theory (see chap. 18, "Biology and Ideology"), although it is important to realize that natural selection was not the only model of evolution available. Spencer favored Lamarck's theory of the inheritance of acquired characters because it better fit his ideology of self-improvement. Huxley would not accept natural selection as the sole mechanism of evolution, preferring to believe that variation was directed in a few consistent directions, instead of being random as Darwin supposed.

Even within the scientific community there were many who rejected naturalistic philosophy, often because they retained deep religious beliefs. Outside science, religious and moral problems influenced many people's response to the theory (see chap. 15, "Science and Religion"). A survey of the popular press reaction by Alvar Ellegård (1958) shows how the more conservative periodicals lagged behind in acceptance of evolution, their authors worrying that the theory undermined both divine providence and the spiritual status of the human soul. Huxley's confrontation with the smooth-talking Bishop "Soapy Sam" Wilberforce at the 1860 meeting of the British Association has become a symbol of the confrontation between evolutionism and conservative religion, although we now know that Huxley was by no means as successful as the popular image of this event implies (see fig. 15.3, p. 356). In the long run, however, conservatives reluctantly accepted the basic idea of evolution. But they needed to see the process as the expression of God's purpose and, thus, remained hostile to the trial-and-

error model of natural selection. The reemergence of a sustained creationist opposition occurred only in the 1920s, however.

There were certainly scientific arguments to be deployed. Darwin made much of the difficulties naturalists often encountered in deciding whether a particular form was a distinct species or merely a variety of another species. He showed how geographical distribution could be explained far more easily in terms of branching evolution rather than as arbitrary acts of creation. The botanists Joseph Hooker and Asa Gray supported Darwin here, while A. R. Wallace undertook a major study of animal distribution, publishing an important synthesis in 1876. Yet increasingly, the emphasis began to fall on an area that Darwin had tried to avoid: the detailed reconstruction of the history of life on earth using fossil and anatomical evidence. Darwin thought the fossil record was so incomplete that it would be impossible to reconstruct the ancestry of any known species in detail. But this left him vulnerable to critics who insisted that unless the "missing links" could be found, evolution remained implausible. By the 1870s, important new fossils had been discovered that seemed to fit the evolutionists' predictions. In Germany, the remains of *Archaeopteryx* provided clear evidence of a form intermediate between reptiles and birds. From America came a series of fossil horses showing a line of specialization leading toward the modern horse that Huxley proclaimed as "demonstrative evidence of evolution" (on these developments, see Bowler [1996]).

Even where fossils were not available, enthusiastic evolutionists such as Ernst Haeckel in Germany used anatomical and embryological evidence to reconstruct the links between the major branches of the tree of life. Haeckel was a leading proponent of the recapitulation theory, which built on the old law of parallelism by assuming that the development of the embryo offered a speeded-up model of the organism's whole evolutionary ancestry. He and his followers (Huxley included himself in this group) proposed hypothetical genealogies to explain the origin of all the vertebrate classes, and even of the vertebrates themselves. Michael Ruse (1996) dismisses this whole movement as inferior science driven by an overenthusiastic support for the idea of progressive evolution. It is certainly true that these evolutionists ignored some of the most important lessons that could have been learned from Darwin. By using the embryo as a model for evolution, they highlighted the progressive development of life in a way that portrayed the human species as its intended goal. Haeckel's version of the tree of life had a main trunk leading through to humans, with everything else dismissed as side branches—a linear model more reminiscent of the old chain of being (fig. 6.5). He had little interest in exploring the kind of adaptive pressures

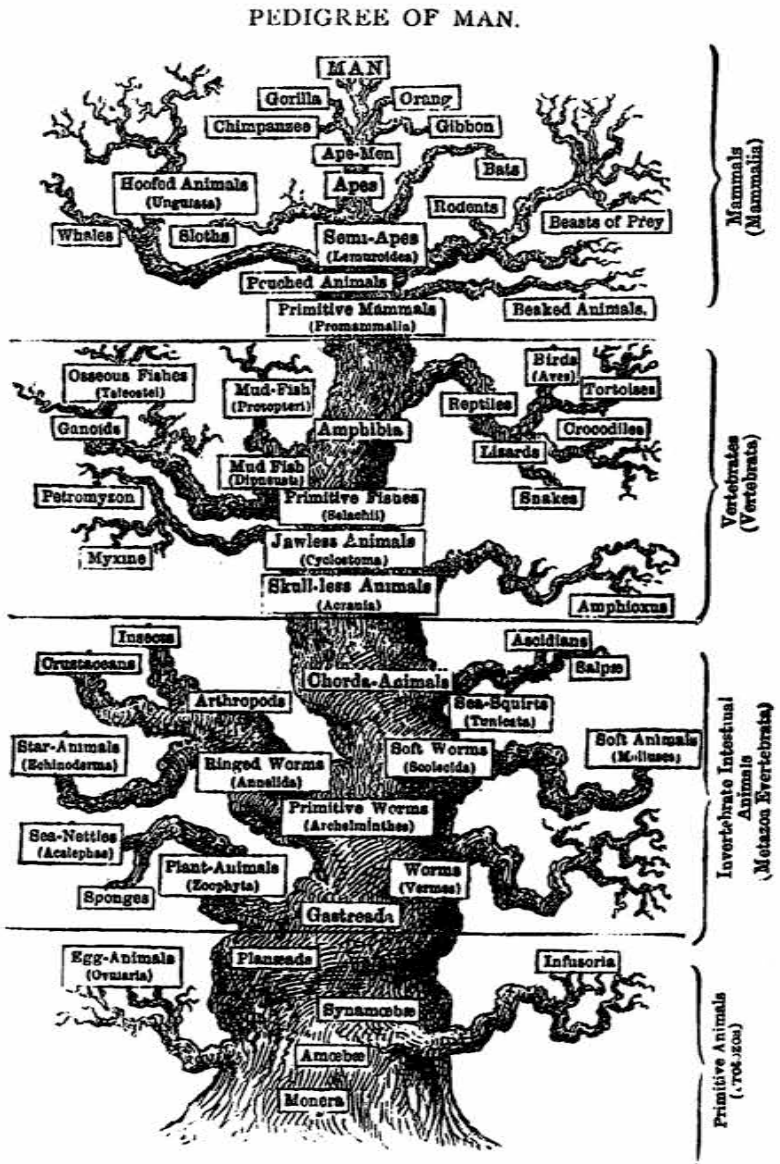

FIGURE 6.5 The tree of life from Ernst Haeckel's *History of Creation* (New York, 1876), vol. 2, facing p. 188. Note how Haeckel combines the linear and branching models of evolution (fig. 6.3, above) by deliberately giving his tree a main trunk with humanity at the top. He thus retains something of Darwin's emphasis on divergence and adaptation but superimposes this onto a linear ascent by treating all those creatures that do not lie on the "main line" as side branches leading off to stagnation.

that might have brought about the changes he was postulating. It is also true that this project to create an evolutionary morphology (the science of animal form) got bogged down as rival hypotheses emerged, with little hope of fossil evidence to determine which was right (see chap. 7, "The New Biology"). But to dismiss this whole generation of evolutionary biology as a waste of time misses the point that it was perceived as the most exciting application of the theory at the time. It certainly confirms that evolution was welcomed because it seemed to endorse the idea of progress, but the debates that were engendered raised substantive issues that are only now being resolved as the techniques of molecular biology (to say nothing of a wealth of later fossil discoveries) are brought to bear on them.

Haeckel called himself a Darwinian, but he combined the selection theory with a generous dose of Lamarckian use-inheritance and a commitment to the idea of progress that owed much to the *Naturphilosophie* of an earlier generation. The selection theory had, in fact, encountered substantial criticism from a host of scientists who found it difficult to believe that a process based on random variation could ever have a purposeful outcome (Gayon 1998; Vorzimmer 1970). Richard Owen accepted evolution but insisted that its course was predetermined by a divine plan (Rupke 1993). The anatomist St. George Jackson Mivart's *Genesis of Species* (1871) outlined a host of objections, some of which are still in use by modern creationists. How, he asked, could natural selection force a transition through the intermediate phase where a structure had lost its old function but was not yet efficient at the new one, for example, when a limb no longer worked as a leg but was not yet a proper wing? Some naturalists shared Mivart's belief that many structures have no adaptive function at all, indicating the existence of predetermined trends not controlled by natural selection. There was also the problem of geological time (see chap. 5, "The Age of the Earth")—by the late 1860s William Thomson was limiting this to a point where many believed that natural selection would be too slow to have produced the ascent of life up to humans.

Equally serious was an objection raised by the engineer Fleeming Jenkin based on Darwin's model of heredity and variation. Like most of his contemporaries, Darwin had no notion of the discrete genetic units that would be postulated by Gregor Mendel—he thought that the offspring would simply blend together any differences between the parents (although this is self-evidently not true for sex). If a beneficial new character appeared in a single favored individual, Jenkin argued that the offspring would only have half the benefit, the next generation only a quarter, and so on. Within a few generations, the beneficial new character would be diluted to insignificance and could not be acted on by selection. Darwin had no real answer to this, and it was Wallace who pointed out that favorable characters do not appear in single individuals. If we think of the population of ancestral giraffes when it first began to feed off trees, it would have shown a range of variation in neck length, with significant numbers at both ends of the range. There would have been no shortage of individuals with longer than average necks to benefit from the action of selection.

By the 1880s, Wallace was one of a relatively small number of biologists still defending the Darwinian selection theory. The theory of evolution itself was secure, but Darwinism was increasingly under fire as critics sought alternatives to the selection theory. This was the period that Julian Huxley later referred to as the "eclipse of Darwinism" (Bowler 1983a). Building on Mivart's work, many argued that evolution was driven by nonadaptive trends somehow built into the nature of life itself. Those who accepted a role for adaptation saw the Lamarckian theory as an alternative rather than a supplement to Darwinism. In America there was a strong neo-Lamarckian movement led by such paleontologists as Edward Drinker Cope. They were sure that the almost linear trends they found in the fossil record could only be the result of some directing agent, in this case the new habit that drove the species toward a more specialized structure. Viewed from the perspective of the late nineteenth century, Darwin's theory was a relic of the past that had played only a fleeting role in forcing scientists to reconsider the case for evolution in the 1860s.

Human Origins

Darwin had avoided discussing the human race in the *Origin of Species*, knowing that this was a particularly sensitive topic. But controversies over the degree of relationship between humans and apes were already underway, and the whole issue had become a battlefield long before Darwin eventually entered the fray with his *Descent of Man* in 1871. Religious thinkers were dismayed that the theory linked us with the animals and thus, by implication, undermined the credibility of the immortal soul. Humans alone had traditionally been endowed with higher mental and moral faculties—so by suggesting that we were only improved animals, evolutionism threatened our unique status and might even undermine the fabric of the social order. In the scientific naturalism favored by Darwin and Huxley, however, it was important to show that there were no supernatural agents in the world, so even the human mind was a product of the activity of the brain, which in turn had been shaped by evolution.

FIGURE 6.6 Comparison of the skeletons of a human (*right*) with those of a gorilla, a chimpanzee, an orangutan, and (twice life-size by comparison) a gibbon; the frontispiece to T. H. Huxley's *Man's Place in Nature* (London, 1863). Huxley argued that the degree of similarity meant that humans had to be classed as Primates and hence, by implication, must share a common ancestry with the apes.

The case for an evolutionary ancestry for humanity was boosted by a revolution in archaeology that took place in the early 1860s. Lyell's *Antiquity of Man* (1863) summed up evidence that Stone Age humans had existed on the earth for tens of thousands of years before civilization emerged. Yet Lyell himself could not accept an evolutionary link between those primitive humans and apes. There was as yet no plausible fossil evidence for a missing link between humans and apes, so those who wanted to argue for an evolutionary connection had to stress the anatomical similarities between humans and the living great apes. Huxley was already engaged in a debate with Richard Owen on the degree of similarity between the human and ape brains. He summed up his arguments for a close link in his *Man's Place in Nature* in 1863 (fig. 6.6). But it was the mental, not the physical, comparison that was crucial, and already philosophers such as Herbert Spencer were beginning to create an evolutionary psychology by which they hoped to explain how the higher mental faculties had been added in the course of evolution (Richards 1987).

Darwin offered his *Descent of Man* as a contribution to this enterprise. He wanted to show that the apparent gulf between animal and human mentalities was not as great as traditionally assumed (fig. 6.7). Like many of his contemporaries, he was increasingly inclined to treat those modern races that the Victorians regarded as "savages" as surviving relics of earlier stages in the ascent from the ancestral ape. They were the equivalent of the

PUNCH'S FANCY PORTRAITS.—No. 54.

CHARLES ROBERT DARWIN, LL.D., F.R.S.

IN HIS *DESCENT OF MAN* HE BROUGHT HIS OWN SPECIES DOWN AS LOW AS POSSIBLE—*I.E.*, TO "A HAIRY QUADRUPED FURNISHED WITH A TAIL AND POINTED EARS, AND PROBABLY *ARBOREAL* IN ITS HABITS"—WHICH IS A REASON FOR THE VERY GENERAL INTEREST IN A "FAMILY TREE." HE HAS LATELY BEEN TURNING HIS ATTENTION TO THE "POLITIC WORM."

FIGURE 6.7 A caricature of Darwin from the magazine *Punch* in 1881. The caption refers to Darwin's theory that humans are descended from a "hairy quadruped," but the picture links him to an even lower animal, the earthworm—the subject of Darwin's last book. He was fascinated by the ability of worms to regenerate the soil and even transform the landscape over a long period of time, retaining an interest in detailed natural history even while dealing with the broadest of theoretical issues.

Europeans' Stone Age ancestors, surviving into the present and in effect showing us what the "missing link" would have been like (see chap. 18, "Biology and Ideology"). Darwin also tried to exaggerate the mental powers of animals: there were as yet no scientific studies of animal behavior, so he could use anecdotal evidence from travelers and zookeepers that often presented an anthropomorphic interpretation of animals' actions. For Darwin the human conscience was merely an expression of the social instincts that our ancestors had been endowed with by evolution. Far from generating instincts for pure selfishness, natural selection (coupled with a Lamarckian inheritance of leaned habits) could promote social instincts in species that normally lived in groups. Our moral values were just rationalizations of instincts imprinted on our ape ancestors.

Darwin saw that it was important to explain why humans gained a higher level of mental powers than their ape relatives. He suggested that perhaps our ancestors stood upright when they moved out of the forests onto the plains of central Africa. This freed their hands for tool making and thus promoted extra intelligence. Most nineteenth-century evolutionary psychologists simply assumed that evolution would steadily add on new stages of mental activity. Their work thus expanded the developmental model of evolution promoted in biology by Haeckel. Darwin's chief disciple in this area, George John Romanes, wrote a series of books on the mental powers of animals and humans, trying to reconstruct the exact sequence in which new mental powers were added. He used the recapitulation theory to portray the mental development of the human child as a model for the whole evolution of animal life. Although fossil discoveries toward the end of the century would challenge this linear model of evolution (see Bowler 1986), its influence on late nineteenth-century thought was profound. And in the end it was turned on its head by Sigmund Freud, who recognized that the animal instincts buried in the unconscious may often be too much for the overlying rational mind to control (Sulloway 1979).

THE RESURGENCE OF DARWINISM

In the decades around 1900 most biologists remained evolutionists, but they believed that Darwinism was dead. New developments in the life sciences were, however, challenging the foundations on which late nineteenth-century evolutionism had been built. To enhance their status as professional scientists, many biologists turned to experimental work and began to look down on the comparative anatomists and paleontologists who had tried to reconstruct the ascent of life on earth. One product of this move was a program of research on heredity and variation that would lead to the foundation of modern genetics (see chap. 8, "Genetics"). The geneticists repudiated the Lamarckian effect and the developmental trends that had upheld the recapitulation theory. They gradually eroded support for neo-Lamarckism, and with hindsight we can see that this paved the way for a reemergence of the Darwinian selection theory. Yet the first geneticists had no more time for Darwinism than they had for Lamarckism. They thought that large genetic mutations created new species without any need for selection. The final phase of the Darwinian revolution emerged from a complex process of reconciliation by which the geneticists were brought round to the view that selection was indeed necessary to explain the accumulation of favorable genes in a population. It turned out that Darwin had been right after all, even though a generation of biologists had turned their backs on his theory.

The first moves were made by biologists who became convinced that heredity rigidly determines the character of the organism. Environmental effects are powerless to alter the characteristics inherited by the child from its parents. In Germany, August Weismann postulated the "germplasm" that was responsible for transmitting the characters from one generation to the next. He argued that it was isolated from the rest of the body, making the Lamarckian effect impossible. Weismann insisted that natural selection was the only way that the transmission of characters could be affected by the environment. In Britain, the statistician Karl Pearson adopted similar views and tried to detect the effect of selection on the variation of wild populations (fig. 6.8). His views were controversial, and Pearson's support for the selection theory generated antagonisms that would alienate him from the founders of genetics. As far as he was concerned, evolution was a slow, gradual process just as Darwin had assumed—but that was exactly the point being challenged by the biologists who would create Mendelian genetics.

The alternative being explored by several of the biologists involved in the "rediscovery" of Gregor Mendel's long-neglected laws of heredity was the theory of evolution by sudden leaps or saltations (Bowler 1989). William Bateson, who went on to coin the term "genetics" and provide the first English translation of Mendel's paper, openly rejected Darwinism during the 1890s. He insisted that studies of variation within species showed that the distinct varieties within them were created abruptly by saltation, not by gradual adaptive change. The Dutch botanist Hugo De Vries, one of the biologists who first drew attention to Mendel's paper, proposed his "mutation theory" based on the apparently sudden appearance of new types

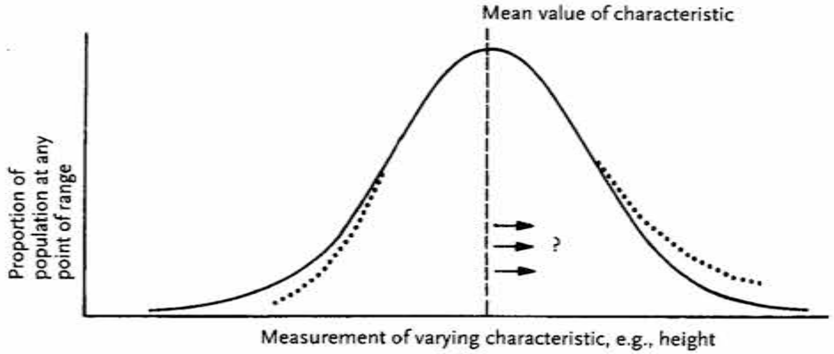

FIGURE 6.8 Diagram to illustrate the distribution of a continuously varying character in a population and the effect of selection on the distribution. The *solid line* is the bell-shaped "normal" curve that would be obtained, for instance, for the variation in height within a human population. The proportion of the population occupying any point in the range (*vertical axis*) is plotted against the measurement of the character (*horizontal axis*). The largest proportion is clumped around the mean value with smaller proportions tailing off to either extreme—most people are of approximately average height, and there are smaller numbers of very tall and very short persons. Biometricians such as Karl Pearson and W. F. R Weldon measured the variation for different characters in wild populations of crabs and snails and obtained curves such as this. But as Darwinists, they then had to show that if the population were subject to selection, there would be a permanent shift in the distribution. If taller individuals were favored in a certain environment, and shorter ones at a corresponding disadvantage, this would generate more tall individuals and less short in the next generation, as indicated by the *dotted lines*. But would the effect of this be to shift the mean value for the population as a whole in the favored direction as shown by the arrows? The measurement seemed to show that such an effect did occur, but it was too small to convince many anti-Darwinian biologists.

within the evening primrose, *Oenothera lamarckiana*. Thomas Hunt Morgan, who eventually established the true nature of mutations, began as a supporter of De Vries's theory and a strong opponent of Darwinism. What drew all of these biologists to the model of heredity that they found in Mendel's laws was their preference for the idea that new characters are created as discrete units. It seemed natural for them to accept a theory in which all hereditary characters are treated as fixed discrete units transmitted from one generation to the next. The fact that Mendel had already worked out the laws governing the transmission of these units—soon to become known as genes—was hailed as a remarkable anticipation of the latest thinking when De Vries and others came across his paper in 1900, more than thirty years after its original publication.

Not surprisingly, the early Mendelians saw their theory as a new alternative to Darwinism, while Pearson rejected the geneticists' model of heredity as incompatible with the continuous range of variation he studied in many wild populations. It took twenty years for a bridge to be built between the two positions by biologists who realized that each side had been looking at only one aspect of the problem. In the meantime, Morgan's studies of true genetic mutations showed that De Vries's large-scale saltations did not reflect the way in which new genetic characters are normally produced (in fact the evening primrose is a hybrid, and the "new" forms De Vries was observing were not true mutations). Genes normally transmit their character without change from one generation to the next, but Morgan and his team showed that every now and again something alters the gene so that it codes for a different character. Large mutations are deleterious and often fatal, but there are many smaller ones that are transmitted to future generations as their carriers breed with other members of the population. By 1920, Morgan had realized that mutations keep up a supply of genetic variation within the species and even began to concede that an effect similar to natural selection would determine what mutations will spread into the population. If a mutated gene corresponds to a character that is beneficial in a new environment, the organisms that carry it will breed more readily and the next generation will contain more organisms with that gene. Conversely, a gene conferring a harmful character will gradually be eliminated. Mutations thus provide the ultimate source of the random variation that Darwin had postulated.

It was also realized that because many characters can be influenced by more than one gene, the genetic model of variation is not incompatible with the continuous range of variation observed by Darwinists such as Pearson. A new science of population genetics emerged to study how genes maintain the variability of populations, and how the range of variation can be altered by natural selection (Provine 1971). In Britain, Ronald Aylmer Fisher published his *Genetical Theory of Natural Selection* in 1930, arguing that all evolution takes place through the slow action of selection on large populations. J. B. S. Haldane also contributed to the theory but realized that the process could work much faster than Fisher supposed when genes conferred major adaptive advantages. In America, Sewall Wright used a different model derived from artificial selection to show that natural selection works best when the species is divided into small subpopulations that only occasionally interbreed. When Wright's mathematical formulas were translated into terms that the field naturalists could understand in Theodosius

Dobzhansky's *Genetics and the Origin of Species* of 1937, the way was open for the final emergence of Darwinism as the dominant model of evolution.

Field naturalists such as Ernst Mayr now began to contribute to the new Darwinism—indeed Mayr has since maintained that he and his co-workers were already finding their way toward a more selectionist model before they became aware of the genetical theory (see Mayr and Provine 1980). In 1942 the British naturalist Julian Huxley, grandson of Thomas Henry, published his *Evolution: The Modern Synthesis*, and the theory has been known ever since as the modern or evolutionary synthesis. Those involved, and a subsequent generation of historians, argued and still argue over exactly what was synthesized to make the theory. Was it a theoretical synthesis bringing together selection and genetics, or a reconciliation between previously hostile areas of biological research made possible by the elimination of rival non-Darwinian ideas? Why was the synthesis more visible in the Anglo-American scientific communities than elsewhere—does this reflect the fact that even genetics developed in a less deterministic way in France and Germany than in Britain and America? These arguments will no doubt continue, fueled in part by the fact that the synthesis has been remarkably successful in holding evolutionism together ever since.

Conclusions

The once-popular notion of a Darwinian revolution following the publication of the *Origin of Species* no longer holds water. Historians have shown that challenges to the idea of divine creation began long before Darwin published and that even the concept of a designed universe could be made more sophisticated so that it could accommodate the idea of development through time. The basic idea of evolution was widely debated following the publication of *Vestiges*, and Darwin's theory was understood in part as a contribution to Chambers's vision of progress. Darwin's more materialistic theory offered some new opportunities to scientists, especially those willing to go along with Huxley's scientific naturalism, but in the end the most radical implications of the selection theory had to wait until the twentieth century before they could be realized. The original Darwinian revolution turned out to be only a transition to an evolutionary interpretation of an already-existing worldview based on faith in the idea of progress as the product of divine providence or of nature's laws. What modern biologists see as most original in Darwin's work served only to shock his readers into acceptance of the general idea of evolution—in the end they could not take natural selection seriously. It took a second revolution associated with the emergence of Mendelian genetics to destroy the developmental view of evolution that had subverted Darwin's proposals and complete the transition to modern Darwinism.

In some senses, of course, the revolution is still not over. The supporters of the modern synthesis did not conceal the difficulties their theory created for traditional beliefs, and in response there was a reemergence of Fundamentalist opposition first articulated in the 1920s. A large number of traditional believers, especially in America, simply reject the theory outright and still look to divine creation. If the Darwinian revolution in science is complete, the revolution in popular attitudes has a long way to go.

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