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CHAPTER 7

THE NEW BIOLOGY

THE BIOLOGICAL SCIENCES BEGAN to take on their modern form in the nineteenth century, and indeed widespread use of the term "biology" only came into use during that period (Coleman 1971). Previously, the life sciences had been studied through natural history and through the physicians' use of anatomy and physiology (although the two areas were linked, e.g., by the interest in plants for drugs). In the nineteenth century, however, a determined effort was made to turn the study of living things into a science matching the prestige of the physical sciences. It would no longer be enough just to collect and classify the diversity of species found at home and around the world. Biologists wanted to understand the detailed internal structure of the different forms of life, and they were increasingly concerned with how those structures were built up, both in the individual embryo and in the evolution of life on earth. Natural history was replaced by comparative anatomy and embryology, sometimes unified as the science of "morphology" (the study of form or structure). This science took place within the dissecting room or laboratory, using ever more complex microscopes and analytical techniques. In the drive to create a professional academic community devoted to the life sciences, the old tradition of field study found itself marginalized.

Detailed studies of the structure of living tissues initiated a major transformation of biologists' ideas about the nature of life by pointing the way toward the theory of the cell. The idea that all living structures are composed of cells, specialized for particular functions, would open new pathways to the study of how those functions operated at the chemical level. It would also transform the study of reproduction by showing how egg and sperm were united to form the basis of the developing embryo. To an increasing extent, though, the model to be followed by all these sciences was derived from experimental physiology. Physicians had always been trained in anatomy (the study of the body's structure) and had used theories about how the parts of the body functioned—a study that began to be known as "physiology" in the course of the eighteenth century. But in the nineteenth century, physiology was transformed by the application of experimental methods, providing an entirely new theoretical framework for understanding how the body worked. This study was still expected to be of use in medicine, since the more one knew about normal functions the better one could understand how things could go wrong. But where earlier physiologists had worked within the framework of medical education, now the subject became a scientific discipline in its own right, based in university science departments as well as in medical faculties (for an old-fashioned but factually detailed study of many of the biologists discussed below, see Nordenskiöld [1946]).

This transformation is normally associated with the application of experimental methods in the life sciences, including vivisection—operations performed for scientific purposes on the bodies of living animals. There had been some use of experiment in ancient medicine, and William Harvey had based his theory of the circulation of the blood partly on the use of demonstrations with live animals. But in the nineteenth century, vivisection became the normal process for attempting to understand how the body functioned. The anatomist might use dead bodies to explore structure, but function could only be investigated by interfering in a controlled way with the processes at work in the living organism. There were moral problems here that exerted considerable effect on how the science developed, but physiologists insisted that causing limited suffering to animals was essential to achieve the greater good of understanding and possibly curing human illnesses.

The laboratory now became the central location for the conducting of scientific physiology, and morphology was linked as closely as possible to this new model. Most of the early developments in this direction took place in France and Germany. When Thomas Henry Huxley and his disciples began to establish the modern discipline of "biology" in Britain during the 1870s (borrowing a term introduced at the beginning of the century), they sought to distance it from old-fashioned natural history by linking physiology and morphology as the twin foundations of a laboratory-based science (Caron 1988). Increasingly, though, it was physiology that determined what the new science should look like: mere description of dead animals was not enough to understand how living organisms actually worked. By

the end of the century, many areas of the life sciences were affected by a "revolt against morphology" driven by the desire to follow physiology into the realm of experiment (Allen 1975).

The application of experimental methods led to new theories of the nature of life and of living processes that we take for granted today. Harvey's discovery of the circulation had transformed physicians' understanding of anatomy and had undermined the credibility of the medieval tradition of physiology. It did not, however, lead to an immediate displacement of medical treatments such as blood letting, which were based on the logic of the old system. In part this was because there was no new system of physiology to make sense of what the body did in the course of respiration and the absorption of food. Some important steps were made toward identifying the functions performed by different living tissues, but there was little knowledge of how those functions were effected. Efforts to create a new science of physiology were hampered by the lack of an adequate chemistry, and it is no accident that modern physiology came into being during the century following Lavoisier's "chemical revolution" and the first steps in the creation of an organic chemistry (the chemistry of complex carbon compounds, including those that make up living bodies). Lavoisier himself made a start by postulating that the body "burned" chemicals derived from food in the oxygen absorbed into the blood from the air—a proposal that would form the basis for a whole series of research programs in the nineteenth century, including many that are seen as the foundation stones of modern biology.

In addition to the impact of experimentalism, most traditional histories of physiology focus on a major theoretical debate over the nature of life. Until the seventeenth century, physicians had followed those ancient philosophers who argued that the physical body was vivified by a nonmaterial soul or vital force. The mechanical philosophy encouraged the reemergence of materialism: the claim that the living body (and by implication the human body) is nothing more than a complex material structure driven by physical forces (see chap. 2, "The Scientific Revolution"). Further development of this materialist approach was hampered by the lack of a suitable chemistry, which might effectively serve as a bridge between the behavior of atoms and molecules and the complex functions of a living body. The development of physiology in the nineteenth century saw a steady advance of materialism, although some eminent scientists stood out against the trend to reduce life to nothing more than physical processes. The elimination of "vitalism" is often presented as a key conceptual advance in the rise of the modern life sciences, but more recent histories take a less blackand-white view. Those biologists who resisted materialism often did so for what seemed to them very legitimate reasons, and some of them did important work precisely because they were still inspired by the belief that life was something more than material activity. In the early twentieth century, eminent physiologists such as J. S. Haldane rejected a simple reductionist materialism, although they seldom sought to revive the old idea of a vital force interfering with the physical world in an almost supernatural manner. Some biologists recognized the need to see organic processes as functions of complex systems that could not be explained away by reducing them to the molecular level. This is the philosophy of organicism or holism, the belief that the whole can be more than the sum of its parts and can exhibit higher-order functions even though the operation of each part is governed solely by physical law.

This chapter will provide a selective overview of some key developments in the establishment of the modern life sciences. It will briefly highlight the rise of morphology, linking this to our studies of other sciences including evolutionism. It will then focus on the expansion of knowledge of organic tissues and cell theory. We then move to physiology and the efforts to uncover the operations of the more fundamental functions of the "animal machine," including respiration and nutrition. The roles of both the experimental method and the new materialism in defining the underlying ethos of the New Science will form themes that traverse the whole story.

The Study of Structure

The eighteenth century had seen a vast expansion in naturalists' knowledge of exotic species and a massive focus on the problem of how to classify the diversity of living things, exemplified by the work of Linnaeus (see chap. 6, "The Darwinian Revolution"). By the early nineteenth century, the project to put classification on more "scientific" grounds led Georges Cuvier and others to insist that the true nature of a species, and hence its true position in the plan of nature, could only be determined from its internal structure (Coleman 1964). Comparative anatomy became the key to a new and more technically sophisticated form of natural history. The location where the research was done was increasingly not the field, where collectors still hunted for new species, but laboratories within the great museums or university departments where the specimens sent back to the metropolis were dissected in ever more minute detail (fig. 7.1). Cuvier and his great rival Geoffroy Saint-Hilaire both worked at the Natural History Museum in Paris, while Richard Owen became the leading British morphologist from a

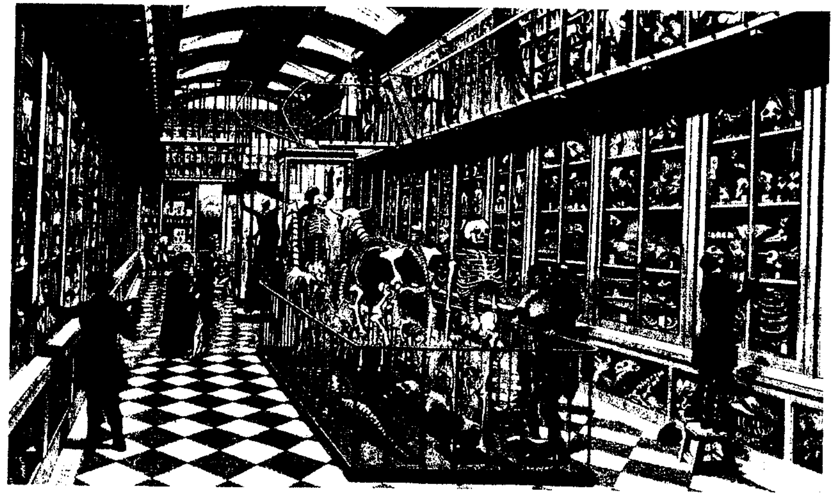

FIGURE 7.1 The gallery of comparative anatomy at the School of Medicine in Paris, created in 1845. This gallery was primarily a center of research where the details of the different skeletal structures could be compared, but similar collections in natural history museums were also used for public display of exotic specimens brought from different parts of the world.

base at the museum of the Royal College of Surgeons (Appel 1987; Rupke 1993). In the later part of the century, though, morphology became increasingly based in the zoology departments of universities, sometimes with overlaps to medicine (on the institutionalization of morphology in Germany, see Nyhart [1995]). Similar developments took place in botany, where the old tradition of classification was replaced by detailed studies of the structure and functions of plants.

Cuvier and his contemporaries revolutionized the science of classification by taking it out of the hands of those who actually studied nature in the wild and bringing it into the carefully controlled world of the laboratory or dissecting room. The old tradition of field study, still visible in Darwin's studies on the *Beagle* voyage, was now becoming marginalized, with a consequent loss of interest in the problems of how organisms actually live in the wild. This would only be regained through the rise of ecology at the end of the century. Darwin himself went on to spend years dissecting a vast collection of barnacles, making his name as a biologist through his publication of the first major study of this group. But even here Darwin was already out of date: he used only a simple hand lens in his study at home. By the middle decades of the century, similar work on other groups was being carried out using an ever more sophisticated array of microscopes, dissecting tools, and staining chemicals, usually within specially constructed laboratories in museums and universities.

Classification was still the main purpose of understanding the internal structure of organisms, but it now formed part of the new science of morphology, the study of form. Cuvier had insisted that to understand the structure of an animal one needed to know about the function the various organs performed, but all too often, the actual function that the structures fulfilled in the life of the organism was ignored. Later critics accused the morphologists of being more interested in dead organisms than living ones. There was an extended debate over the relative significance of form and function, with many morphologists following Geoffroy Saint-Hilaire in insisting that there were "laws of form" that determined the various possible structures independently of their actual function (Russell 1916). It was within this tradition that ideas of nonadaptive evolution flourished as alternatives to natural selection during the "eclipse of Darwinism" at the end of the century (see chap. 6, "The Darwinian Revolution"). Morphologists such as Ernst Haeckel welcomed the theory of evolution because it allowed them to insist that the relationships they were uncovering between different forms of life were real, that is, the product of genealogical descent by natural processes rather than patterns in the mind of the Creator. But they were reluctant to follow Darwin's own close studies of how animals functioned in the wild, including how they were affected by changing climates or the invasion of rival species. Instead, they were more inclined to see evolution as the unfolding of orderly patterns driven by internal biological forces (Bowler 1996).

To understand how life had evolved, the morphologists turned to the study of comparative embryology (fig. 7.2). In Haeckel's terminology, it was assumed that ontogeny (the development of the individual organism) recapitulates phylogeny (the evolutionary history of the species). Embryology had in fact made great strides in the early nineteenth century. The old preformation theory, in which the embryo simply expands from a preformed miniature in the fertilized egg, was replaced by a sophisticated model of epigenesis, in which the very simple form of the egg undergoes a complex series of transformations by which the various structures of the organism are gradually built up. In 1828 Carl Ernst von Baer, who had discovered the true mammalium ovum in the previous year, showed how individuals within each of the main groups of living organisms undergo a distinct process of differentiation by which the specialized organs that characterize the group are formed. There is no single ladder of development—the history of the animal kingdom is best understood as a branching tree, just as Darwin would proclaim in his theory of evolution. Significantly, though, Haeckel subverted this vision by giving the tree a single main trunk running toward the human form. But in one respect, Haeckel's synthesis of embryology and evolutionism built on the latest developments in the study of living structure at the microscopic level. He was able to trace ontogeny (and hence by implication phylogeny) from a single cell, the fertilized ovum, through a complex process of differentiation in which that cell divided and subdivided, eventually forming a spherical body cavity as the foundation from which the embryo would be built (fig. 7.3). This focus on the fertilized ovum as the foundation for development would provide the basis for later work by August Weismann and others on the process by which the chromosomes of the cell nucleus transmit the information of heredity from parent to offspring (see chap. 8, "Genetics").

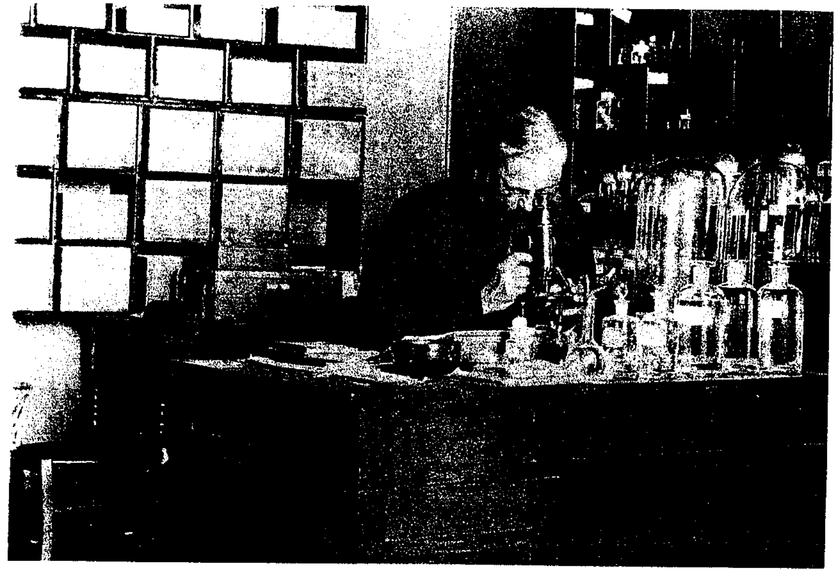

FIGURE 7.2 Anton Dohrn working at his microscope in 1889 in the Zoological Station he founded at Naples (reproduced with the permission of the archives, Stazione Zoologica "Anton Dohrn"). Microscopic examination of "primitive" creatures and their embryological development was routinely used at this time in an effort to reconstruct the history of life on earth, and marine biological stations allowed biologists to study live specimens with the best-available equipment, such as the microscope used here by Dorhn. Significantly, however, Dohrn fell out with Haeckel over the precise structure of the tree of life, and the evidence they produced could not resolve their differences.

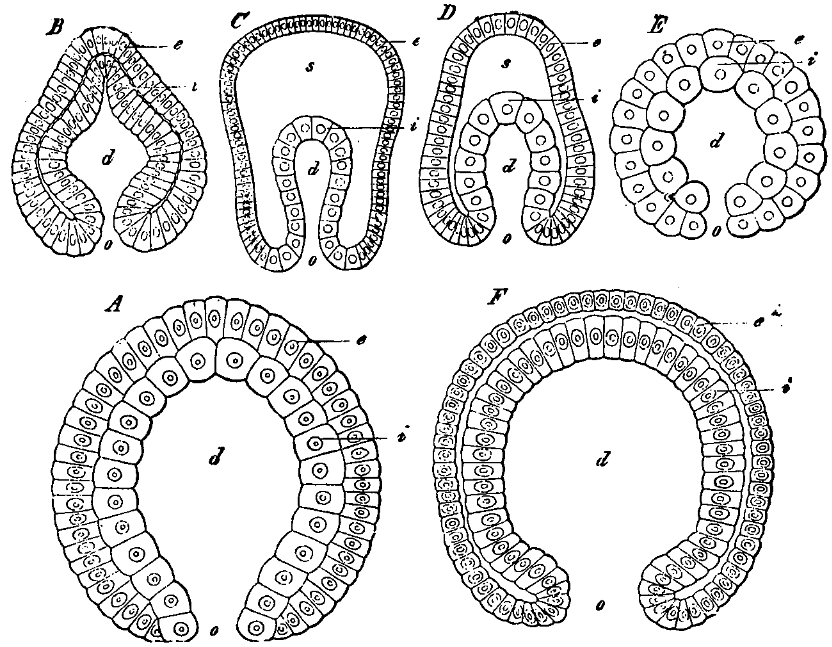

FIGURE 7.3 Haeckel's depiction of the very early "gastrula" stage of development in different organisms, from his *Evolution of Man* (London, 1879), 1:193. The bottom two are (*left*) a primitive zoophyte and (*right*) a human. Note how Haeckel shows the two layers of cells of which this stage of the embryo is built. He argued that the hollow gastrula represented an early common ancestor of the whole animal kingdom.

The idea that the cell was the fundamental unit of life, and that all larger organisms are thus composed of cells, had emerged in parallel with these developments in embryology. Cells had been observed in plant tissues by early microscopists such as Robert Hooke, but their nature and function remained a mystery until the improved microscopes of the nineteenth century allowed a more fine-grained analysis of tissue structures. In 1847 the German botanist Jakob Mathias Schleiden and the zoologist Theodor Schwann proclaimed their "cell theory," in which cells were the basic units from which all living tissues were constructed (fig. 7.4). They differed on how the cells were formed, however, Schleiden holding that new cells appeared within old ones by crystallization around a newly formed nucleus, while Schwann thought they formed from the featureless material surrounding the existing cells. At this point the theory could thus be understood in many different ways, but in 1855 another German, the embryol-

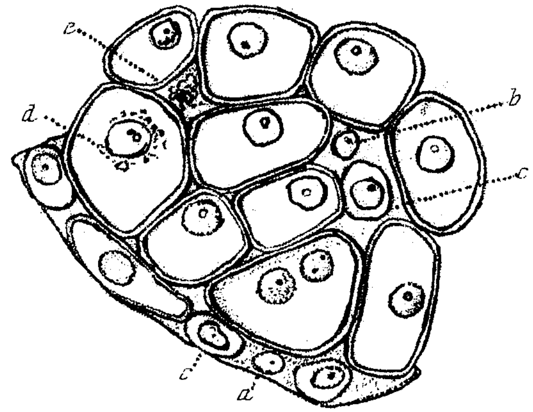

FIGURE 7.4 Microscopic study of the structure of a plant showing the cells and their nuclei, from Theodor Schwann's *Microscopical Researches* (London, 1847), facing p. 27. Schwann showed that all tissue, animal and plant, was composed of cells and argued that the cell was the basic unit of life.

ogist Robert Remak, showed that, in the early stages of growth, cells are formed by a process of division apparently initiated in the nucleus. In his *Die Cellularpathologie* of 1858, Rudolf Virchow proclaimed the final version of the cell theory: cells are the fundamental units of all life and new cells are formed only by the division of existing cells—"Omnis cellula e cellula." For Virchow, this latter point was a key factor in the defense of a vitalistic philosophy in which living things were driven by forces that somehow transcended those of the physical world. Only life could generate life, and theories of the spontaneous generation of living tissue from inorganic chemicals were necessarily false. Rejection of spontaneous generation was common among conservative thinkers, and Virchow was inclined to conservatism in both his philosophy and his politics. One historical study argues that Virchow's vision of the body as a unified and coherent assemblage of specialized cells was inspired by his preference for a political system in which all individuals find their true purpose in life within an ordered society (Ackerknecht 1953).

This vitalistic interpretation was not the only one, however. Other biologists had focused on the fluid material within the cells, largely ignoring the nucleus, whose function was little understood at the time. In the 1840s, Jan Purkinje and Hugo von Mohl defined this material as "protoplasm" and suggested that it was the basic material of life. On this model, the cell was important but only because its wall served to separate the protoplasm from the environment—it was the activity of the protoplasm itself that made life possible. Perhaps more important, this focus on the material substance of the protoplasm, rather than the ordered structure of the cell, encouraged a more materialistic view of life. If one could hold out the hope of chemistry eventually explaining the processes that the protoplasm performed to maintain life, then there was no need for special vital forces. This was the message proclaimed in T. H. Huxley's popular essay of 1868, "The Physical Basis of Life." Six years later, Huxley reinforced his essentially materialistic view in a talk titled "On the Hypothesis That Animals Are Automata, and Its History" in which he traced the continuity between nineteenth-century materialism and Descartes's original view that animals are nothing more than machines (both reprinted in Huxley 1893). At this level of debate there was a genuine interaction between the morphologists who studied how cells were assembled into larger organisms and the physiologists who were now applying the experimental method to understand the processes that maintained life.

The Functions of the Living Body

William Harvey's theory of the circulation of the blood, published in 1628, is sometimes presented as the foundation stone of modern physiology. The discovery undermined the traditional theory of how the body functioned, proposed by the Roman physician Galen, but it did not in itself explain the purpose of the blood being circulated through the lungs and then through the rest of the body. Perhaps for this reason it had little impact on the actual practice of medicine. Harvey's theory certainly prompted further research, including the microscopist Marcello Malpighi's discovery of the capillaries that joined the arteries to the veins in the muscles. But Descartes's suggestion that animals could be understood as just complex machines was incapable of forming a basis for a serious research tradition. Perhaps the heart was a pump, but what powered it and the other muscles in the body was unknown, as were the function of both digestion and respiration. The chemistry of the time had nothing to offer as a means of understanding these processes. Nevertheless, the study of physiology—the functioning of the animal and human body—came into existence as a recognizable discipline within the medical faculties of eighteenth-century universities. Most active was the Swiss biologist Albrecht von Haller, whose *First Lines in Physiology* (1747) offered an early survey. He was best known for defining the difference between those parts of the body that are irritable (contract when touched) and those that are sensible (transmit sensations through the nerves to the

brain). But Haller's physiology was still only a somewhat more animated version of anatomy: it sought to establish the functions of the parts of the body more carefully, but it still offered no real explanation of how those functions operated (see chap. 19, "Science and Medicine"; for a broad survey of the history of physiology, see Hall [1969]).

Some historians would make the same point for the more sophisticated tissue doctrine of Marie-Francois-Xavier Bichat, expounded in his *Anatomie générale* of 1801. If there is a great divide separating the thought of the eighteenth and the nineteenth centuries, as Michel Foucault (1970) argues, then Bichat's efforts to classify the vital functions and associate each with the particular type of body tissue within which it was performed still fits into the eighteenth-century mold (Albury 1977). Traditionally, Bichat has been regarded as the archetypal vitalist; for him the vital functions were the sum total of the forces that resist the physical world's tendency to destroy life—which is why the body decays so rapidly after death. Each tissue had its own vital function, such as sensitivity or irritability, and the existence of these functions was a self-evident deduction from the facts of observation. The sheer variability of organic functions made it obvious that the vital forces were not governed by the mechanistic and predictable laws of the physical world. To make physiology scientific, these unique forces had to be identified, classified, and localized in the body, a technique that paralleled the eighteenth century's fascination with the classification of biological species. If this aspect of Bichat's thought is stressed, there is a clear gulf between his approach and that of the next generation, typified by François Magendie's relentlessly experimental technique of trying to understand how the functions operated. Yet Bichat was also a pioneer of vivisection and hence one of the founders of experimental physiology. Perhaps, as John E. Lesch (1984) suggests, his work had two dimensions, one relating to medicine and one to surgery. Physiology at this point was trying to establish itself within the new academic environment created by the French revolutionary government, and to some extent it sat uncomfortably among medicine, surgery, and natural science.

In another respect, Bichat was well aware of the latest developments in related areas of science. In 1777, the chemist Anton Lavoisier had suggested that his oxygen theory of combustion could be applied to explain the phenomenon of "animal heat" (Goodfield 1975). An animal's body is warm because a process equivalent to the burning of its food material is taking place in its lungs. In the 1780s Lavoisier worked with the physicist Pierre Simon Laplace, using an ice calorimeter, to show that the amount of heat generated was approximately the same in both combustion and respiration. Here was a direct application of a materialistic approach to physiology: a major vital function now seemed to be potentially explicable in purely physical terms. Bichat was well aware of this theory and supported the modification of it that supposed that the oxidation took place in the tissues of the body, not in the lungs, the blood being responsible for conveying both oxygen and food materials to the tissues. But he remained convinced that many other vital functions were not capable of being reduced to physical processes. In this sense, Lavoisier set the scene for the vitalist-mechanist debate of the following century, in which some would follow Bichat while others would argue for the eventual reduction of all vital processes to physical ones. But Bichat's own position warns us of the complexity of the issues involved: the vitalists cannot be dismissed as backward looking thinkers hoping to retain a role for a mystical or spiritual dimension in science.

This debate would be conducted primarily in the physiological laboratories of France and Germany, with Britain now lagging far behind the Continental developments. There is a long-standing assumption that early nineteenth-century German biology was deeply affected by the mystical values of the antimechanist and romantic *Naturphilosophie.* But as Lenoir (1982) insists, the influence of *Naturphilosophie* has been overstated. Much German biology is best described as teleomechanist: it assumed that the body obeys lawlike principles, but interpreted those principles as working for the goal of maintaining life. There was thus no barrier to the application of experiment on living things, on the assumption that physicochemical processes were involved. An important model for the new biology was provided by the research school established in chemistry by Justus von Liebig (Brock 1997). Liebig was appointed professor of chemistry at Giessen in 1824 and established an Institute of Chemistry there. This became a magnet for students from all over Europe, who came to imbibe Liebig's message of the importance of laboratory-based experiment for the study of organic and animal chemistry. The institute's motto was "God has ordered all His creation by weight and measure." In keeping with the new quantitative ethos in experimental philosophy, Liebig insisted on the importance of accurate measurement and analysis. He regarded biological functions as the results of chemical and physical processes going on in the body, invoking the modified form of Lavoisier's theory of respiration to explain animal heat. The aim of the quantitative program outlined in his *Animal Chemistry* of 1842 (reprint, 1964) was to examine carefully what went into the human or animal body at one end and what came out at the other, in effect seeking to use physiological processes like nutrition and respiration to explain the body's sources of energy. Liebig's belief that the degradation of proteins explained muscle activity while the oxidation of carbohydrates and fats generated only heat would soon be abandoned. His methodology was nevertheless an inspiration to later physiologists, although Liebig refused to abandon vitalist philosophy. Like Bichat, he seems to have thought that there were vital forces resisting decay. But he assumed that these forces were lawlike and worked in harmony with the laws of physics and chemistry. They were not inherently capricious, and there was no analogy with the soul or the mind. In effect, he was thinking of a vital energy that was interchangeable with other forms of energy.

One of the most influential departments promoting the new approach to biology was at Berlin under Johannes Müller. Originally influenced by the mysticism of *Naturphilosophie,* Müller turned to careful observation and experiment, working both in morphology and physiology. Some of his most important work was done on the sensory and motor nerves, building on the work of Charles Bell and François Magendie (discussed below). Müller articulated a law of specific nerve energies, which posited that however a sensory nerve is stimulated, it always gives rise only to a particular specific sensation. Despite his commitment to observation, though, Müller's early exposure to a more mystical approach ensured that he remained committed to a vitalism that was far more prescriptive than Liebig's. He was convinced that the living body is governed by a creative force that generates purposeful structures, the ensemble of different species reflecting the divine plan of the universe.

Three of Müller's students turned their backs on his vitalism and helped to found the most influential materialist school in nineteenth-century biology. They were Hermann von Helmholtz, Carl Ludwig, and Emil du Bois Reymond. There was a strong link with liberal political principles, the challenge to romanticism being seen as a challenge also to conservative ideology. It was no coincidence that the movement was founded in 1847, immediately before the year in which many European countries were convulsed by revolution. Their materialism was as much a reaction against the mysticism of *Naturphilosophie,* which they saw still at work in Müller's vitalism, as it was the outcome of demonstration through the new experimental techniques. They saw the advances being made in physics and chemistry and assumed that a program based on similar principles would have the same effect in biology. There were some important results, including du Bois Reymond's work on the electrical nature of nerve activity. Helmholtz also worked on the nerves and virtually founded the science of physiological optics, but he then moved to physics and became one of the founders of the law of the conservation of energy. In effect, the materialists viewed the animal body as a machine working in accordance with this law: there was no special vital form of energy associated only with life. This was equivalent to the program that T. H. Huxley proposed in his "Physical Basis of Life," although Huxley focused on the protoplasm within the cell as the prime locus for the crucial biochemical processes.

It has to be said that although the materialist-reductionist program played an important role in nineteenth-century debates in the philosophy of science, its implementation proved much more difficult than its early proponents imagined. At one time it was assumed that Friedrich Wöhler's synthesis of urea in 1828 drove the first nail in the coffin of vitalism. That a chemical known previously only as a byproduct of organic activity should be synthesized from material of a purely nonorganic origin must surely have convinced everyone that there was no need for a vital force. But further historical studies of the reception of Wöhler's work have shown that the synthesis was not perceived as having such far-reaching consequences at the time (Brooke 1968). The whole picture of a single classic experiment undermining the philosophy of vitalism turns out to be a myth, and vitalistic ideas continued to influence major biologists for at least another generation. Working out the details of how physiological processes functioned was not an easy task, even using experiments on living animals. It was the French experimentalists, using a less dogmatic approach to the study of living functions, who made perhaps the more substantial contributions to the founding of a scientific physiology.

The Experimental Method

Although the German school was founded on the use of systematic observation and experiment, there were some who could not bring themselves to experiment on living animals. Müller himself felt this way and later turned to comparative anatomy because he was aware that physiology could not be advanced without vivisection (Huxley remained an anatomist for the same reason). To study function, it was necessary to interfere in a controlled way with a living body and observe the results (fig. 7.5). We have already noted that in France Bichat was using vivisection from the start of the century, so his legacy can be traced as much through his contribution to experimental physiology as through his vitalism. His successor as the leading experimental physiologist of early nineteenth-century France was François Magendie, who gained a reputation as a brutal vivisectionist, indifferent to the suffering of the animals he used in his experiments. Ma-

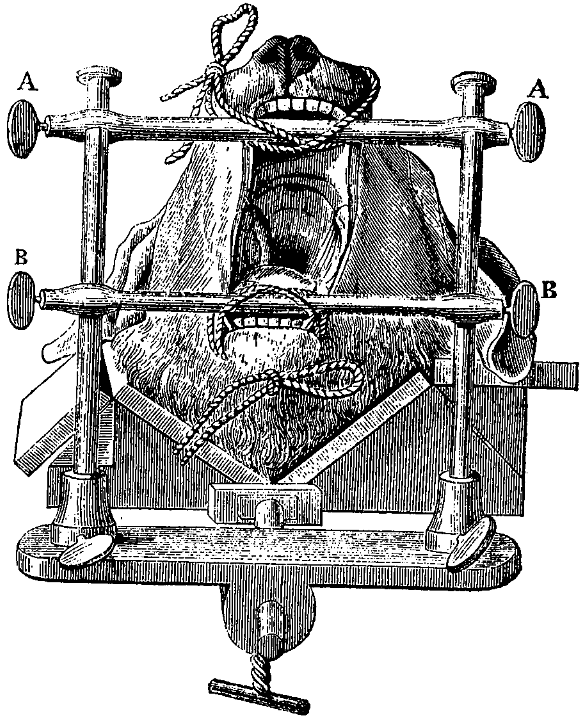

FIGURE 7.5 Apparatus for restraining the head of a dog during a vivisection experiment on the salivary glands or on the nerves of the neck, from Claude Bernard's *Leçons de physiologie opératoire* (1879), 137. Vivisection, or experimentation on live animals, was thought to be essential for understanding how the vital processes worked. But many nonscientists were outraged at the apparent indifference of the scientists to the suffering of their animal subjects, and the antivivisection movement became an early focus for popular opposition to science. This image was reproduced in an antivivisectionist pamphlet, *Light in Dark Places*, by Frances Power Cobbe, distributed in London (1883) by the Victoria Street Society for the Protection of Animals from Vivisection and the International Association for the Total Suppression of Vivisection.

gendie is remembered as the codiscoverer of the Bell-Magendie law that recognizes that the anterior (frontal) nerves running from the spinal cord govern the motion of the muscles, while the posterior (rear) nerves convey sensation to the brain. Significantly, the Scottish anatomist Sir Charles Bell hypothesized the law on the basis of a single experiment done in 1811—he would not follow up the discovery because he was reluctant to engage in further vivisection. When Magendie turned to the problem a decade later, he undertook a whole series of experiments with living animals that put the law on a firm foundation (Lesch 1984, 175–79).

Magendie's program for a scientific physiology rested on the application of experimental techniques, not on any philosophical commitment to materialism. He used experiment to develop explanation in terms of physical processes as far as possible and criticized Bichat for allowing vital forces to play an active role in his theories. Yet in the beginning of his career he seems to have accepted that there might be limits to how far the search for materialist explanations could go—perhaps the actual processes going on within the nerves might prove impossible to explain in purely physical terms. But the vital force could play no role in science so long as the physiologist was unable to postulate laws governing its behavior. This was what has been called a "vital materialism" as opposed to the rigid mechanistic materialism of the German school; it pushed materialism as far as possible without being dogmatic on the question of whether the body was governed solely by physical processes. In his later career, Magendie dismissed the vital force as a romance, a mere excuse to cover processes we do not yet understand, although he still refused to speculate explicitly about the complete elimination of such a force through future investigations. For Magendie, it was the experimental method that guaranteed that future work would be based on hard facts. Speculating about the ultimate nature of life was not part of the scientific process.

Magendie's best-known student at the Collège de France was Claude Bernard, who started as a laboratory demonstrator and went on to make a reputation for himself as a skilled and methodical experimenter. He was made professor of general physiology at the Sorbonne in 1854 and in the same year became a member of the Académie des Sciences. In 1855 he succeeded to Magendie's position at the Collège de France. Bernard's research focused on the role of the liver in maintaining blood glucose levels, on the digestive function of the pancreas, and on the action of poisons such as carbon monoxide and curare. He was admired for the simplicity of his experimental techniques and designs and for his skill at keeping his animals alive through to the end of his investigations (Holmes 1974). His *Introduction to the Study of Experimental Medicine* of 1865 (translated in 1957) became a classic statement of the role of experiment in biology.

Significantly, Bernard, like Magendie, sidestepped the mechanism-vitalism debate by focusing on the body as a system designed to maintain the *milieu interior,* or the internal environment, within which physiological functions could proceed. Even if all of those functions were purely

physical in nature, it would be pointless to reduce physiology to physics because the living body was a self-regulating system that could not be accounted for in terms of those laws. In effect, the body is more than the sum of its parts; it operates as a unified whole that transcends its individual functions. This would later become known as the philosophy of holism or organicism and would form the most influential current of thought opposing mechanistic materialism in the twentieth century. The question of how such complex systems came to be constructed became a key problem for evolution theory, and it is significant that many physiologists and biochemists have remained suspicious of that theory's ability to explain the production of this degree of complexity in purely materialistic terms.

On the whole, however, physiology and the biomedical sciences tended to move ever more firmly into the mechanist camp, seeking to explain every function solely in terms of physics and chemistry. Further research continued to drive back the limits within which purely vital functions could be postulated, leaving most biologists convinced that the whole vitalist program had merely held back the development of their science. It has now become almost an article of faith that modern biology was founded on a program of explaining all physical functions in physicochemical terms. The emergence of biochemistry as an independent discipline in the early twentieth century also contributed to this process (Kohler 1982). Yet the refusal of so many early physiologists to dogmatize on the issue of materialism, and the continued efforts of later workers to defend a role for the body as an organized whole, warn us not to place too much emphasis on this philosophical debate. To a significant extent, the emergence of modern physiology rested on the application of the experimental method within an essentially pragmatic worldview that merely sought to extend natural explanations as far as possible.

Historical studies of the later developments in which mechanistic explanations became dominant have been hampered by the sheer complexity of the technical issues involved. But some important studies have driven home the point that the main driving force of theoretical innovation was not always the urge to promote reductionist materialism. Philip Pauly's study (1987) of the German-American physiologist Jacques Loeb—who achieved notoriety as an advocate of the mechanistic view of life—shows that he was an experimentalist who remained impressed by the complexity of the body's "engineering." It was Loeb's *The Mechanistic Basis of Life* of 1912 that caught the public's attention, but he also wrote *The Organism as a Whole* four year later. The eminent British physiologist J. S. Haldane, who made important advances in the study of respiration, openly repudiated mechanistic materialism, using the analogy of the dependence of the parts of the body on the whole to bolster an ideology in which the individual is subordinated to society (Sturdy 1988). In Germany, too, early twentieth-century biologists such as Hans Driesch resisted the overrigid application of mechanist principles. More generally, there was a reaction against the mechanistic view of the previous century, with a number of scientists exploiting a holistic view of nature (Harrington 1996). A detailed study by Frederick L Holmes (1991, 1993) of the process by which the biochemist Hans Krebs worked out the citric acid cycle in animal tissues (the Krebs cycle) shows that he was deeply influenced by the concept of the organism as a balanced whole. The experimentalist program has certainly helped to eliminate the concept of nonphysical forces from biology, thus realizing one aspiration of materialist philosophy. But some of its most eminent practitioners have retained the sense that the organism must be treated as a system whose structure is so complex and well-integrated that biology will never form a mere subdepartment of the physical sciences.

Institutionalizing the New Biology

Morphology had established a place for itself in the natural history museums founded in many European cities in the early nineteenth century. It gradually adapted itself to the university system but always tended to fall between the two stools of anatomy (in the medical faculties) and natural history. The shift into museums transformed natural history from a discipline devoted to the collecting and describing of species into a centrally located research enterprise where resident experts studied specimens sent to them by fieldworkers of a far lower professional standing (see chap. 14, "The Organization of Science"). It was physiology, however, that would decisively transform the educational system by helping to create the specialized and highly technical departments of what would become known as biology. In the process, natural history was marginalized—and eventually so was morphology, although to begin with, it had ridden into the new world on the coattails of the new experimentalism. But even physiology at first struggled to gain a professional locus for itself because its emphasis on a more scientific study of living processes offered both opportunities and threats to the established tradition of medical education. It was also seized on by popular writers arguing for a more materialistic perspective.

These problems were obvious in France, where even Magendie and Bernard struggled to create a professional focus for the new physiology. Magendie gained the support of both Cuvier and Laplace, but there was no section devoted to physiology in the Académie des Sciences. Both Magendie and Bernard taught at the Collège de France, and Bernard exploited links with the Société de Biologie, a group of physicians who favored the new scientific approach. It was in Germany that the rapidly expanding university system created a framework within which institutes and departments of promoting the new biology could be established. Building on the model provided by Liebig's laboratory at Geissen, Müller and others established programs that often linked physiology and morphology. One of the earliest applications of the sociological approach to the history of science was the suggestion that competition between the different German universities formed a particularly favorable environment for the establishment of new departments in fashionable subjects such as this.

Britain lagged behind, partly because physiology was associated with a more materialistic approach that seemed hostile to the academic elite's enthusiasm for natural theology. It was Darwin's bulldog, T. H. Huxley, who became the most outspoken proponent of systematic laboratory training as an integral part of medical education. As the older universities were modernized and new ones created, this program began to take effect, although it was dogged by a strong antivivisection movement based on a concern for animal rights (French 1975; see fig. 7.5). At Cambridge, Huxley's protégé Michael Foster was appointed prelector at Trinity College and in 1883 was appointed to a university chair with the resources to establish a physiology laboratory (Geison 1978). Foster's *Textbook of Physiology* (1877) played a key role in establishing laboratory-based training in medicine. Huxley introduced summer schools for high school teachers in London based on laboratory courses, with his young disciples as the demonstrators. Here morphology and physiology were presented as twin components of a truly scientific study of living things, form and function being seen as inseparable parts of what was increasingly being called "biology" (Caron 1988). In America, the rapid expansion of research-based universities in the later decades of the century created the opportunity for a similar expansion of the new biology (Rainger, Benson, and Maienschein 1988). Johns Hopkins became the model for the new breed of university within which experimental biology flourished, and its graduates fanned out across the country to found other departments.

The Revolt against Morphology

By the last decades of the nineteenth century, animal physiology had emerged as the paradigm for the new experimental biology. It was paralleled by developments in botany, as Julius Sachs and others began to focus on plant physiology, to some extent eclipsing the old focus on classification and the study of geographical distribution. William Thiselton-Dyer spread the new botany into Britain, just as Foster spread the new animal physiology. It was within this rapid expansion of experimentally based studies that what Allen (1975) has called the "revolt against morphology" took place, completing the transition to the modern framework within which the life sciences are studied. Although pioneering figures such as Müller and Huxley tried to associate a laboratory-based study of form (based on the new microscope techniques) with the experimental study of living functions, it became increasingly clear to many of the next generation that morphology was still essentially a descriptive science. It used the study of dead organisms to throw light on their evolutionary affinities, but it could offer no insights into how those structures functioned in the living body. Nor, despite the emphasis on comparative embryology, could it explain how the structures were actually created within the developing organism. More recent studies have questioned whether there was a sudden revolt or merely a gradual transformation, but the end result was the same: descriptive biology was eclipsed by the study of function (Maienschein 1991).

One consequence of this process was the rapid specialization of the life sciences into a number of distinct disciplines, which did not always communicate as well as they might because their founders were intent on carving out their own institutional framework. Embryologists abandoned the recapitulation theory as a guide to evolutionary relationships and followed Wilhelm Roux's proclamation of the need for an *Entwickelungsmechanik*, a science that sought to explain how the embryo develops in terms of physicochemical processes. This would lay the foundations of modern experimental embryology, although some of the pioneers (including Hans Driesch) found it hard to abandon the old idea that there were more purposeful directing forces involved. This work also focused attention onto the processes within the fertilized ovum that prepared the way for the development of the embryo, playing a key role in the emergence of the theory of the chromosome and hence the gene as the determinant of the future organism's characters (see chap. 8, "Genetics"). E. B. Wilson and others founded the science of cytology to focus on the processes governing life at the cellular level. At the same time, the new science of Mendelian genetics focused on the experimental study of how characters are transmitted from one generation to the next. Although T. H. Morgan's theory of the gene would unite chromosomal studies with the Mendelians' breeding experiments, genetics lost touch with embryology and paid little attention to the

process by which the gene's information was expressed in the developing organism.

The experimental disciplines were, in general, hostile both to the morphological tradition and to the older form of natural history that morphology had marginalized earlier in the nineteenth century. Classification and the reconstruction of evolutionary genealogies were dismissed as old fashioned, and even the revived Darwinism based on the genetical theory of natural selection struggled to find a home within the new biology. In one important respect, however, the experimental approach reinvigorated a topic that had been studied within the older natural history tradition, leading to the emergence of the discipline of ecology. Naturalists had always been interested in the relationship between the organism and its environment, and Darwinism had kept this interest alive because adaptation was the driving force of natural selection. But now both plant and animal physiologists began to think in terms of relating the functions they studied within the body to the physical conditions of the surrounding environment, extending the experimental techniques already in use. Most influential were the plant physiologists, including Eugenius Warming in Denmark and Frederick Clements in America (see chap. 9, "Ecology and the Environmental Sciences"). Ecology remained a fragmented discipline, however, and it too remained quite distinct from many of the other specialized forms of biology that had established themselves within the early twentieth century. The drive to create a range of disciplines focused on the experimental study of different living functions thus ended up fragmenting the life sciences into a group of distinct and sometimes hostile professional groups.

Conclusions

The life sciences underwent major transformations in the course of the nineteenth century that established the field of biology in something like its modern form. Natural history was marginalized, although some field naturalists, including amateurs, continued to play a role in areas such as taxonomy and the study of geographical distribution. The emphasis switched to laboratory-based research in the great universities and museums, with the field naturalist demoted to the mere collector who transmitted new information for processing at the center. But the pressure to develop an intrusive, experimental science of life, emanating from the biomedical areas of the life sciences, allowed physiology gradually to emerge as the model for what a truly scientific biology should look like. Eventually even morphology found itself eclipsed as a purely descriptive discipline with no real explanatory power. The great museums were themselves marginalized as mere repositories of material to be described and classified, activities little better than stamp collecting as far as the experimentalists were concerned. University departments and medical schools became the focus for the most prestigious research. Topics such as evolutionism, which sought to straddle the old and the new techniques, found themselves in almost the same predicament as the old natural history. In the course of these developments, the old theory of a distinct vital force was gradually abandoned, with increasing attention focusing on the drive to work out explanations based on physics and chemistry. Not all the pioneers were dogmatic materialists, however, and many biologists remain convinced that the complex interactions that sustain life can only be understood if the organism is treated as a coordinated whole.

Expansion of the new biology had been funded by the public's ever-increasing demand for improved medical techniques, but some legacies of the new biology have now become a focus for concern. The massive specialization of research disciplines led to a fragmentation of knowledge and expertise that some biologists are struggling hard yet to overcome today. Bridges have to be built, often with great difficulty, between areas such as genetics and embryology—although any old-fashioned morphologist would have told you that it was pointless to study the transmission of characters between the generations without also taking an interest in how those characters were developed in the individual organism. Evolution theory has also had to take on board the fact that changes in the ways genes are expressed may have had profound effects on the emergence of novelties in the history of life on earth. More seriously, perhaps, the isolation of ecology from other specialized areas of biology has fragmented our response to the current environmental crisis. Even the old disciplines of taxonomy and biogeography, long neglected along with the research departments of the great museums, are being hailed as essential factors in our effort to salvage the biosphere. If we do not know how many species there are, or where they live, how can we save them? The new biology created a wealth of opportunities in the biomedical sciences that have transformed our lives through treatments based on discoveries about how the body operates. But a study of the social transformations within the scientific community that created the life sciences as we know them today reveals that specialization and the relentless urge to focus research in the laboratory have their downsides too. If biology is to have a role in dealing with the environmental crisis, as well as satisfying our demand for better medical facilities, some of the developments on which the new biology was based may have to be reconsidered.

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