process or phenomenon that can be studied reliably until a taxonomic foundation has been laid. The fact that the evolutionary answers are usually supplied almost automatically once the taxonomic analysis has been completed is especially rewarding. It is therefore not surprising that so many of the leading evolutionists of the past 100 years have been taxonomists by background and primary interest. It is still true that a taxonomist is singularly well qualified to point out evolutionary problems and solve them.

THE HISTORY OF TAXONOMY

Diversity has interested humans ever since the beginning of our species. No matter how ignorant a native tribe may be in other matters biological, invariably it has a considerable knowledge of local plants and animals as well as names for them and often even a rudimentary classification. However, the development of a scientific theory of classification is a remarkably recent phenomenon. Simpson (1961) gives a valuable survey of the history of taxonomy and the development of its concepts, and Mayr (1982*a*) describes in considerable detail the various periods in this development. There are also histories of the study of higher taxa, such as that of Smith, Mittler, and Smith (1973) for entomology.

Several early Greek scholars, notably Hippocrates (460–377 B.C.), enumerated types of animals, but there is no indication of a useful classification in the surviving fragments of their work. There is no doubt that Aristotle (384–322 B.C.) was the father of biological classification. He lived for some years on the island of Lesbos, where he seems to have devoted himself almost entirely to the study of zoology, especially the study of marine organisms. He not only studied morphology but also paid much attention to embryology, habits, and ecology. Emphasizing that all attributes must be taken into consideration, he said, "Animals may be characterized according to their way of living, their actions, their habits, and their bodily parts" (*Hist. Anim.* 1.1. 487*a*). He referred to such major groups of animals as birds, fishes, whales, and insects; in the insects, he made distinctions between mandibulate and haustellate types and winged and wingless conditions. He also used terms for lesser groups, such as Coleoptera and Diptera, which persist today. He established numerous collective categories, or genera, using as differentiating characters blooded versus bloodless, two-footed versus four-footed, hairy versus feathered, with or without an outer shell, and so forth. All this was a tremendous advance over anything that had previously existed, and Aristotle's thinking completely dominated animal classification for the next 2000 years. Nevertheless, he did not supply (or even attempt to supply) an orderly, fully consistent classification of animals (Mayr 1982*a*; Pellegrin 1986).

Interest in natural history and in the study of animals as things important in themselves steadily decreased after the death of Aristotle. Animals were written about not to provide knowledge about them but for the sake of moralizing; they became symbols of virtues (courage, diligence) or of objectionable behavior. Most animal books up to Gesner (1551) and Aldrovandi (ca. 1600) were encyclopedias. Only from about 1550 on did the knowledge of animals make more rapid progress, as documented by the writings of William Turner (1508–1568), Pierre Belon (1517–1564), and Guillaume Rondelet (1507–1566); however, the recognized taxa were on the whole those of folklore, such as birds, fishes (including all sorts of aquatic organisms), and shells.

Downward Classification

Plant classification experienced a great flowering in the period from Cesalpino (1519–1603) to Carolus Linnaeus (1707–1778), not only in the writings of these two great taxonomists but also in those of Magnol, Tournefort, Rivinus, Bauhin, Ray, and various lesser figures. Their method of *downward classification* was the principle of logical division, which consisted in dividing a larger (superordinated) group by *dichotomy* into two subordinated groups: animals—with or without blood, animals with blood—hairy or not hairy, and so forth. This principle dominated taxonomy up to the end of the eighteenth century. Animal taxonomy made little conceptual progress in the seventeenth and eighteenth centuries, although the work of Willughby (1635–1672) on birds and that of Reaumur (1683–1757) on insects revealed a remarkable advance in knowledge. Natural history in the eighteenth century was dominated by two great figures, Buffon (1707–1788) and Linnaeus.

Linnaeus, sometimes called the father of taxonomy, largely adhered to the principles of downward classification by logical division. His thinking was that of an *essentialist* for whom species reflect the existence of fixed, unchanging types (essences). However, in a period during which the number of new species and kinds of organisms grew at an exponential rate, he was a desperately needed methodological innovator. Speedy and correct identification was what the naturalist required most, and this was facilitated by Linnaeus's careful keys, his rigorous system of telegraphic-style diagnoses, his standardization of synonymies, and his invention of *binominal nomenclature*. Because of his authority Linnaeus was able to impose his methods, and this brought consensus and simplicity back into taxonomy and nomenclature, where there had been a threat of total chaos.

The actual classifications adopted by Linnaeus were of mixed value. For the groups with which he was most familiar, for instance, insects, he produced classifications that are still largely acceptable. By contrast, his classifications of other groups, such as birds, amphibians, and lower invertebrates ("Vermes"), were inferior to those of earlier authors.

Buffon was not a taxonomist and had little interest in classification and the higher categories. However, in some respects he had perhaps as great an impact on the ensuing history of systematics as Linnaeus did. First of all, by using the sterility barrier (instead of degree of morphological difference) as the species criterion, he prepared the way for the biological species concept. More important, by his attacks on scholasticism and his emphasis on the biological interpretation of characters (and on the utilization of as many characters as possible), he laid the foundation for a new approach to classification.

Upward Classification

By the middle of the eighteenth century the shortcomings of the method of downward classification by logical division were increasingly recognized. It was actually a method of identification, not of classification, and since the arrangement it produced depended entirely on the sequence in which the differentiating characters were used, it was blatantly artificial. This method was incapable of producing order in a large fauna. As a result, it was gradually replaced by the entirely different method of *upward classification*. This method consists of assembling species by inspection into groups of similar or related species and forming a hierarchy of higher taxa by again grouping similar taxa of the next lower rank. As stated by Buffon (1749): "It would seem to me that the only way to design an instructive and natural method is to group together things that resemble each other and to separate things that differ from each other." This thought was systematically applied by the botanist Adanson (1763) and was practiced by nearly all post-Linnaean zoologists, who delimited taxa by inspection and through an evaluation of numerous characters. Characters were weighted, usually not by a priori principles (such as physiological importance) but by an a posteriori determination of a covariance of characters. (For a discussion of the problems of weighting, see Chapter 7.)

Concurrent with the methodological shift from downward to upward classification was a major philosophical change. A strong belief in a linear, teleological aspect of the universe, as reflected in the *scala naturae* and in Lamarck's concept of evolution, was replaced by a belief in the existence of *archetypes* (idealistic morphology) (Desmond 1982). Cuvier recognized five phyla (embranchments), and von Baer, along with Owen and the comparative morphologists in the pre-Darwinian period, thought they were able to arrange all species of animals into a limited number of groups, each representing a distinct "type." As a descriptive device such "typology" was clearly legitimate (Schindewolf 1969), but it must not be confused with the typological thinking of essentialism.

Four other developments characterized the period between Linnaeus and Darwin. First, specialization became more pronounced. The days when authors such as Ray, Linnaeus, and Lamarck could successfully deal with the taxonomy of both animals and plants were over by 1800. Indeed, more and more authors became specialists in a single group, such as birds, beetles, or butterflies. Second, classifications became more hierarchical. Above the species Linnaeus recognized only genus, order, class, and kingdom, but soon the categories family and phylum were added, and numerous additional ones came later. Third, philosophical guidelines were expressly rejected, and classifying became an entirely empirical enterprise. Fourth, the search for a natural system was intensified, with the term *natural* serving as the antonym of *artificial*. That system was considered most natural which succeeded best in grouping together the species that had the most in common.

Impact of *The Origin of Species*

The one question that taxonomists were unable to answer before 1859 was why the members of a taxon are more similar to each other than they are to members of other taxa. Darwin supplied the explanation through his theory of evolution by common descent. "Natural" groups exist because the members of a natural taxon are descendants of a common ancestor and therefore have a much greater chance to be similar to each other than do unrelated species. Classifications proposed prior to 1859, based on the grouping of similar species, continued on the whole to be acceptable after 1859, since similar species are ordinarily descendants from a common ancestor. Darwin, however, did more than provide the theoretical basis for a natural system. He also provided in Chapter XIII of the *Origin* (1859) a set of clear, practical criteria to be applied during the construction of a classification. These criteria are discussed in Chapter 6.

A major preoccupation of taxonomists in the first 50 years after the publication of the *Origin* was to substantiate the theory of common descent. This was expressed in the search for missing links between seemingly unconnected taxa, in the reconstruction of "primitive ancestors," and more generally in the construction of phylogenetic trees. This endeavor led to a boom in the fields of comparative systematics, comparative morphology, and comparative embryology.