3 Classification and System in Flowering Plants: Historical Background
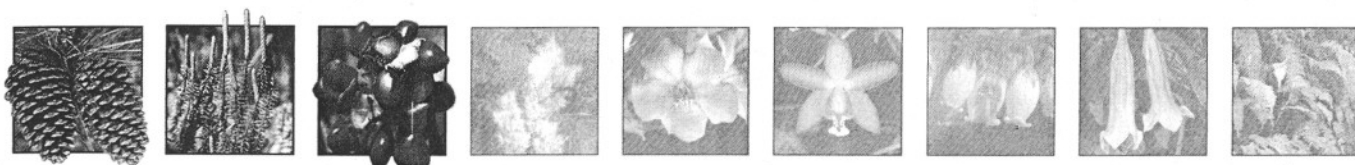
Throughout history, scientists have tried to determine the best way to classify living things. Their ideas on how to do this have changed considerably over time. In this chapter we discuss the main ways that botanists have classified plants, and some of the reasoning behind those classifications. This is only part of the history of systematics; discussion of the complex relationships between professional and amateur botanists and the general public is largely ignored. These relationships are an integral part of the historical background of our discipline, even if we know all too little about them (but see, for example, Allen 1976).

If you look at the phylogenetic trees in Chapters 7 through 9, you will see that it is possible to base classifications on them that capture precisely the clades in those phylogenies (see Chapter 2). Both phylogenies and classifications are hierarchical and are made up of groups nested within groups. However, some classifications in use today—in particular, evolutionary classifications—do not try to represent phylogenies in this way. Indeed, they are not strictly hierarchical. What they are trying to represent can be understood only in the context of a long history stretching back before anyone had any idea about evolution. Understanding classifications thus means that we need to understand their history.

In the past, both users and makers of classifications had quite different ideas about nature and about the role of classification than they do today, yet we tend to assume that our and their ideas are the same. The problem is made worse because many terms have changed meaning over time. The term system is a prime example. It now refers to sets of relationships in genealogies (de Queiroz 1988), but in the late eighteenth century, system was used as a term to belittle classifications based on a single character—except in England, where it referred to what European botanists would have called method, classifications based on many characters!

Finally, plant systematists, perhaps even more than other systematists, have long distrusted theory, and have considered classification a theory-free, "empirical" operation (see Stevens 1986, 1990, 1994, 1998a, and Kornet 1991 for discussion). Theories should not affect a systematist's observations or classifications. For this reason, plant systematists have often been unwilling or unable to explain the reasons for their decisions regarding classification.

This chapter describes some of the history of botanical classification in order to show how earlier, often non-phylogenetic, ideas about nature were incorporated into current classifications. First we discuss the long-standing and continuing tension between the makers of classifications, most of whom want to understand relationships (although note that the term relationship has meant different things to different people), and many users of classifications, who simply want names to be stable. Then we discuss how relationships are understood and how nature is visualized, how higher taxa are delimited, and how the circumscription of some of the major groups has changed. (Here we discuss only higher taxa—genera and above; for a discussion of species concepts, see Chapter 6 and Stevens 1992, 1997b.)

Classification, Nature, and Stability

For hundreds of years, botanists have tried to develop a classification that was "natural." Until recently we have assumed that history of systematics is in part the history of a single "natural" system that has been gradually developing over the centuries. Its principles were first outlined by Caesalpinus. Tournefort and Linnaeus described "natural" genera, and Linnaeus suggested a number of "natural" families, although he did not describe them. The "natural" method then received a major boost from A.-L. de Jussieu in his great *Genera plantarum* of 1789, in which he described both genera and families and placed the latter in classes. This Jussieuan foundation is the basis of our current classification, and although new families have been added, the limits of existing families have been modified, and higher taxa such as orders have been added, nothing fundamental has changed.

Unfortunately, the word natural has no fixed meaning; rather, authors have used it to mean something that

agrees with their own ideas about nature, or about constructing classifications or systems. Eighteenth-century systematists had ideas about nature that were very different from ours—they were certainly not evolutionary—and their systematic practice and classifications are best interpreted in terms of how they understood nature. Nineteenth-century systematists built on the work of their predecessors. Although they generally did not describe clearly their understanding of nature, which was changing, the way they discussed and depicted relationships was not much different from that of the preceding century. And many aspects of nineteenth-century classification persisted through the twentieth century.

Some historians of classification see a trend from analytic ways of grouping that were particularly common in the eighteenth century toward more synthetic procedures in the nineteenth century. In analytic grouping procedures, one or a few characters are used successively to define groups, so that organisms are divided up into smaller and smaller groups. The whole process is rather like using a key. In synthetic grouping, many characters are used and groups are built up ("synthesized") (Mayr 1982).

The distinction between the two procedures is not always clear. Even in the twentieth century some botanists used single-character, analytic (divisive) systems (such as John Hutchinson, who divided dicotyledons into woody and herbaceous groups, a classification that even Linnaeus had dismissed as "lubricious"; see Hutchinson 1973). On the other hand, Jussieu's method for recognizing relationships, developed in the later part of the eighteenth century, is synthetic.

Classifications have been expected to do much more than reflect nature, however. They have also been expected to be (1) easy to use, (2) stable, (3) an aid to memory, (4) predictive, and (5) concise—a set of goals that are sometimes in conflict. These goals of classification were spelled out by Andreas Caesalpinus in 1583 (see Greene 1983, Vol. 2: 815–817). Thus the systematist must not only describe nature (whatever he/she thinks nature is), but also serve a community of users, many of whom may have no interest in the systematist's ideas of nature. Before the twentieth century, those users were largely medical personnel, but they now include a broad array of biologists and non-biologists (even interior designers).

Stability of names has been a perennial problem. Systematists have often wanted to leave the names of taxa unchanged—even if those names conflicted with their views of relationship—lest the users of their classifications become upset

Andreas Caesalpinus
(1519–1603, Italian)

(Stevens 1994: Chapter 10; 1997a). Even George Bentham and J. D. Hooker, authors of the great three-volume *Genera plantarum* (1862–1883), circumscribed some taxa to reflect custom and convention; that is, they constructed some taxa that were not natural, even by their own definition of the word. Bentham, at least, ignored some of his own taxon circumscriptions when it came to discussing distributional patterns (Stevens 1997a). In this book we have attempted to change our classification so that it better reflects relationships, but it is highly likely that some readers will wish we had not changed so much. This point of view is, if nothing else, traditional!

J. S. L. Gilmour (1940) promoted the idea that the best classification had maximum general utility, although this leaves open the definition of "utility." The needs of groups of people who use classifications may change over the years, and needs may conflict (Stevens 1998b); the result may even be classifications that conflict. Certainly Gilmour's ideas sharpened the conflict between those who wanted classifications to reflect history and those who were not at all interested in relationships.

As early as 1778, however, Lamarck had suggested a solution to the problem: The characters used in the formal classification did not have to be those used for identification. The keys (see Appendix 2) that he promoted link users and experts. Easily visible characters could be used in keys, and these would not necessarily be the same as the sometimes inconspicuous characters used to distinguish the groups recognized in the formal classification. Keys made it easy to give plants their correct names, so groups in classifications did not—and do not—have to be easily recognizable.

A general respect for authority has also affected classifications. Some plant groups have been recognized for a long time, for example, the Labiatae, Liliaceae, Cruciferae, and Compositae. Many of these do not end in the conventional -*aceae*, which indicates that they are not based on particular genera, and the groups may even pre-date "scientific" classification. The fact that such groups have always been recognized is sometimes used as evidence that they are "natural" groups. If they have been historically recognized by the acknowledged masters of the discipline, so the argument goes, they must be correctly delimited. Systematists have been generally reluctant to modify such groups.

These paradigmatic groups are generally ones that are obvious in the European flora, a fact that reflects the European origin of botanical systematics. Not only did the discipline originate in Europe, but it was dominated by Europeans for centuries. Not until Asa Gray (1810–1888) was there a North American botanist considered by Europeans to be fully their equal, and only with Charles Bessey (1845–1915) did North American botany become fully independent (Dupree 1959; Cuerrier et al. 1996). In other parts of the world, especially those that were then colonies of European nations, this domination persisted longer, and it was especially evident in the floras of countries that were written by European botanists and based on material held in European institutions.

Understanding Relationships

We mentioned in the preceding section that eighteenth- and nineteenth-century systematists saw nature quite differently from the way we do

Asa Gray
(1810–1888, American)

now. How can we know what they were thinking? The analogies they used when describing patterns of relationships that they saw in nature and the diagrams they prepared to show these patterns are particularly good sources of information.

Although it is obvious to us that relationships can often be represented as treelike diagrams, the reason is that we share a common set of assumptions about how organisms came to be the way they are. Thus, throughout this book, we diagram relationships somewhat like pedigrees, with extant organisms linked by extinct ancestors (this sort of diagram is known as a **Steiner tree**).

Many of our predecessors did not share this view of nature. Put yourself in the world before Darwin and before ideas of evolution. How would you imagine plants are related to each other? What would the word *relationship* mean? In fact, we find that many eighteenth- and nineteenth-century botanists thought of relationships as being like the relationships between countries on a map or stars in a constellations; that is, they were reticulating.

Antoine-Laurent de Jussieu described many of the families whose evolution we now attempt to study. His genera and families have been interpreted for two centuries as though they were more or less distinct groups, but this is not how he saw them. For Jussieu, relationships in nature formed continuous series that lacked any clear breaking points. Any divisions in these series were the work of man, not of nature. Jussieu emphasized that groups were linked, and his natural families, such as the Compositae, were natural precisely because they were examples of this continuous nature; not surprisingly, genera in such families were difficult to recognize.

For Jussieu, as for his colleague Lamarck, the taxonomic hierarchy was simply a set of words, each of which individually referred to a part of the

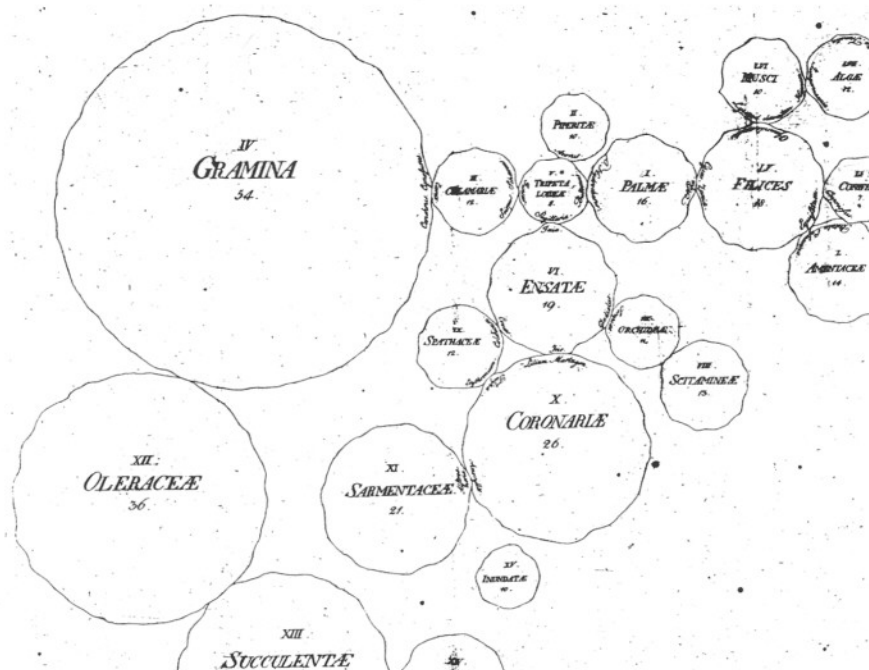**Antoine-Laurent de Jussieu**
(1748–1836, French)

Figure 3.1 A portion of P. D. Giseke's "genealogical-geographical" map (1792).

continuum and together allowed the whole to be recalled to mind. Complications arose from Jussieu's descriptions of the groups he recognized. These groups were rarely wholly characterized by the features he listed for them, and a family description often referred only to characters of genera in the middle of the sequence in which he placed them (i.e., in the middle of the continuum).

A particularly interesting diagram from about this time is P. D. Giseke's "genealogical-geographical" map of 1792 (Figure 3.1). In this diagram, circles of various sizes, representing families, are placed at varying distances from one another. Giseke took pains to say that the relationships he showed were not those between "grandfather and grandson," but rather between "cousins or relatives by marriage." He noted whether or not there were intermediates between the families shown in the diagram, and he carefully distinguished between different kinds of relationships as he described the complex, two-dimensional spatial relationships between groups.

Much later, Bentham and Hooker's *Genera plantarum* (1862–1883) reflected the principles first outlined by Bentham in 1857. Both Bentham and Hooker thought that groups showed reticulating relationships, and that their boundaries were sometimes, or even often, indistinct. All in all, their ideas were not too different from those of Giseke.

Through much of the nineteenth century, and even much of the twentieth, botanical relationships have been portrayed as highly complex and reticulating. Even when tree diagrams were used to show evolutionary relationships, extant groups were linked directly to other extant groups. (These diagrams are known as **minimum spanning trees**.) Such diagrams imply that groups that exist in the world today are the ancestors of other groups that also currently exist, which doesn't make much sense in terms of evolutionary processes.

A more evolutionary view would be to say that two extant groups are descended from a single extinct ancestor. The direct links between extant groups were drawn in part because many botanists, from at least as early as 1786 (Johann Georg Forster), have disliked talking about ancestors, whether because ancestor-descendant relationships could not be seen directly or, later, because the fossil record was simply too poor to detect them. There are a few examples of early trees with extinct ancestors, but these are much less common (for illustrations, see Lam 1936 and Voss 1952).

In addition to showing that groups were linked simultaneously to many other groups, the goal of these complex diagrams was often to indicate the relative "highness" or "lowness" of groups. This aim can be seen in the work of Charles Edwin Bessey, a major figure in North American botany at the end of the nineteenth century. He produced numerous diagrams showing relationships, and in the latter part of his career these diagrams showed extant groups joined directly (Figure 3.2) (Cuerrier et al. 1996).

Bessey drew these "trees" to show major trends in advancement (and sometimes also reversals), and his classifications are to be read as sequences that in part reflect these diagrams. It is interesting that Bessey was attempting to make systematics more philosophical, and he had specifically dismissed maplike representations of nature. In fact, his freestanding "trees" are more like archipelagos or maps, even if they have been given an axis. They are conceptually similar to the representations of nature he dismissed, being quite like those of Linnaeus and Jussieu. Furthermore, although Bessey repeatedly emphasized that classifications should reflect phylogeny, the way he produced classifications made that goal very difficult to achieve.
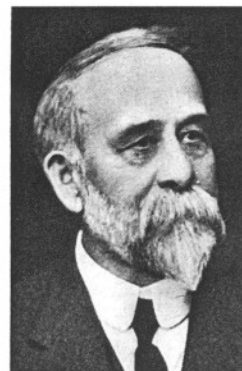
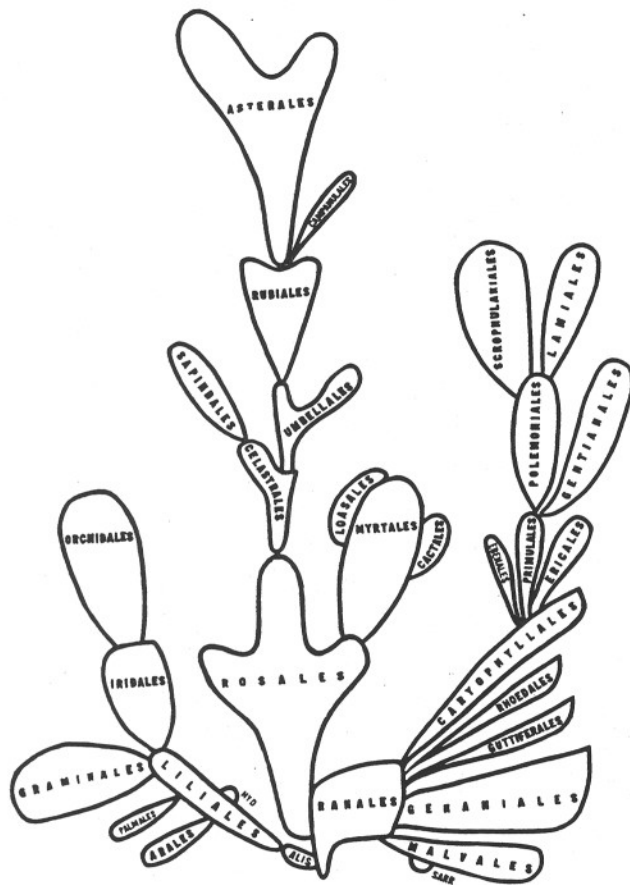**Charles Edwin Bessey**
(1845–1915, American)

Figure 3.2 One of Charles Bessey's freestanding "trees." (From Bessey 1915.)

Other major classification systems, such as that of Arthur Cronquist (1981), are also minimum spanning trees (Figure 3.3) that sometimes even allow reticulations between groups. They are certainly not readily interpretable in phylogenetic terms. An unwillingness to specify only historical connections between groups is associated with a tendency to emphasize parallel evolution, parallel tendencies, or even ideas of **orthogenesis** (directed evolution), as is particularly evident in Cronquist's earlier work. If two groups are not related directly, the argument goes, the occurrence of the same characters in these groups must be explained by independent evolution.

H. F. Wernham, in an influential series of papers (1911–1912), asserted that the Sympetalae were polyphyletic—as were monocots, dicots, and even angiosperms as a whole. He felt that all important characters had evolved in parallel several times in closely related but independent lineages. In fact, suggestions that there were large-scale parallelisms in patterns of relationships are quite common from the late eighteenth century onward, and some researchers have even seen quite close parallelisms between the series into which animals and plants could be placed. The existence of such parallelisms was taken as evidence that the "real" pattern of relationships in nature had been discovered!

Rolf Dahlgren's name has become associated with diagrams representing a cross section of a phylogenetic tree ("Dahlgrenograms") (Figure 3.4). Groups are represented by bubbles of different sizes between which relationships are implied—though not clearly shown—by the way the diagram is drawn. These diagrams have
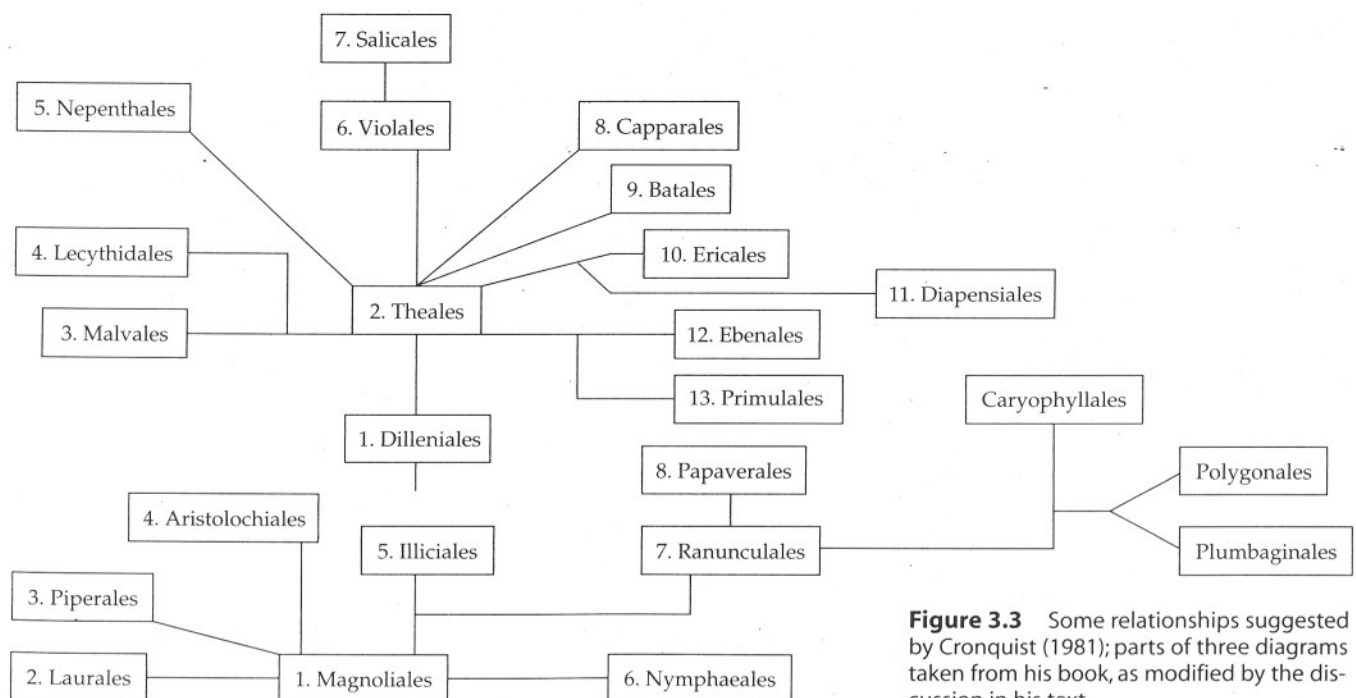

Figure 3.3 Some relationships suggested by Cronquist (1981); parts of three diagrams taken from his book, as modified by the discussion in his text.
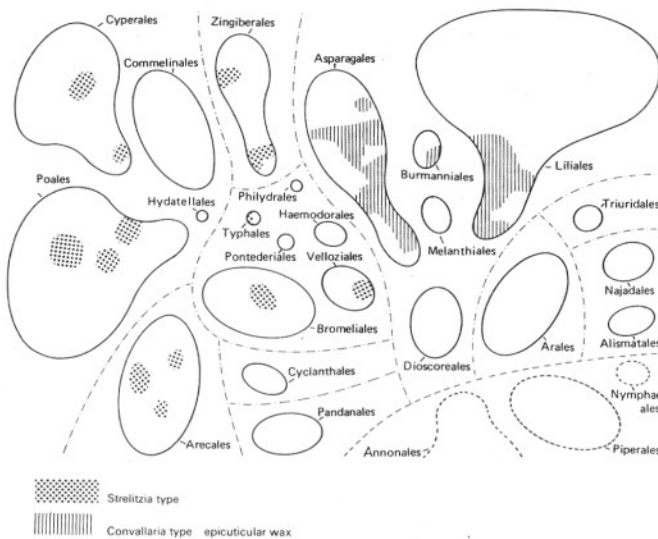
Figure 3.4 An example of a "Dahlgrenogram," a diagram representing a cross section of a phylogenetic tree. The diagram on the right is a three-dimensional representation of the diagram on the left. (From Dahlgren et al. 1985.)

been much used to display results of broad surveys of variation of characters, such as the distribution of iridoids or the types of plastids in sieve tubes. Conceptually, Dahlgrenograms are more closely related to Bessey's cactuslike diagram (see Figure 3.2) or Giseke's "genealogical-geographical" map (see Figure 3.1) than to the phylogenies used in this book. (Note, however, that Dahlgren himself was much interested in phylogeny.)

Indeed, for some authors the fact that such diagrams did not have evolutionary implications was a virtue. They permitted one to think about general relationships, without worrying about evolution (Heywood 1978). Note that in this context, again, the term *relationship* can't mean evolutionary or, still less, phylogenetic relationships.

Classifications and Memory

The use of classification as an aid to memory was critical in a time before computers existed and when even books were not common. A classification had to have a moderate number of families, and these had to be divided into subgroups that were neither too small nor too large. Linnaeus emphasized the value of system, grouping organisms in tens; this approach allowed him to place all of the fewer than 10,000 plant species that he thought existed into groups at just four hierarchical levels.

Jussieu, whose classification was imposed on what he saw as continuous natural variation, recognized only taxa that he thought were neither too small (there had to be at least two included members) nor too big (100 members may have been the uppermost limit). Thus, he recognized no monogeneric families, and the Compositae,
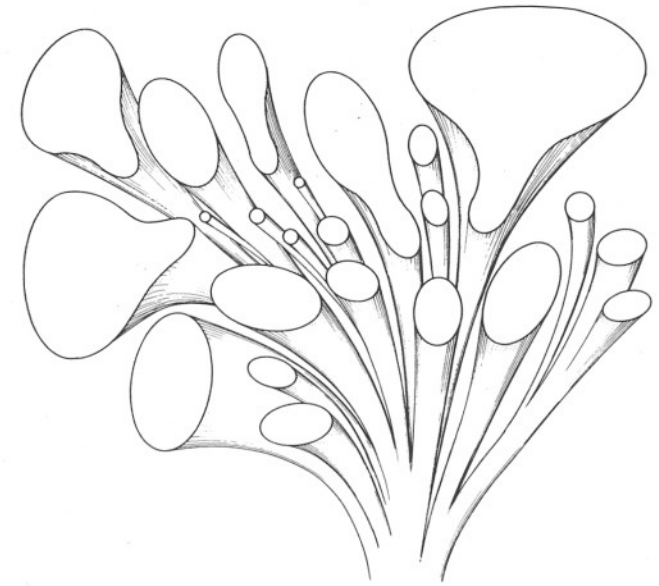
which he thought were very "natural" but had well over 100 genera, were divided into three families.

Similarly, Bentham and Hooker, and some of their colleagues, such as Asa Gray, had agreed before the monumental *Genera plantarum* was written that 200 was the upper limit of families to be recognized; otherwise there would be too many to memorize (201 was the final figure). Bentham and Hooker also agreed that the best size for taxa was 2 to 6, rarely up to 12, included members. Yet some of the families they accepted had hundreds of genera.

Bentham and Hooker reconciled their intention of having a fixed, low number of often quite large families and the need to have small taxa at all hierarchical levels by interpolating formal or informal groupings wherever needed. As a result, all groups in the *Genera* above the level of genus have fewer than 14 included members. Such small groups are best suited for storage in and recall from memory, and the emphasis on recognizing large genera and families also minimized the number of names in general used and reduced the burden on the memory (Stevens 1997a, 2002).

The Formation of Higher Taxa

The idea that almost all plants belong in genera with two or more species was suggested by Conrad Gessner around the middle of the sixteenth century (Morton 1981). However, similar groupings of plants (and animals) are evident in classifications of local peoples worldwide (Atran 1990; Berlin 1992). The recognition of such groupings is based on their **salience**, or obviousness and importance to the observer. This idea of salience is based on things like the degree of similarity among members of a group, their commonness, and their utility for humans.

Joseph Pitton de Tournefort
(1656–1708, French)

The basic units in such classifications often are named with binomials, or, more generally, a noun + adjective construction.

In herbals and other early botanical literature, plants are grouped in various ways (alphabetical arrangements are common), although why these groupings were recognized is often unclear. In 1694, Joseph Pitton de Tournefort provided clear guidelines for describing genera (see Dughi 1957). Generic characters should be recognizable in all members of the genus, he argued, and should be visible without the use of a microscope. When possible, these characters should be taken from features of the flower and fruit.

Tournefort called groups based on these features primary genera. However, if these genera were too big, features from other parts of the plant could be used to characterize smaller genera (see also Walters 1986 and references). Groups characterized by nonreproductive features he called secondary genera. He also suggested that it was important to keep the total number of genera to about 600 (Stevens 1998a). This number is in line with the basic units in folk taxonomies worldwide (see Berlin 1992). Tournefort's classification indeed has much in common with folk taxonomies.

Carolus Linnaeus focused on genera, and his descriptions were much more detailed than Tournefort's. Linnaeus believed that individual genera and species existed in nature, and the ranks of genus and species were distinct ranks in the organization of nature, whereas larger groupings were matters of human convenience. He emphasized that features of the flower and fruit should be used to distinguish genera, and hence he combined most of Tournefort's secondary genera with the primary genera. Vegetative features distinguished species. But, as Linnaeus observed, "Characterem non constituere Genus, sed Genus Characterem" (Linnaeus 1751: 119)—loosely interpreted, genera exist in nature independently of the features used to characterize them, certainly independently of any rigid application of "generic" characters.

This and similar dicta, when coupled with the way Linnaeus went about recognizing and describing genera (for instance, he did not always change generic descriptions as he added new species to them), make his actual practice seem almost unprincipled at times (Stafleu 1971; Stevens 2002). Like Tournefort, Linnaeus con-

Carolus Linnaeus
(1707–1778, Swedish)

sidered large groups unwieldy, and he preferred small taxa at all hierarchical levels. Indeed, it has recently become common to think of Linnaeus as being some kind of essentialist, a person who believes that taxa have certain kinds of fixed characters without which they cannot be formally recognized (again, a loose interpretation). However, this is at best a great oversimplification (Winsor 2001; Stevens 2002).

Today's genera are ultimately built on this Linnaean foundation. Although many taxonomists, at least in theory, tolerate genera distinguished by characters other than those of flowers and fruits, in practice reproductive characters have served as a major source of generic-level differences. Nevertheless, many important nineteenth-century taxonomists certainly did not believe that there was a rank of genus (or family, for example) in nature, and by the middle of the century this was true of the rank of species too (Stevens 2002).

By the 1870s it even seemed that most genera were known, but this state of affairs did not last long. Genera were groups of species separated by morphological gaps of adequate size (see below). Hall and Clements (1923: 6) called for "experimental and statistical studies of the generic criteria in use" in a paper whose title indicated that they wanted to clarify how systematists detected phylogenies, but their aim was really to maintain the status quo, the conventional (broad) delimitation of genera (and species) because of "the significance of system, and of the mechanism of memory" (Hall and Clements 1923: 7). Moreover, they provided no new way of detecting phylogenies.

The idea that there were families of plants was specifically suggested by Pierre Magnol in 1689 (see Adanson 1763–1764, Vol. 1: xxii–xxvii). Magnol used characters taken from all parts of the plant, or sometimes, an "affinité sensible" that could not be expressed in words. He did not recognize all the families he might have because he wanted to keep their number small. He listed 76 families.

Linnaeus described classes and orders (= families) in his sexual system. Plants were assigned to groups primarily on the basis of stamen number and arrangement, and secondarily on the basis of ovary number (more exactly, on the number of stigmas or styles). For example, *Datura* and *Verbascum*, both of which have two carpels but only a single style, were placed in the Pentandria Monogyna.

Linnaeus also outlined a natural method, the goal of botany, in which genera were grouped into natural families (he recognized 67 in the year 1751, with a substantial residue of unplaced genera). He stressed the need for characters unique to a family and found in all its members, since without such characters the natural method would be like a bell without a clapper, as he graphically described the problem. However, Linnaeus was unable to provide such characters for even the most natural of families, such as the Umbelliferae (Apiaceae).

Michel Adanson
(1727–1806, French)

Although his largely artificial sexual system and his natural genera both rely almost exclusively on characters taken from the flower and fruit, when it came to natural families, Linnaeus (1751: 117) observed, "Habitus occulte consulendus est"—that is, "the habit should secretly be consulted." Habit, for Linnaeus, comprised all other parts of the plant, including features such as leaf vernation, and could also be used to distinguish families. He regretfully noted that his natural method was incomplete because plants showed relationships in several directions, like territories on a map; some plants were not yet discovered; and the habits of plants were poorly known (Linnaeus 1751: 26–36, 137).

The need, then, was to find features that indicated higher-level relationships. Between 1763 and 1789 three authors outlined the issue in ways that defined the debate over the ensuing two centuries. In a series of tabulations (Adanson 1763–1764), Michel Adanson showed that every characteristic of plants *varied within* natural groups; he concluded that no character was essential for defining a group and that groups could be defined only by combinations of characters. A classification could be produced only by an exhaustive comparison of all parts and properties of plants.

Adanson did not state clearly how this classification was to be carried out, but his contemporaries, such as Marie Jean Antoine Nicolas Caritat de Condorcet (1743–1793), noted that this might entail mechanization in the recording of characters (no easy task two centuries before the personal computer!). Other naturalists, presumably not wanting to have to look at every character in every plant, needed clear guidelines for deciding whether some characters were more important than others. Jean-Baptiste de Lamarck (1778) came up with a numerical weighting scheme (the first one known in botany) that assigned similarity values to features that depended on how widely they were distributed in plants (e.g., how common a calyx was), although he took into account not simply presence or absence, but also the nature of the feature.

Jussieu (1789) built up "groups" by synthesis, successively forming species, genera, and families; ideas of general similarity seem to have guided this synthesis. He then showed

Jean-Baptiste-Pierre-Antoine de Monet de Lamarck
(1744–1829, French)

how different features characterized groups of successively smaller circumscription. He described these characters as if they were invariable at the level they characterized, and he strongly disagreed with Adanson's contention that there were no invariable, essential characters.

Augustin-Pyramus de Candolle (1813) saw a proper subordination of characters as being the third and final stage in detecting relationships, following the stages of "blind groping" and general comparison. This subordination of characters was similar to the way in which Jussieu had described the distributions of characters. (Candolle tended to give the same character equal weight, at least in related taxa.)

Note that Jussieu's emphasis on synthesis was compatible with his belief that there were no groups sharply separated from other such groups in nature; gradual synthesis produced the continuity in relationships that was a feature of continuous nature. Indeed, Jussieu confidently expected plants yet to be discovered to be intermediates that filled in the apparent gaps between groups. Candolle, on the other hand, tended to emphasize analysis. He asserted that there were distinct groups in nature, noting that botanical discoveries were not filling in the morphological gaps between groups, and he looked for features that characterized these groups.

Augustin-Pyramus de Candolle
(1778–1841, Swiss)

During the nineteenth and twentieth centuries, the fundamental differences between Jussieu's and Candolle's understanding of nature were almost never discussed, and no accepted rationale for weighting characters was developed. Whether or how to weight remained a bone of contention for the next century and a half. Arguments between self-styled Jussieuans and Adansonians over weighting in the latter part of the nineteenth century centered more on what characters should be used, and how, and less on whether or not to use all characters.

A number of systematists, especially those in France and Germany, adopted concepts of **types**. These might be the common form in a group, or represent a "perfect" flower—a radially symmetrical form such as a peloria mutation in a bilaterally symmetrical group, or a bisexual flower in a monoecious or dioecious group. (The original peloria mutation, which excited Linnaeus so much when he found it that he initially wanted to name it as a new genus, *Peloria*, was a mutant of *Linaria* (Plantaginaceae) with five spurs radiating from the center of the flower, not the normal one in the abaxial position).

Such types could provide a way of understanding the diversity of form in a group and of relating one group to

another. They were also in some ways an alternative to conventional weighting schemes, but typological thought, although widespread, never became systematized. Not only did the word type reflect a variety of very different ideas, but typological thought in general was equated by some (mostly English-speaking individuals) with speculation. Ideas of essences (i.e., essential characters, as described earlier) and types are often linked.

Acceptance of evolution did not inspire any new way of detecting relationships. Furthermore, Charles Darwin (1809–1882) provided no indication of how to rank taxa; he did, however, emphasize that relationships could be represented as groups subordinate to other groups (Figure 3.5). Systematists like George Bentham (1875) understood this—when coupled with the idea of evolution—to mean that the only difference between taxa occupying the highest and the lowest ranks of the hierarchy was one of degree. Taxa might be distinct, yet ranks were not fundamentally different; neither ranks nor individual taxa had essences. This only compounded the problem of deciding at what rank to recognize a particular group, unless reference was made to previous taxonomic practice—that is, an appeal was made to established practice or convention.

Up until the middle of the twentieth century, systematists continued to delimit groups very much in the same way that they had at the beginning of the nineteenth century, although of course they knew much more about the basic morphology and anatomy of plants. Similarity in general morphology and anatomy came to indicate closeness in evolutionary or phylogenetic relationships, but there was no way of deciding which particular characters indicated such relationships and which did not.

Systematists sometimes tried to distinguish between characters that were adaptive, and therefore less valuable in assessing relationships, and those that were not

George Bentham
(1800–1884, British)

adaptive and thus more valuable. Groups were still circumscribed by morphological gaps, but there was no agreement as to when a gap was large enough for a group to be recognized at a particular rank. Indeed, gap size has tended to be inversely proportional to the size of the groups involved (Davis and Heywood 1963).

For about 170 years it has been recognized that the application of criteria to evaluate closeness of relationship and to rank taxa has been inconsistent. So, for example, families in the Malvales have often been considered equivalent to tribes in the Rosaceae. It is not surprising that arguments over how broadly or narrowly taxa should be circumscribed have remained unresolved.

John Gilmour (1940; see also Winsor 1995, 2000) reopened discussion about the general issue of how to group organisms when he observed that the use of characters to establish evolutionary relationships tended to be circular: Characters important in establishing evolutionary relationships were those important in delimiting groups, and vice versa. He suggested that groups in natural classifications were simply those that had many characters in common.

John Scott Lennox Gilmour
(1906–1986, British)

Such groups had the useful property that they could be used for a wide range of purposes; they were general-purpose classifications.

Gilmour believed that attributes (characters) of plants were sensory data, which, he thought, were facts. Classifications were "clips" that held these data together, so if different principles of classification were used, the clips—and so the groups recognized—would be different. Evolutionary classifications, by their very definition, would always be special-purpose and so not of general use or interest.

What became known as phenetics or numerical taxonomy owes much to Gilmour's ideas. Pheneticists produced groups on the basis of overall similarity, in hopes that this process would produce an objective, stable, and repeatable classification (Sokal and Sneath 1963; for more on this topic, see Chapter 2 and Vernon 1988). (Interestingly, Gilmour himself was not sympathetic to the use of computers that his approach encouraged.) The assumption that characters were observable facts soon proved to be a considerable oversimplification; what appeared to be basic characters could be subdivided. Furthermore, different numerical algorithms produced different phenograms (see Chapter 2), and hence could be the basis of different classifications, but it was often unclear why one algorithm should be preferred over another.

Phenetic theory and, in particular, practice had little effect on higher-level systematics in North America. It
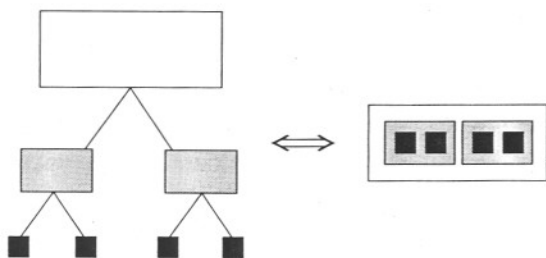

Figure 3.5 Although Charles Darwin's work did not provide any insights on how to rank the various taxa, he understood that some groups were subordinate to others.

had rather more influence in England, where botanists were perhaps particularly distrustful of what they saw as being evolutionary speculation (Vernon 1993; Winsor 1995); good systematists, it was claimed, always had been more or less Gilmourian.

It has generally been conceded that genera, and particularly families, are less "natural" than species. However, what such comparisons might mean is unclear, because systematists have not been clear as to what is meant by "natural." Is it that the rank of genus (for example) is a rank in nature, or that genera are discrete groups, or that members of a genus are more closely related to one another than they are to members of another genus?

In any event, there always have been dissenting voices. Linnaeus claimed that genera and species were equally natural. A.-L. de Candolle thought genera were more natural than species because genera were named as such by the common man (a similar idea was expressed by H. H. Bartlett). In a much-cited paper, Edgar Anderson (1940) reported on a survey that he had carried out to find out whether systematists thought genera or species were more natural. Some systematists who monographed groups, at least, were inclined to think that genera were more natural than species, despite the often expressed views to the contrary. So were biogeographers such as Ronald Good, and it should not be forgotten that the genus is the basic unit of much of the biogeographic work that has focused on global patterns of diversity and relationships.

Early in the nineteenth century, Charles-François Brisseau de Mirbel (1776–1854) suggested that there were two main kinds of families (and genera). Whereas *familles en groupes* ("families in groups") were very natural and clearly circumscribed, *familles par enchaînement* ("families by chaining") were less natural and had less clear limits. All genera in the first kind of family tended to be united by one or more characters, but they were often difficult to distinguish from one another.

In the second kind of family, individual genera were linked individually, forming a chain of similarities; these genera were often easily distinguished, even if the family was not. Similar distinctions, as between definable and indefinable families, have persisted (Davis and Heywood 1963: 107). It is perhaps ironic that some indefinable families, like Rosaceae and Ranunculaceae, have turned out to be largely monophyletic, while definable families like Lamiaceae or Liliaceae are strongly paraphyletic or polyphyletic.

Today most systematists realize that they need phylogenies. Before his untimely death in a car accident in 1989, Dahlgren had begun to elaborate relationships following more thoroughly phylogenetic principles. Such principles—especially the use of synapomorphies to diagnose monophyletic groups—were conceptualized by Willi Hennig (1950, 1966) and Warren H. Wagner (1969, 1980); they are outlined in Chapter 2. These principles provide criteria for deciding which particular features indicate phylogenetic relationships.

For almost a quarter of a century, students of Wagner and others produced Wagner trees, although most studies using them involved only a few taxa. In the late 1970s papers by Bremer, Wanntorp, and others popularized morphological Hennigian studies. A decade later, papers by Bremer (1987) and Jansen and Palmer (1987) suggested that both molecular and morphological data divided Asteraceae in a novel and exciting way. It was to be the combination of massive amounts of molecular and morphological data with methods of data analysis inspired ultimately by both Hennig and Sokal and Sneath that would transform both our ideas of higher-level relationships in land plants, and indeed how systematists work (Stevens 2000a).

In phylogenetic studies, at least, collaboration is the order of the day. No longer are systems as it were "owned" by individuals, as phrases such as "Engler's system" or "Cronquist's system" might suggest. Collaboration is common in producing and analyzing the data, as well as in suggesting possible classificatory interpretations (Angiosperm Phylogeny Group 1998; Grass Phylogeny Working Group 2001; Angiosperm Phylogeny Group 2002; see also Endersby 2001).

The arguments in systematics—often rather confused—now focus on the use of statistical methods for evaluating the support of hypotheses of phylogenetic relationships, and the proper use of evolutionary models, as in maximum likelihood methods. Perhaps surprisingly, little advance has been made in understanding the relationship between morphological observations and hypotheses of phylogeny (Stevens 2000b).

There is still disagreement over the relationship between phylogenies and the classifications that are based on them. Some systematists think that an important element shaping classifications should be how different one group looks from another; others think that classifications should be based strictly on phylogeny—that is, that all taxa should be monophyletic. The latter is the approach taken here (see Chapter 2).

This division is independent of the arguments for and against the PhyloCode, a discussion in which history has been invoked by all sides. However, not only is there little evidence for some of the particular historical arguments advanced, but history seems largely irrelevant (Stevens 2002).

A final point bears on the weight or importance of particular kinds of characters in the detection of relationships. Whole suites of characters deemed to be important come into and go out of fashion over the years. Thus in 1883 Ludwig Radlkofer proclaimed the following century to be that of the anatomical method in systematics, and in 1924 Hermann Ziegenspeck produced the "Königsberger Stammbaum," a tree showing the serological relationships of all plants (with fossils placed in their appropriate positions).

Other features, such as plant chemistry, chromosome number, and the morphology of sieve tube plastids, have all had their moment of glory. Because it was realized that single-character classifications were suspect, botanists often have restricted themselves to providing extensive surveys showing patterns of variation in individual characters. Unfortunately, despite claims that classifications synthesize all available data (Lawrence 1951; Constance 1964), prior to the advent of the computer there was no way of really integrating all the data that systematists produced. Furthermore, the coverage of systematic data has often been sadly inadequate.

Generalized anatomical surveys such as those that Radlkofer favored became unfashionable well before the end of his "century of the anatomical method." Developmental studies were not popular in systematics, despite remarkable work by J.-B. Payer in the middle of the nineteenth century. Although this work was dismissed by systematists such as J. D. Hooker, it is still widely cited in the comparative developmental studies that are adding so much to systematics today.

There has been some tension between floras, with their proper emphasis on geographically circumscribed treatments focusing on characters that help in the identification of the plants (see Frodin 2000 and Appendix 2), and monographs that deal with taxa wherever they are found and emphasize characters indicative of relationships, whether or not they can be used in identification. Major floras still often take more than 50 years to complete and are similar in their goals (and in the time it takes to finish them) to the Colonial Floras promoted by the Directors of the Botanic Gardens at Kew, England, in the later part of the nineteenth century. Accessible to a wide variety of scientists, they have helped stabilize usage of taxon names, although too little attention has been paid to just how the contributors to these floras reached the taxonomic conclusions that they did (Stevens 1997a).

Plant Groupings over the Years

It is impossible to do more than mention a few of the main changes in ideas about relationships in the years prior to the advent of phylogenetic methodology (see Lawrence 1951 for summaries). Some of the differences between what are now called monocotyledons and dicotyledons were already evident to Theophrastus in 300 B.C., but John Ray (1627–1705) was the first to make a major distinction between the two, although he subordinated it to his primary division into trees and herbs. Cotyledon number was the main character used by Jussieu in 1789 to divide plants, and it has almost always retained its prime position.

Jussieu placed the monocotyledons before the dicotyledons because they were simpler (monocots appeared to lack a corolla and had only a single cotyledon), and he began the dicots with such plants as Aris-

tolochiaceae and many Caryophyllales (his nomenclature is modernized here); all, he thought, lacked a corolla (petals) and so were the simplest in the series of increasing complexity that his arrangement represented.

Many plants with catkins have flowers of different sexes, often on different individuals, and so they seemed to Jussieu to be by his criteria the most complex; these he placed near the end of the dicots, and thus near the end of his whole sequence. He placed the conifers (but not the cycads, which he included with the ferns) at the very end, probably in part because some genera have many cotyledons and so represented the culmination of the cotyledonary series. The distinctive nature of gymnospermy was demonstrated by Robert Brown in 1826, but "gymnosperms" (conifers and cycads) were not finally excluded from the angiosperms until much later in the century.

Two major arrangements adopted subsequently are associated with the names of A.-P. de Candolle and Adolf Engler. However, there has always been a plethora of alternative systems: In the twentieth century, Lam, Melville, Meeuse, and Hayata, to name just a few, all proposed their own sometimes very different systems. Candolle (1813) began his system—which he said was not to be interpreted as being linear—with the Ranunculaceae on the grounds that one should place well-known organisms first. Simple plants tended to be least well known; the Ranunculaceae had, he thought, the most complex flowers and were well known.

Candolle's series followed the sequence (1) Thalamiflorae (superior, sepals and petals distinct), (2) Calyciflorae (often a hypanthium, sepals and petals distinct), (3) Corolliflorae (sympetalous plants), (4) Monochlamydeae (only a single perianth series) (see Chapter 4 for discussion of these floral terms). Monocots followed the dicots, and gymnosperms, not named as such, straddled the end of the dicot series and the beginning of the monocots.

Although Bentham and Hooker largely followed the Candollean sequence, their classification delimits taxa that are quite often substantially different, and hence implies different relationships. Furthermore, they noted that they adopted the dicot sequence Thalamiflorae–Gamopetalae–Monochlamydeae for convenience only, and that many Monochlamydeae, in particular, were probably related separately to Polypetalae (i.e., plants having distinct petals); they were not much happier with Gamopetalae. Their Gymnospermae was a fourth dicot group placed just before the monocots.

Engler's system is basically a modification of that of Adrien de Jussieu (1843). Jussieu, like his father, Antoine-Laurent, allowed that the basic sequence should be simple to complex. However, he thought that monocots and dicots should be placed in parallel, not in series. Hence his dicot sequence began with plants that were absolutely simple, rather than those that Antoine-Laurent thought were most similar to monocots. Within the dicots, Adrien

Heinrich Gustav Adolf Engler
(1844–1930, German)

placed dioecious groups, divided into angiosperms and gymnosperms, first, and Amentiferae (i.e., species with reduced, wind-pollinated flowers borne in catkins or aments) were placed first within the angiosperms. The other three major groups of dicots that he recognized followed the morphological sequence (1) apetaly (petals lacking), (2) polypetaly (petals distinct), (3) monopetaly (petals fused).

Engler excluded gymnosperms from the angiosperms and divided dicots into Archichlamydeae and Sympetalae. The angiosperms began with groups such as Piperaceae and Chloranthaceae before proceeding to Amentiferae and polypetalous plants. The basic arrangement is unchanged in recent editions of this system (Engler 1964), although Piperaceae have been moved. There is some debate whether Engler thought that the Amentiferae really were primitive, but some who used the Englerian sequence (or its precursors) certainly did think this to be the case.

Bessey's system combines features of both main ways of arranging plants. Bessey's dicta—guidelines for the production of phylogenies (Bessey 1915)—have been particularly influential. Many of these dicta are specific evolutionary trends, and the identification of such trends long remained a major component of evolutionary thought. Recent systems, of which perhaps the most notable are those of Dahlgren (1983; Dahlgren et al. 1985), Thorne (1999, 2000), Takhtajan (1997), and Cronquist (1981), are largely variants of Besseyan and Englerian ideas combined (Cuerrier et al. 1996), although Thorne and particularly Dahlgren (as discussed earlier) paid more attention to phylogenetic principles.

Despite all these varying approaches, by the early 1980s something of a consensus about ideas of relationships seemed to be developing (Stevens 1986), and in North America Cronquist's system was much in use. Well documented and with descriptions that incorporated both anatomical and chemical information, it starts with families that are still considered to be members of basal angiosperm lineages, although they are now often placed in groups that are differently circumscribed. Elsewhere in Cronquist's system, particularly in groups like the Rosidae, Dilleniidae, and Liliidae, there is little in common between the groups that he recognized and those that are recognized here.

Indeed, the consensus of the late twentieth century ignored those who still followed Englerian ideas, and it has not survived the effects of cladistic theory (see Chapter 2) and the recent spate of major molecular and morphological studies that utilize it (see Chapters 8 and 9). The changes are caused by the existence of clear goals, large amounts of new data, and new methods of data analysis, as well as the realization that the systematist is no longer describing relationships in nature, but proposing hypotheses of phylogeny. Although many important aspects of phylogenies remain unclear—for instance, the relationship of monocots to other angiosperms—the broad outlines of a new arrangement are evident (Angiosperm Phylogeny Group 1998, Angiosperm Phylogeny Group 2002) and are reflected in the relationships discussed in Chapters 8 and 9 of this book and the sequence followed there.

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