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10

History and Development of Classification

The arrangement of plants into an organizational scheme is called plant **classification**. Humans by nature are inquisitive and have always asked questions about the plants they encounter. Historical information indicates that some civilizations classified plants. Early societies were dependent on some plants or plant parts for food, shelter, weapons, or tools. No doubt some type of selection process occurred, with some plants being superior for a particular use, and these plants were given names to aid societies in communication.

The earliest records for naming and classification date back many millennia. In approximately 4000 B.P. (2000 B.C.), the *Atharva Veda* in ancient India provided medicinal use of plants. In this work, a "botanist" named Parashara wrote what was termed *Virkshayurveda*. This treatise dealt with the property of soils, described various forest types in India and the morphology of leaves and cells, and delimited a considerable number of present-day plant families. Other treatises on medicinal plants used by the Aztecs, Assyrians, Chinese, and Egyptians have also been discovered.

Naming and classification is evident even in the early Judeo-Christian record, as we read in Genesis 2:19-20: "...Now the Lord God...brought them to the man [Adam] to see what he would name them; and whatever the man called each living creature, that was its name. So the man gave names to all the livestock, the birds of the air and all the beasts of the field" (New International Version).

In the western world, the beginnings of botany as a science can be traced to the ancient Greek philosophers who lived between 370 and 285 B.C. An inspection of the historical development of plant classification can be grouped into systems: the form system of plants, the sexual system of plants, early "natural" systems, post-Darwin "natural" systems (1860-1950), and contemporary classification systems.

FORM SYSTEM OF PLANTS

The early philosophers and medical personnel of Greece and Rome wrote some of the early botanical works published in Europe.

An outstanding student of Aristotle and Plato was **Theophrastus** (370-287 B.C.). He classified approximately 500 plants on the basis of habit or form—notably herbs, shrubs, and trees—in his *Historia planatarum*. He distinguished between the annual, biennial, or perennial lifespan. He also provided the basis for floral morphology by distinguishing between superior and inferior ovaries, polypetalous and gamopetalous corollas, and determinate and indeterminate inflorescences. He probably gained much of his botanical knowledge from the cultivated plants grown in early Athenian gardens.

Pliny the Elder (23-79 A.D.), a Roman scholar and naturalist, wrote an encyclopedic set of books termed *Historia naturalis*. In this series he discussed such diverse plant topics as horticultural practices, medicinal uses, plant anatomy, and trees used for timber. He used a similar classification as the Greeks and also incorporated many of his predecessors' errors. His contributions are considered one of the most important of the early botanical works. His life was terminated by an eruption of Mt. Vesuvius.

Dioscorides, a contemporary of Pliny, was a physician in Emperor Nero's army. He traveled extensively in the Mediterranean region studying plants. His *de Materia medicia* (first century A. D.) was illustrated and included medicinal information and descriptions of about 600, mostly Mediterranean plants. This work was widely used by Europeans for the next 1500 years.

In about 512 A.D., the *Anicia Julianna Codex* was prepared from material originally written by Dioscorides for the daughter of a Byzantine emperor. This work was illustrated in color and was copied and recopied many times without major revisions during the Middle Ages.

Albertus Magnus (1193-1280) wrote *de Vegetabilis*, in which he described various garden vegetables. He accepted Theophrastus' classification but introduced for the first time the difference between monocotyledon and dicotyledon seeds.

Little information of real botanical significance was added following the fall of the Roman civilization. It was not until the fifteenth and sixteenth centuries that there was real awakening. During this period, sometimes called the **Age of the Herbals**, many new plants were described and illustrated. This was enhanced by the new art of printing illustrations by woodcuts and moveable type. The authors of these books were concerned with providing information on medicinal plants, and therefore these works became known as **herbals** and the authors as **herbalists**.

In Eastern Asia, herbals were compiled before and during this beginning of botany in Europe. In China, *Cheng lei Pen Tsào* was written by Tang Shen in 1108 and it went through twelve editions by 1600. Hsu Yung wrote *Pen Tsa O Fa Hui* in 1450 and Li Si Chen wrote *Pen Tsao Kangmu* in 1590.

During this herbalist period, plant information was not of much value from a classification standpoint. Some herbals were well known for their fine illustrations of living plants. These included works by **Otto Brunfels** (1489-1534), **Jerome Bock** (1498-1554), **Leonhart Fuchs** (1501-1566), **Charles Clusius** (1526-1609), and **Mathias de l'Obel** (1515-1568), known as the Father of British Botany.

One significant taxonomic contribution is worth mentioning. A pupil of Fuchs, **Gaspard (Kaspar) Bauhin**, attempted to use a binomial system of nomenclature in several publications such as *Prodromus theatri botanici* (1620) and *Pinax theatri botanici* (1623).

Andrea Caesalpino (1519-1603), an Italian physician, organized an herbarium of 768 dried and mounted plants in 1563, some of which are still preserved. His work, *De plantis* (1583), described 1520 species of plants, arranged as either herbaceous or woody. He further realized the value of using flower and fruit characters over characters of form or habit. It is said that he had a good grasp on the concept of what we today call genera, and he greatly influenced later botanists.

The first real advance in taxonomy and classification in many years was made by an English blacksmith, **John Ray** (1628-1705, Fig. 10.1). After graduating from Trinity College, he traveled extensively in Europe observing plants. In his two main works, *Methodus plantarum nova* (1682) and *Historia plantarum* (1686-1704), he expanded the principle that all parts of the plant should be considered for classification.

Ray's classification system first divided plants in the old way of Theophrastus—into herbs (Herbae), shrubs, and trees (Arborae). He further divided them into 25 classes of dicotyledons and four classes of monocotyledons. Some of his groupings represent some present-day families such as Brassicaceae (Tetrapetalae), Lamiaceae (Verticillatae), Fabaceae, and grasses (Staminae). His writings dealt with approximately 18,000 species.

A French contemporary of John Ray was **Pierre Magnol** (1638-1715). Finding Ray's classification too cumbersome, he grouped plants into 76 families in his *Prodromus historiae generalis, in qua familiae per tabulas disponutur* (1689). Magnol is therefore the first to use the family concept emphasized today. His name is honored by the beautiful woody genus *Magnolia*.

Joseph Pitton de Tournefort (1656-1708) was a student of Magnol and became a professor of botany at the Jardin de Roi. Tournefort traveled extensively in Europe and Asia Minor collecting plants; he even climbed Mt. Ararat. He was the first to give descriptions of genera. He grouped flowers with petals and without petals (apetalous), corollas with separate and united petals, and regular and irregular corollas. It is noteworthy that he still grouped the plants into herbs and trees, but he did not recognize plant sexuality. In his *Eléments de botanique* (1694), enlarged in 1700 to *Institutiones rei herbariae*, he described 698 genera and 10,146 species. Some of his genus names, such as *Abutilon, Acer, Betula, Quercus*, and *Ulmus*, were used by Linnaeus.

Rudolf Jacob Camerarius (1665-1721) was the director of the botanical garden at Tübingen, Germany. He is known for his letters to botanists reporting his crossing experiments between different plants. In a letter dated 25 August 1694 to a professor at Giessen, titled *De sesu plantarum epistola*, he described how pistillate flowers would not set seed without staminate flowers being present. He referred to the stamens as the male sex organs, the style and ovary as the female sex organs, and pollen as necessary for seed development. For the first time, sexual reproduction was established for the flowering plants.

SEXUAL SYSTEM OF PLANTS

By the turn of the eighteenth century, there had been a gradual accumulation of plant material, and much of it did not fit the known classification schemes of the day. It was during this historical-botanical period that a young Swedish botanist, Carl Linnaeus (1707-1778, Fig. 10.2), came on the classification scene. Linnaeus was born into the family of a poor clergyman, at Råshult, Sweden. During his early childhood years, he showed an interest in

Figure 10.1 John Ray (1628-1705), an English blacksmith, wrote an early classification of plants. Courtesy of the Royal Botanic Gardens, Kew.

Figure 10.2 Carl Linnaeus (1707-1778), the "Father of Biological Classification," as a young man holding the plant named *Linnaea borealis* (the genus was named after Linnaeus by Gronovius). Courtesy of the Royal Botanic Gardens, Kew.

the flowers of the garden and constantly asked for the names of the plants. He enrolled at the University of Uppsala, where he came under the guidance of an elderly professor, Olaf Rudbeck, who treated Linnaeus like a son. Under Rudbeck's guidance, he published his first paper on the sexuality of plants in 1729.

In 1732 Linnaeus obtained a small travel grant of approximately $125 (U.S.) from the Academy of Sciences of Uppsala for a botanical exploration of Lapland. In five months, Linneaus traveled over 7600 km and returned with over 537 specimens. The results of the excursion were published in *Flora lapponica* (1737).

Young Linnaeus was encouraged to study medicine in mainland Europe, and in 1735 he traveled to the Netherlands where he obtained his degree at Harderwijk. While in the Netherlands, he became closely associated with two Dutch botanists—Hermann Boerhaave and J. Gronovius. Their influence was most invigorating to Linnaeus, for in the span of two years he wrote *Systema naturae* (1735), which was the basis of Linnaeus' sexual classification of plants, animals, and minerals; *Critica botanica* (1737); *Flora lapponica* (1737); *Hortis cliffortianus* (1737); and *Genera plantarum* (1737). This latter work is important because of the 935 genera described; five revisions and two supplements later would bring the total to 1336 genera.

Linnaeus made short visits to England and France. When his former teacher Rudbeck died in 1742, he returned to Uppsala as Professor of Medicine. In 1753, then as Professor of Botany, he published *Species plantarum*. This work described approximately 1000 genera and 7300 species, all given binomial Latin names and arranged according to the sexual system of *Systema naturae*, which was published earlier (Table 10.1). Linnaeus was not the first to use binomial nomenclature (as discussed earlier), but he was the first to do so consistently. This is why *Species plantarum* and its published date of 1 May 1753 is chosen by contemporary botanists as the beginning point for plant nomenclature. Carl Linnaeus can truly be called the Father of Biological Classification.

Table 10.1 Outline of the classes of the classification used by Linnaeus in *Species plantarum*.

Class Number	*Name*	*Number of Stamens*	*Present-day Example*
1.	Moandria	1	*Canna*
2.	Diandria	2	*Veronica*
3.	Triandria	3	*Poa*
4.	Tetrandria	4	*Protea*
5.	Pentandria	5	*Campanula*
6.	Hexandria	6	*Lilium*
7.	Heptandria	7	*Aesculus*
8.	Octandria	8	*Vaccinium*
9.	Enneandria	9	*Laurus*
10.	Decandria	10	*Rhododendron*
11.	Dodecandria	11-19	*Euphorbia*
12.	Icosandria	$\leq$ 20 on calyx	*Opuntia*
13.	Polyandria	$\leq$ 20 on receptacles	*Ranunculus*
14.	Didynamia	Stamens didynamous	*Lamium*
15.	Tetradynamia	Stamens tetradynamous	*Brassica*
16.	Monadelphia	Stamens monodelphous	*Malva*
17.	Didelphia	Stamen didelphous	*Faba*
18.	Polyadelphia	Stamen polyadelphous	*Hypericum*
19.	Syngenesia	Stamen syngenesious	*Aster*
20.	Gynandria	Stamen united	*Cypripedium*
21.	Monoecia	Plants monecious	*Carex*
22.	Dioecia	Plants dioecious	*Salix*
23.	Polygamia	Plants polygamous	*Acer*
24.	Cryptogamia	Nonflowering plants	*Pteris*

Linnaeus' greatest contribution to botany was his new system of naming plants. He gave a general (genus) name and a trivial (specific epithet) name to each plant, geographical areas where the plant was found, herbarium specimens seen, and references for publications.

Many students studied with Linnaeus and spread the "Linnean gospel" throughout the world. In 1761 he was nobilized and was known from this point as Carl von Linné.

The last years of his life were spent in ill health and he died in 1778. After his death, his widow sold his personal library and herbarium to an Englishman, Dr. James E. Smith, in 1784 for the sum of £1000. These collections later became the property of the Linnean Society of London, which was founded by Smith in 1788. Today they are carefully preserved at Burlington House, on Piccadilly, at the headquarters of the Society (Fig. 10.3).

Figure 10.3 The climate-controlled vault at The Linnean Society of London, where Linnaeus' original specimens are housed.
Courtesy of The Linnean Society of London.

Linnaeus was not as rigid with his sexual system of classification as many have been led to believe. Many times he included species in a genus that did not follow his system definition. He would use the technical characters of a plant species to confirm their general arrangement. In this way, many genera fit a more natural classification.

Early in his career, Linnaeus believed that species were unique, genetically true-breeding, and monotypic. The variation he observed he attributed to climate or soil difference. In later years, he began to maintain that many species and even genera had developed through hybridization, a concept not normally thought of as applying to Linnaeus. His attempt at bringing together species that were more alike is indicated by Linnaeus' sixth edition of *Genera plantarum* (1764), where genera in 58 "natural orders" were presented. His sexual system was retained for identification purposes only.

Species plantarum did not end with Linnaeus. It underwent various revisions until the beginning of the 1800s. It was published in six volumes between the years 1797 and 1830 by the German botanist Karl Ludwig Willdenow (1765-1812), who included species from all over the world. Linnaeus' home has been restored and is preseved in Sweden (Fig. 10.4).

Figure 10.4 The restored home of Carl Linnaeus in Sweden.
Courtesy of W. F. Grant.

EARLY "NATURAL" SYSTEMS

During the latter part of the eighteenth century, many explorers and botanists soon found that the wealth of international plant specimens could not be classified satisfactorily with Linnaeus' sexual system. A better one was desperately needed. Botanists began to realize that some natural affinity occurred among plants and incorporated a natural arrangement of the plants in their works.

Michel Adanson (1727-1806), a Frenchman exploring the African flora, rejected Linnaeus' sexual system in favor of a natural one for his groupings, which today corresponds to orders and families. This was recorded in his work *Families des plants* (1763).

A French contemporary of Linnaeus, **Bernard de Jussieu** (1699-1777), was not satisfied with Linnaeus' system and attempted to improve upon it, modifying it into a more natural arrangement. His system was published by his nephew **Antoine Laurent de Jussieu** (1748-1836, Fig. 10.5), along with his own concepts, in *Genera plantarum secundum ordines naturalis disposita* (1789). The plants were classified into 15 classes and 100 orders, which are recognized today as families (Table 10.2). This first comprehensive attempt at natural classification is the beginning point for conserved family names of flowering plants as stated according to the International Code of Botanical Nomenclature.

Figure 10.5 Antoine Laurent de Jussieu (1748-1836), a French contemporary of Linnaeus. Courtesy of the Royal Botanic Gardens, Kew.

Augustin Pyramus de Candolle (1778-1841, Fig. 10.6), the senior member of the famous botanical Swiss-French family, developed further the classification system of A. L. de Jussieu in his *Théorie élémentaire de la botanique* (1813), in which 135 orders (today's families) were described. Along with his son **Alphonse de Candolle** and grandson **Casimir**, he published the enormous *Prodromus systematis naturalis regni vegetabilis* (1824-1873), which included descriptions of almost 59,000 species of gymnosperms and dicotyledons. The ferns were placed with the monocots and the gymnosperms with the dicots, while the algae, mosses, liverworts, fungi, and lichens were placed in the Cellulares (plants without vascular tissue). Even though other natural systems were proposed during this time period, the de Candolle system was dominant until about 1860. The de Candolle library and specimens are housed at the Conservatoire et Jardin Botanique, Genève, Switzerland. An interesting note about the popularity of the de Candolle classification was its sequence, starting with the polypetalous, hypogynous Ranalian groups, similar to present-day systems.

A Scottish botanist, **Robert Brown** (1773-1858, Fig. 10.7), was known not for any classification system of his own, but for his observations on floral and seed morphology. He was the first to show that the gymnosperms (Pinophyta) were a separate group of plants with naked ovules, in contrast to the angiosperms which have the ovules enclosed in ovaries. Brown was the first to establish the families Asclepiadaceae and Santalaceae, to write about the morphology of the grass flower, and to understand the nature of the cyathium of the Euphorbiaceae. Davis and Heywood (1973) say that "it is difficult to understand how Brown could have written as he did without some intimation of evolution."

Between 1825 and 1845, at least 24 classification systems were proposed. They all

Table 10.2 Outline of the de Jussieu classification of plants.

Number Group	Modern Examples
1. Acotyledones/Monocotyledones	Algae, fungi, mosses
2. Stamens hypogynous	Cyperaceae, Gramineae (Poaceae)
3. Stamens perigynous	Iridaceae
4. Stamens epigynous,	Orchidaceae
Dicotyledones, Apetalae	
5. Stamens epigynous	Aristolochiaceae
6. Stamens perigynous	Polygonaceae, Proteaceae
7. Stamens hypogynous	Amaranthaceae, Nyctaginaceae
Dicotyledones, Monopetalae	
8. Corolla hypogynous	Boraginaceae, Labiatae (Lamiaceae)
9. Corolla perigynous	Ericaceae
10. Corolla epigynous, anthers united	Cichoraceae
11. Corolla epigynous, anthers distinct	Rubiaceae
12. Stamens epigynous	Araliaceae, Umbelliferae (Apiaceae)
13. Stamens hypogynous	Cruiciferae (Brassicaceae), Ranunculaceae
14. Stamens perigynous	Leguminosae (Fabaceae), Rosaceae
15. *Declines irregularis*	Amentiferous plants, conifers

Modified from Naik, 1984; Porter, 1967.

Figure 10.6 Augustin Pyramus de Candolle (1778-1841), the senior member of the famous de Candolle family of botanists.
Courtesy of the Royal Botanic Gardens, Kew.

Figure 10.7 The Scottish botanist Robert Brown (1773-1858), the first to recognize gymnosperms as a separate group of plants.
Courtesy of the Royal Botanic Gardens, Kew.

were nothing more than a minor revision of the concepts of de Candolle and Brown. Three individuals worth mentioning briefly were the French botanist **Adolphe T. Brongniart** (1801-1876), who considered the apetalous plants to be reduced from the polypetalous; **John Lindley** (1799-1865), an Englishman who felt that plants had developed along lines of simple to more complex morphology; and the Viennese botanist **S. L. Endlicher** (1805-1849), who divided the plant kingdom into thallophytes (algae, fungi, and lichens) and cormophytes (mosses, ferns, and seed plants). Endlicher's system was widely used in Europe, but was neglected in England and North America.

George Bentham (1800-1884, Fig. 10.8) and **Sir Joseph Hooker** (1817-1911, Fig. 10.9) were British botanists who worked out of the Royal Botanic Gardens at Kew, just outside of London. They published their classification system in a three-volume work called *Genera plantarum* (1862-1883). This work described 202 orders (present-day families) and included all known seed plants at that time (over 97,000) according to the Bentham and Hooker system. This system followed that of de Candolle but also differed somewhat. All genera were described in Latin from observed living material at Kew or from herbarium specimens Bentham and Hooker had seen. Their work gave a synopsis of each family and the geographical range of each genus. This system was a real landmark in botany for its scholarship and quality.

It could be noted that the most famous North American botanist at this time, **Asa Gray** (1810-1888), combined the Bentham and Hooker system with that of de Candolle for his own use.

POST-DARWINIAN "NATURAL" CLASSIFICATION SYSTEMS (1860-1950)

With the publication of Charles Darwin's (Fig. 10.10) *The Origin of Species* in 1859, the complete direction of classification and biological thought was altered. The theories of Darwin seemed to bring together all of the dissatisfaction that botanists had held toward Linneaus' sexual system and later toward the de Candollean system.

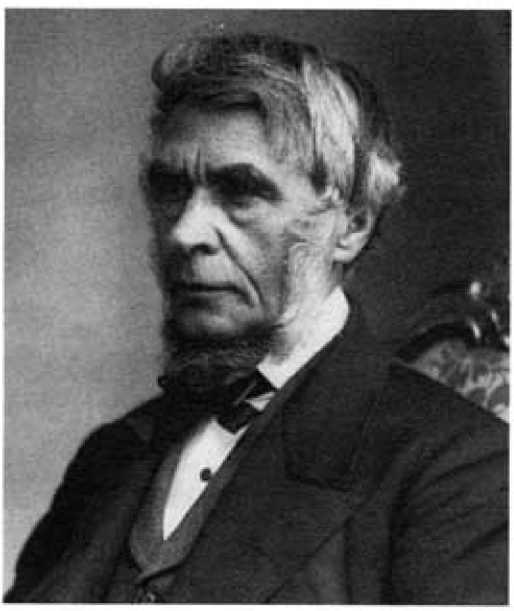

Figure 10.8 The famous British botanist George Bentham (1800-1884), who worked at the Royal Botanic Gardens with Sir Joseph Hooker.
Courtesy of the Royal Botanic Gardens, Kew.

Figure 10.9 The famous British botanist Sir Joseph Hooker (1817-1911), a close friend of Charles Darwin.
Courtesy of the Royal Botanic Gardens, Kew.

The systems that developed are based on the theories of descent and evolution, and the idea that the present-day life forms are a product of natural evolutionary processes. The authors of the various classification systems attempted to organize plant groups from the most simple to the most complex and to demonstrate ancestral relationships. As more and more data became available and more botanists began to study plants, it was inevitable that different views would be forthcoming and different classification systems would be produced.

August Wilhelm Eichler (1839-1887), a German, modified earlier systems to reflect a better relationship between plants. The plant kingdom was divided into non-seed plants (Cryptogamae) and seed plants (Phanaerogamae). The former group was divided into Thallophyta, Bryophyta, and Pteridophyta. The seed plants (Phanaerogamae) were divided into the gymnosperms and angiosperms, and the angiosperms were broken down into monocots and dicots. This breakdown by Eichler was based on the assumption that plants with a complex flower organization are more "advanced" in their evolutionary development. Eichler's system was the foundation for Adolf Engler's system (see below) and was never widely accepted. The system of Bentham and Hooker remained the dominant system in North America and England.

Another German, **Adolf Engler** (1844-1930, Fig. 10.11), and his associate, **Karl Prantl** (1849-1893), adopted the major feature of Eichler's classification and published a 20-volume work, *Die natürlichen Pflanzenfamilien* (1887-1899), which provided a way to identify all the known genera of plants from algae to flowering plants. The work was illustrated and included keys. These features, along with information on anatomy, embryology, morphology, and geography, and with descriptions and good publicity, helped botanists to adopt the system within a few years.

Many of Engler's changes to Eichler's system show the influence of earlier systems, but he still followed the basic phylogenetic breakdown. A main feature of the system is that the monocotyledons are placed before the

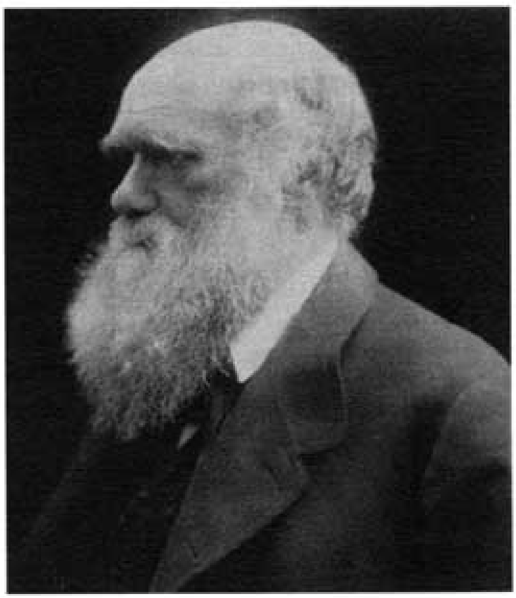

Figure 10.10 Charles Darwin, whose ideas on the origin of species revolutionized botanists' view of the classification of plants. (Darwin autographed this photo, "I like this photograph very much better than any other which has been taken of me. Ch. Darwin.")
Courtesy of the Royal Botanic Gardens, Kew.

Figure 10.11 Adolph Engler (1844-1930), who, with his associate Karl Prantl, became famous for completing the only detailed classification of plants from algae to flowering plants.
Courtesy of the Royal Botanic Gardens, Kew.

dicotyledons, and the catkin-bearing (ament-type) plants are placed before other families, indicating that these plants were considered to be more primitive than the rest.

A slightly revised edition of the system was last published in 1964 by Engler and **L. Diels** as *Syllabus der Pflanzenfamilien*. Up to the present time, Engler's system is still used by most herbaria in their arrangement of species and is followed by writers of many manuals and floras. It is still the only system that treats all plants (algae to flowering plants) in such depth.

Richard von Wettstein (1862-1931, Fig. 10.12), a botanist from Austria, published a system that is rather similar in many respects to Engler's. In his *Handbuch der systematischen Botanik* (1901) and fourth revision (1930-1935), he rearranged many of the dicot families. He felt that the monocots were derived from the order Ranales in the dicots and that unisexual flowers lacking perianth were the simplest, with perfect flowers derived from them. He also considered more contemporary literature. His system was more phylogenetic than Engler's system.

The system of Wettstein was not widely accepted, especially in North America. However, his theory that monocots were derived from dicots differed from Engler's ideas. Some of the present-day contemporary systems have adopted many of his more specific conclusions to phylogenetic relationships.

The first North American to make a contribution to the general system of classification was a student of Asa Gray, **Charles E. Bessey** (1845-1915, Fig. 10.13). The ideas of Bessey have greatly influenced the thinking of authors of late-twentieth-century systems. Bessey began his career at Iowa State University, but after a short time went to the University of Nebraska where he spent most of his career. In creating his system, entitled "The Phylogenetic Taxonomy of Flowering Plants," he was the first to develop a scheme that was "truly phylogenetic" (Lawrence, 1951). He rejected many of the Eichler/Engler ideas. Bessey's system was founded on various guiding rules or "dicta," which he used to determine the level of being, simple or advanced, of a group of plants. Some of his 28 dicta are as follows (Bessey, 1915):

> (1) Evolution is not always upward, but often it involves degradation and degeneration. (2) In general, homogeneous

Figure 10.12 The Austrian botanist Richard von Wettstein (1862-1931), who published a classification system similar to Engler's.
Courtesy of the Royal Botanic Gardens, Kew.

Figure 10.13 Charles E. Bessey (1845-1915), whose ideas provided the basis for some of the current systems of plant classification.
Courtesy of Iowa State University Library/University Archives.

> structures (with many and similar parts) are lower, and heterogeneous structures (with fewer and dissimilar parts) are higher. (9) Woody stems (as of trees) are more primitive than herbaceous stems, and herbs are held to have been derived from trees. (12) Historically simple leaves preceded branched ("compound") leaves. (16) Petaly is the normal perianth structure, and apetaly is the result of perianth reduction (aphanisis). (19) Hypogny is the more primitive structure, and from it epigyny was derived. (24) In earlier (primitive) flowers there are many stamens (polystemonous) while in later flowers there are fewer stamens (oligostemonous). (27) Flowers with both stamens and carpels (monoclinous) precede those in which these occur on separate flowers (diclinous).

From these rules he constructed a phylogenetic diagram that has been called "Bessey's cactus" or "*Opuntia besseyi*" by many American botanists. His ideas differed from the Engler and Prantl system in that 1) he thought angiosperms were derived from a cycad-type ancestor, similar to that of the fossil Bennettitales, whereas, in the Engler and Prantl system, flowering plants originated from some unknown gymnosperm that was similar to a conifer; 2) he felt that angiosperms developed from the Ranales group from a plant with floral features that were similar to this group, while Engler and Prantl felt that dicots and monocots were derived from some catkin-bearing (amentiferous), floral-reduced ancestor and then obtained a perianth; and 3) he made his main separation of subclasses based on the floral cup characters of hypogynous, perigynous, and epigynous, while Engler and Prantl felt that the major separation should be based on apetalous, choripetalous, and sympetalous.

A Swedish botanist, **Carl Skottsberg** (1880-1963), developed a modified Engler system to the plant kingdom. He borrowed some concepts from Wettstein in his publication *Vaxternas Lir* in 1932-1940. He maintained the separation of the pteridophytes and gymnosperms, but thought that the class Gnetinae should include the Ephedrales and Welwitschiales. He also felt that, within the flowering plants, some undiscovered dicot gave rise to the monocots. He deviated from the ideas of Engler and Wettstein in proposing that the apetalous families originated many times independently and were recognized throughout the dicots.

Hans Hallier (1868-1932), a German botanist, proposed a phylogenetic system that is similar to Bessey's. He believed that the dicots developed from magnolia-like ancestors, with the monocots being more advanced and developing from an unknown ancestor. Both Bessey and Hallier developed their systems independently of one another.

The British botanist **John Hutchinson** (1884-1972, Fig. 10.14) worked at the Royal Botanic Gardens, Kew. The system he proposed in his *Families of Flowering Plants* (1926, 1934; 3rd ed. 1973) was somewhat like Bessey's but had major differences. He considered the angiosperms to be monophyletic in origin from a hypothetical seed plant. He considered the herbaceous or woody habit of the plant to be very important. The woody dicot groups developed from the Magnolias and the herbaceous groups were supposedly derived from herbaceous members in the Ranales. The monocotyledons were thought to have evolved from ancestral individuals in the Ranales. Hutchinson also proposed more orders than usual with fewer families in each order. The

Figure 10.14 The British botanist John Hutchinson (1884-1972), who proposed a family classification for the flowering plants.
Courtesy of the Royal Botanic Gardens, Kew.

orders were derived from ancestral precursors to the present-day orders and not from each order directly.

Hutchinson's system has not been accepted by many botanists, even though the arrangement of many families, especially within the monocotyledons, has been very helpful. The greatest criticism is leveled at his initial separation of herbaceous from woody groups. This has split some families that are similar in flower morphology and appear as natural units, except for the difference in habit (herbaceous versus woody).

A completely different approach to classification systems was used by the German **Karl Mez** (1866-1944). Mez believed that relationships between various large groups of flowering plants could be ascertained by using serological antigen-antibody reactions. By comparing the protein reactions of different groups (e.g., genera, families, etc.), close or distant, affinities could be determined. Mez produced a "family tree" for the plant kingdom, but it was severely criticized. Few botanists today follow Mez's ideas.

Oswald Tippo (b. 1911) at the University of Illinois attempted to do a broad classification of the higher groups of the plant kingdom in 1942. He used detailed information from other authors, studying various groups (both living and fossil), and divided the plant kingdom into various subkingdoms and phyla. He theorized that the pteridophytes were not a homogenous group and that seed plants and pteridophytes lack a demarcation between them. The Magnoliales were thought by him to be the most primitive flowering plants.

CONTEMPORARY CLASSIFICATION SYSTEMS (1950 TO PRESENT)

During the years 1950 to 1983, intense interest was generated in developing a more acceptable classification for the plant kingdom. A few individuals such as **Harold C. Bold** (1909-1987) and **Robert Whittaker** (1921-1980) confined their efforts to the larger groups of plants. Others concentrated on the angiosperms and, using Bessey's original ideas, attempted to construct a more natural system.

In 1950, an American, **A. Gunderson** (1877-1958), proposed a new classification system for the dicotyledons based on anatomy, cytology, and morphological data. The dicots were divided into 10 groups that were further separated into 42 orders. He ignored previously used floral characters, such as polypetaly and sympetaly.

Another American botanist, **Lyman Benson** (1909-1994), proposed a modified system of rearranged orders and families, taking ideas from both Bessey and Engler. He published this in the form of a two-dimensional chart in 1957, which was revised in 1979. The chart covered angiosperm groups only. Benson did not feel that any contemporary plant order was derived from any other living order, but believed that orders developed from precursor groups that are now extinct. He theorized that the flowering plants' origin was uncertain, but that they originated from some woody Ranales. The orders were not connected. The monocots, however, developed from the same general Ranales or Alismatales area. His separation of orders into Corolliflorae and Ovariflorae groups was purely arbitrary and not natural. Benson's system is easy to use when teaching students, but has not been followed by many botanists.

G. Ledyard Stebbins (1906-2000, Fig. 10.15), of the University of California, Davis, has made many outstanding contributions to botany. In 1974, he discussed the basis of classification of flowering plants. He applied information from genetics (mutation, population,

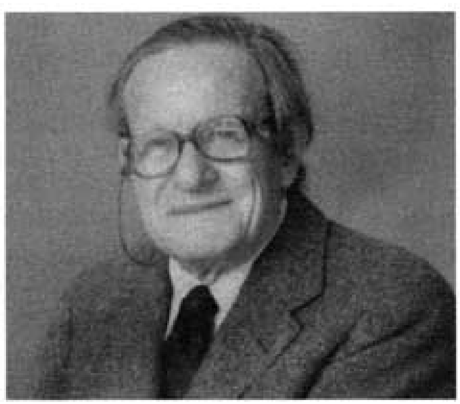

Figure 10.15 The outstanding American geneticist G. Ledyard Stebbins (1906-2000). Courtesy of G. L. Stebbins.

recombination, etc.), geology, microevolution, **natural selection**, reproduction, paleobotany, and ecology to the relationships within angiosperms. Stebbins proposed no new classification to the higher groups (families and orders), but modified the system of Cronquist. His broad-discipline approach allows the reader the freedom to view the complexity of data as applied to a natural classification system of flowering plants. This contemporary approach, allowing freedom for differing views and ideas toward the same data, or as new data become available, is refreshing as compared with the dictatorial "dicta" of Bessey.

Armen L. Takhtajan (b. 1910, see Figs. 10.17 and 10.19), working in Leningrad, has developed over many years a phylogenetic system of the angiosperms. His system, published in English in 1961, 1964, 1969, 1980, and 1997 (published earlier in Russian), reflects the influence of the Hallier system. He felt that Hallier's system gave a better insight into flowering plant phylogeny than did Bessey's. Takhtajan subdivided the Magnoliophyta (angiosperms) into two classes: Magnoliopsida (dicots) and Liliopsida (monocots)—Magnoliata and Liliatae in earlier versions. He divided these into various subclasses with endings of -anae, rejecting the -florae ending used previously. In the Magnoliopsida, he recognized 7 subclasses, 20 superorders, 71 orders, and 333 families, while in the Liliopsida were found 3 subclasses, 8 superorders, 21 orders, and 77 families. He considered the flowering plants to be monophyletic, not polyphyletic, in origin. He considered the order Magnoliales to be the most primitive, and from this branch the various angiosperm groups developed; the Liliopsida (monocots) were derived from a precursor in the Nymphaeales (water lily) group. The latter idea has received the most criticism from botanists, who feel that the two groups are similar due to convergent evolution instead of divergent change. In spite of these criticisms, Takhtajan's ideas have been relatively well accepted by the botanical community. Takhtajan's relationships among groups can be seen in "Takhtajan's flower garden" (Fig. 10.16).

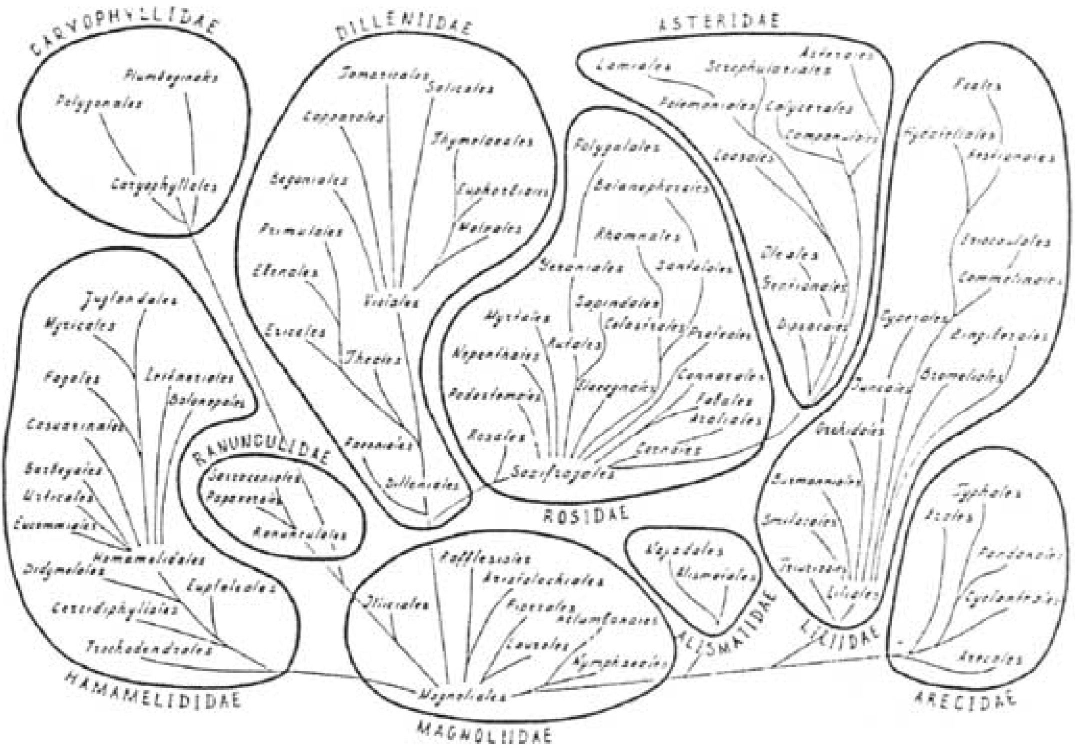

Figure 10.16 "Takhtajan's flower garden," which shows the putative relationships between the orders and subclasses of the flowering plants.
From Takhtajan, 1980.

Arthur Cronquist (1919-1992, Fig. 10.17) at the New York Botanical Garden first presented a system for dicotyledons in 1957, and in succeeding years (1966 and 1968) he refined it to include all flowering plants. His system is based on a vast literature search (including the Russian literature), personal communication with other botanists, and individual study in the field and with herbarium specimens. His system takes its initial basis from Bessey, followed by a modification and refinement of Takhtajan's phylogenetic system. His "evolutionary tree" (more like two small shrubs) derives the two classes Magnoliopsida (dicotyledons) and Liliopsida (monocotyledons) from the primitive Ranales group. In the class Magnoliopsida are 6 subclasses, 55 orders, and 352 families; the Liliopsida has 5 subclasses, 18 orders, and 61 families (Fig. 10.18). Cronquist's system is based on the idea that the orders within the subclasses were derived from one another. However, it should be pointed out that Cronquist emphasizes continually that the correctness of some of his arrangements are somewhat arbitrary or open to reinterpretation and new information.

Cronquist discussed his system in great depth in *An Integrated System of Classification of Flowering Plants* (1981). Here the student will find a discussion; key to all classes, subclasses, orders, and families of flowering plants; a commentary; and vast reference sources. Due to its thoroughness, many botanists in the world today are following Cronquist's system or a slight modification of it. In this book I have followed the Cronquist system in the arrangement of families in Chapters 8 and 9. This was done not because I feel the system is the most phylogenetically correct of the present systems, but because (1) it offers a contemporary system based on all types of research evidence that reflects our best knowledge about flowering plant relationships, (2) it provides more in-depth literature on the various plant taxa than any of the other systems currently being discussed and used by botanists for the individual who wishes to search further, and (3) it provides a logical,

Figure 10.17 Two authors of well-known contemporary systems of flowering plant classification: left, Armen Takhtajan; right, Arthur Cronquist.
Courtesy of A. Cronquist.

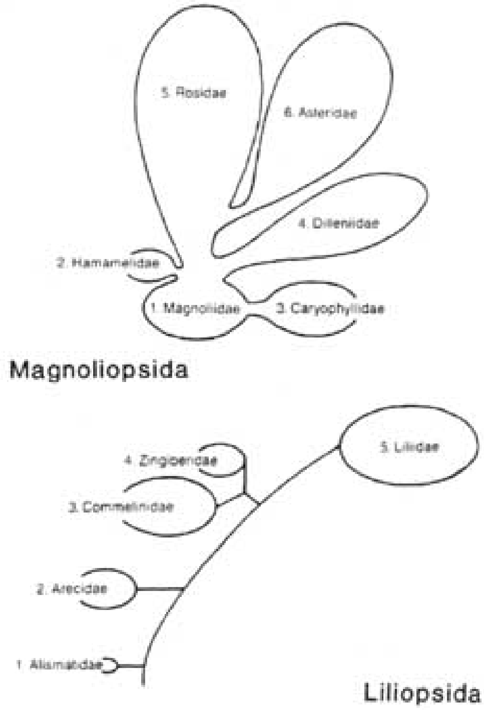

Figure 10.18 Putative evolution among the subclasses of Magnoliopsida and Liliopsida according to Cronquist. The number of species in each group is proportional to the size of the balloons.
From Cronquist, 1988.

orderly (if not natural) way for the student to learn about flowering plants.

A similar system to Takhtajan's and Cronquist's systems for classifying flowering plants has been proposed by a former curator of the Rancho Santa Ana Botanical Garden in California, **Robert F. Thorne** (b. 1920, Fig. 10.19). Thorne's system is centered around the angiosperms, which he has divided into ten subclasses: Magnoliidae, Alismatidae, Liliidae, Commelinidae, Ranunculidae, Caryophyllidae, Dilleniidae, Rosidae, Asteridae, and Lamiidae. The three monocot subclasses contain 9 superorders, 24 orders, 16 suborders, 114 families, and 82 subfamilies (170 subfamilies and undivided families), 2,778 accepted genera, and 57,885 accepted species. Similarly, the seven dicot classes contain 22 superorders, 51 orders, 366 families, 310 subfamilies (585 subfamilies and undivided families), 21 Asteraceae tribes, 10,885 genera, and 199,355 species. The synopsis of this updated classification of Angiospermae can be found with nomenclatural additions by James L. Reveal on his website:http://www.inform.umd.edu/PBIO/fam/thorneangiosp99.html. In Thorne's "evolutionary shrubs," he placed the superorders near the extinct precursor protoangiospermae in the center, where the "most primitive" characters are thought to have been retained. He next radiated out the various taxa from the "point of origin," with the orders that were most unlike the ancestral group placed furthest from the center (e.g., Asterales, Fig. 10.20).

Thorne states that his classification system is different from other systems because he stresses relationships and similarities of taxa rather than the "importance" of presumed phylogenetically significant characters. In spite of Thorne's claims, many botanists consider the system to be similar to Cronquist's and Takhtajan's systems; but in actuality, it is similar only in principle.

Another contemporary system needs to be considered. **Rolf M. T. Dahlgren** (1932-1987, Fig. 10.21) of Copenhagen presented a phylogenetic diagram. His wife, Gertrud Dahlgren, has combined their ideas in a two-dimensional diagram (Fig. 10.22). The class Magnoliopsida (angiosperms) is divided somewhat arbitrarily into two subclasses: Magnoliidae (dicots) and Liliidae (monocots).

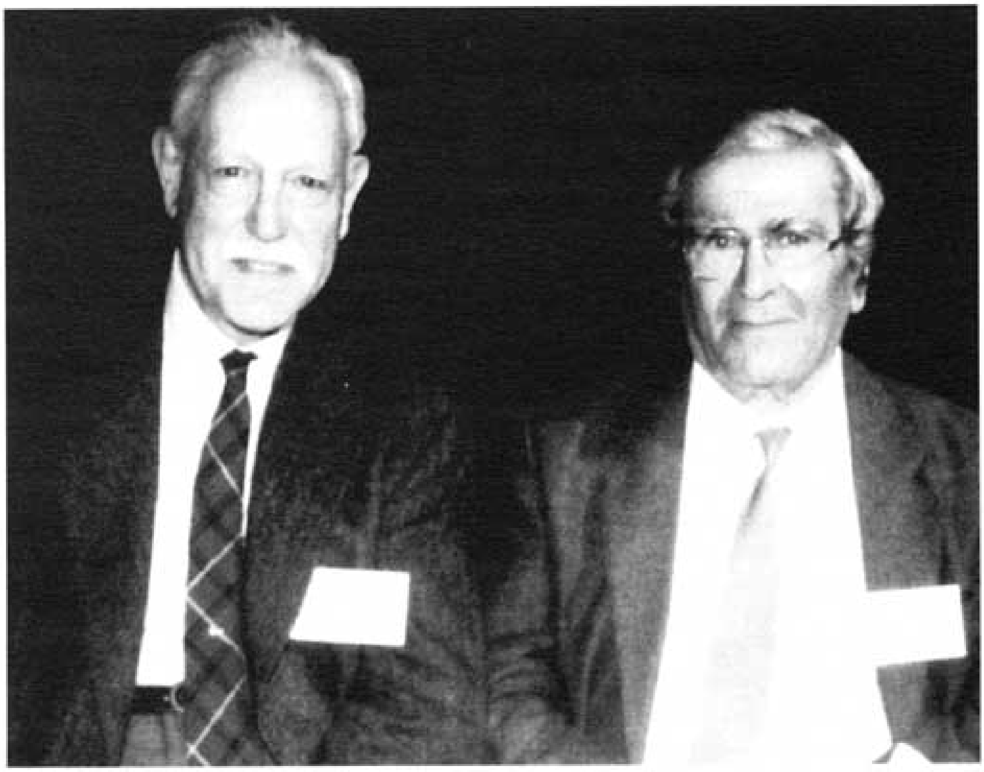

Figure 10.19 The American botanist Robert F. Thorne (left) with Armen Takhtajan at the Missouri Botanical Garden, 7 October 1990.
Photo by DWW.

The Magnoliidae is broken down into 25 superorders, with the Liliidae having 10 superorders. Dahlgren considered flowering plants to be monophyletic in origin and believed that various specialized characters (e.g., presence of phloem companion cells, 8-nucleate embryo sac, etc.) would only have developed once in the angiosperm precursor. The system as portrayed by Dahlgren shows irregularly shaped branches to be most similar when close to one another, and the size relates to the number of species in each. He used the ending -florae, like Thorne, for superorders.

In spite of splitting up some orders into more families in the superorder Liliiflorae, the system is very similar to that of Takhtajan. To help understand how more recent contemporary classification systems have been influenced by previous workers, a flow chart showing the history of classification is given in Figure 10.23. From this chart, it can be seen that the author(s) of a system had some influence on a succeeding system; a few individuals, such as Hallier and Bessey, profoundly influenced current contemporary systems; the current systems of Cronquist, Dahlgren, Stebbins, Takhtajan, and Thorne for the flowering plants have more similarities than differences; and the systems of today may be much different from the classification systems of tomorrow, as new data are forthcoming.

A classification system is only one person's ideas of possible relationships among plant groups. How data are used, perceived, interpreted, and applied depends on the investigator's background, environment, and personal bias. The "natural picture" portrayed by the fossil record "data bank" at hand is most incomplete and sketchy. Therefore, botanists have to rely on **extant** micro- and macromorphological data to interpret the past—data that may give incorrect results and conclusions. Just because a taxon is morphologically and chemically "similar" to another taxon does not mean that a relationship is assured. A case in point can be seen in Figure 10.24. The late C. V. Morton, of the Smithsonian Institution in Washington, D.C., found an old leather bag of

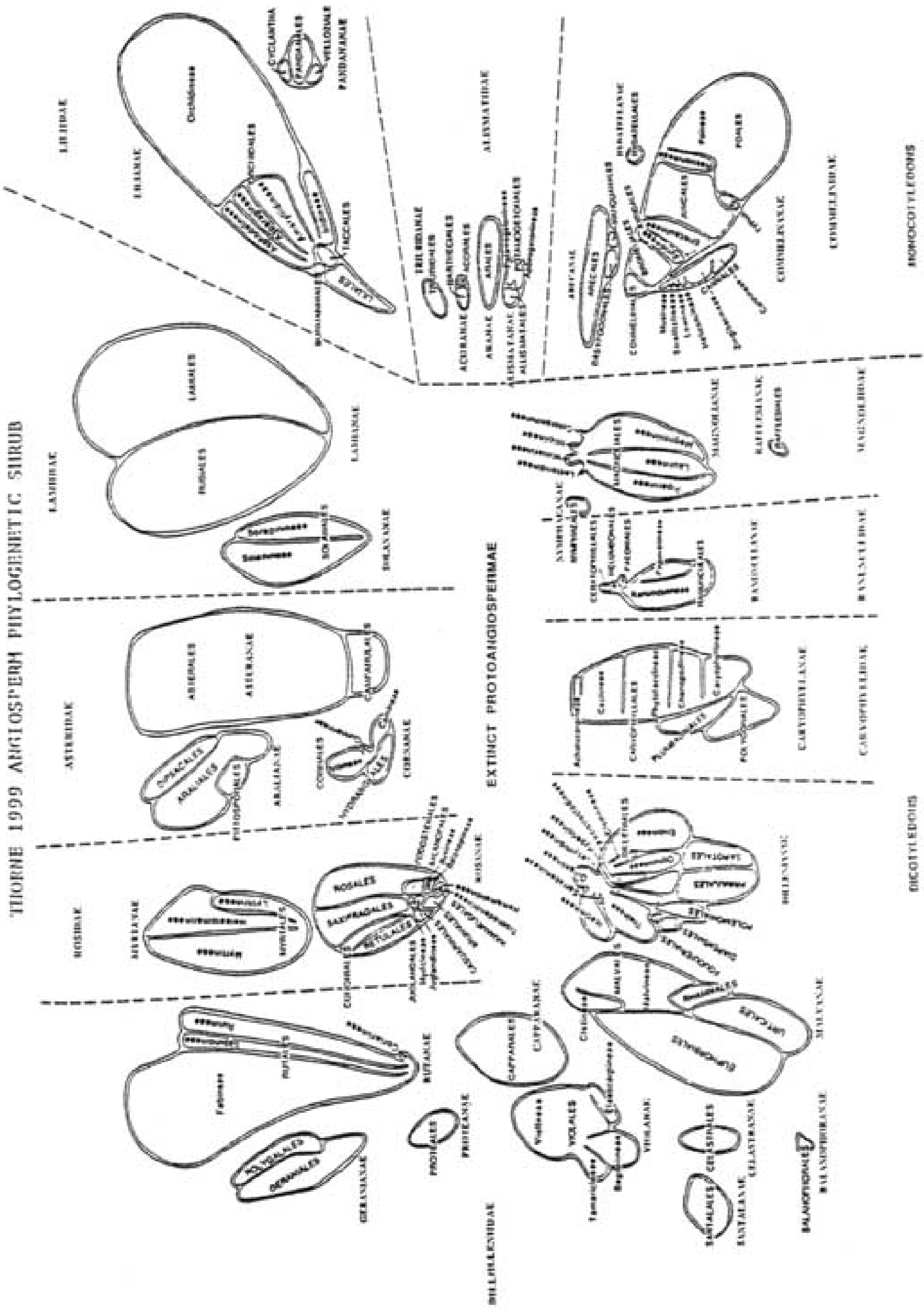

Figure 10.20 Thorne's grouping of flowering plant groups in relation to a hypothetical extinct protoangiosperm. Courtesy of R. F. Thorne.

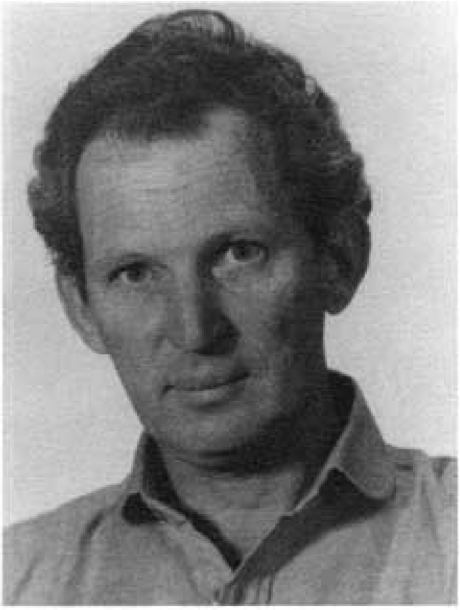

Figure 10.21 The Danish botanist Rolf Dahlgren (1932-1987).
Courtesy of the Botanical Museum and Herbarium, Copenhagen.

ancient paper clips left by his predecessor, Mr. Maxon. He placed these on a fiber board on his office wall, gave them descriptive names, and arranged them along morphological evolutionary lines in a "phylogenetic bush" of the fictional class Papyroclippopsida. Those paper clips manufactured before 1900 are below the recent fossil line; those manufactured after are above. Some evolutionary lines became extinct; others, such as the newer plastic ones, have no fossil record. A predator enters the picture in the form of a staple remover. A phylogenetic joke? Yes, but the above point is emphasized.

A reflection on the various classification systems reveals that for almost 300 years botanists have attempted to show a natural view of the botanical world. As time progressed, along with knowledge and evidence, various ideas and concepts were proposed, accepted and built upon, or rejected. Botanists working in different countries and disciplines added to the pool of information. Interestingly, different individuals working independently reached similar conclusions. This was to be expected because each botanist should ultimately be using the same data base for information.

In spite of what appears to be many workers developing morphological classification schemes, very few individuals are really involved on a worldwide basis. Most younger botanists prefer to address less speculative issues. As a result, the "champions" of morphological botanical classification may soon be leaving the botanical scene without many younger workers taking their places. Why? Further reflection may be in order. Today, more than at other times in botanical history, intelligent, inquisitive young people have many other areas of botany (or biology for that matter) in which to work. This was not the case in years past. Research funding from various granting agencies (whether private or public) also reflects this trend, with large sums of money going to support contemporary experimental, chemical, and molecular research and less support being given for more speculative, morphological issues.

In spite of this contemporary trend, there are some encouraging signs: (1) During the past 40 years there has been an explosion of various types of botanical knowledge, especially in molecular systematics, which has been used in constructing recent classification systems. This will be discussed in more detail later in this chapter. (2) The origin of the systems has taken on an international flair: American, Swedish, English, and Soviet Armenian. (3) A cooperative influence can be seen in each system—in the ways each author of a system has influenced another and in their phylogenetic ideas and conclusions. The openness and undogmatic interchange of ideas and theories today can only enhance and encourage thinking young minds to begin to explore unanswered questions of how, when, where, and why.

CONTEMPORARY PHENETIC METHODS

The classification systems discussed thus far in this chapter were based on observations of a small or large number of characters with the intuitive ordering of the individuals or taxa into groups that convey a relationship. However, most modern systematists prefer to follow a methodological approach to classification.

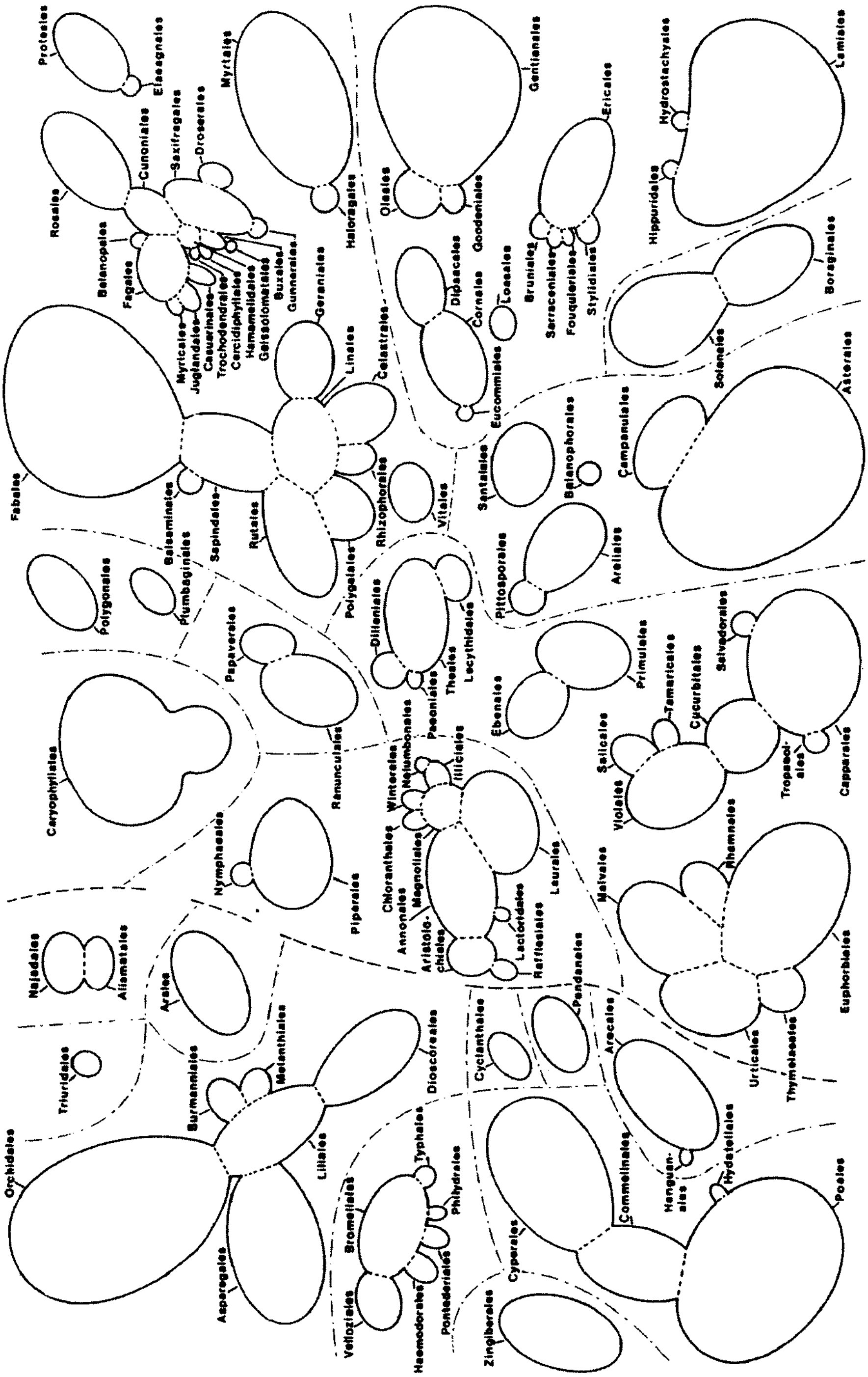

Figure 10.22 Diagram, published after Dahlgren's death, showing his and his wife's views of angiosperm classification of superorders and orders. From G. Dahlgren, 1989. Used by permission of Academic Press Inc. (London) Ltd. and G. Dahlgren.

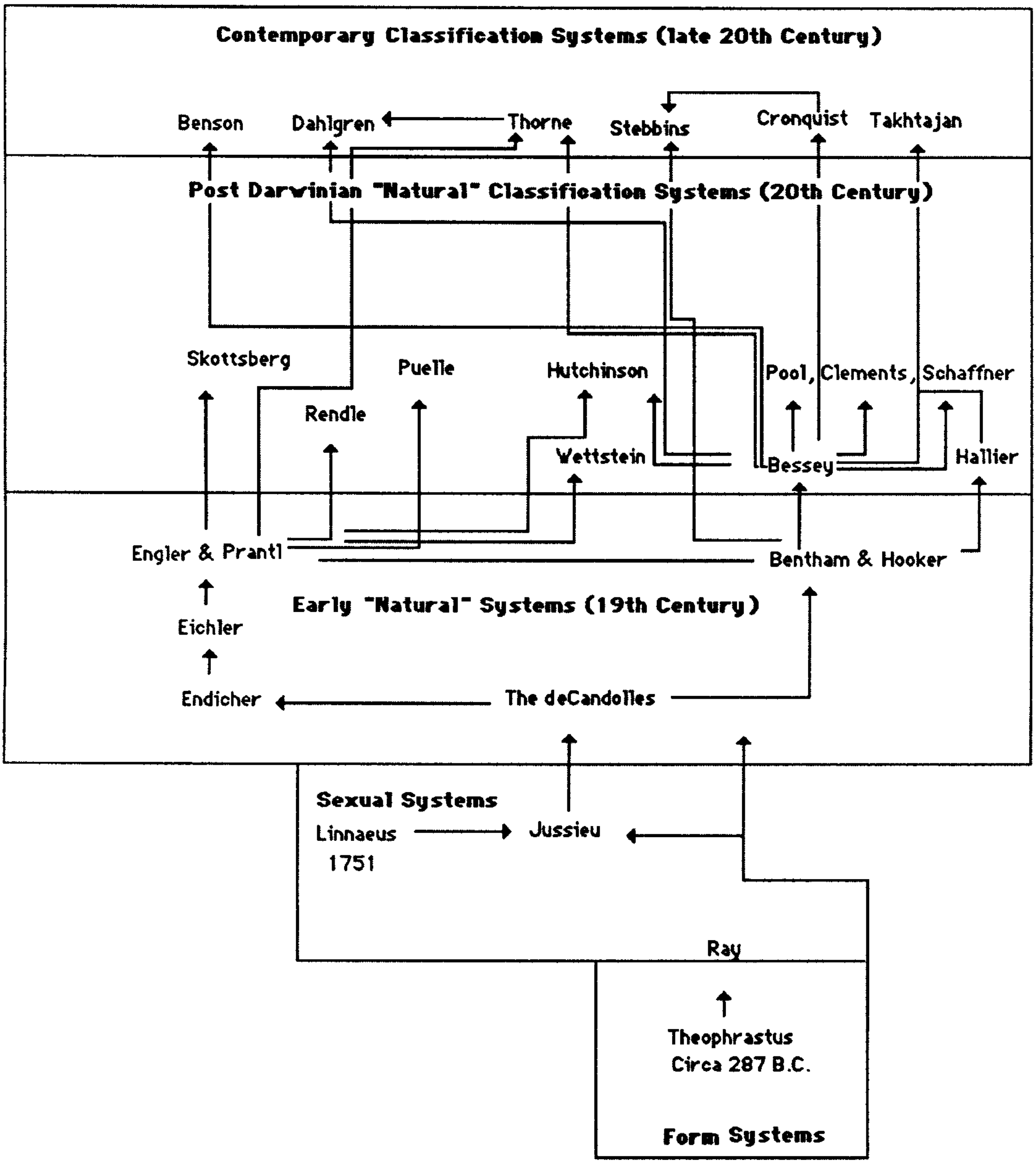

Figure 10.23 Outline of various authors' attempts to develop a "natural" system of classification for the flowering plants. Arrows indicate the interrelationships of the systems.

One approach is the **phenetic classification** method that seeks to express natural relationships based on similarities between characteristics of organisms. This is done without consideration of origin or evolutionary significance. The resulting similarity may appear to be practical and "natural," but may not reflect evolutionary or genetic history. The methods do not produce new data or new classification principles, but are methods of reorganization and presentation of information.

The beginning of this view towards classification developed in the 1950s and 1960s around numerical methods of analyses and the development of computers, and became known as **numerical taxonomy** or **taximetrics**. The

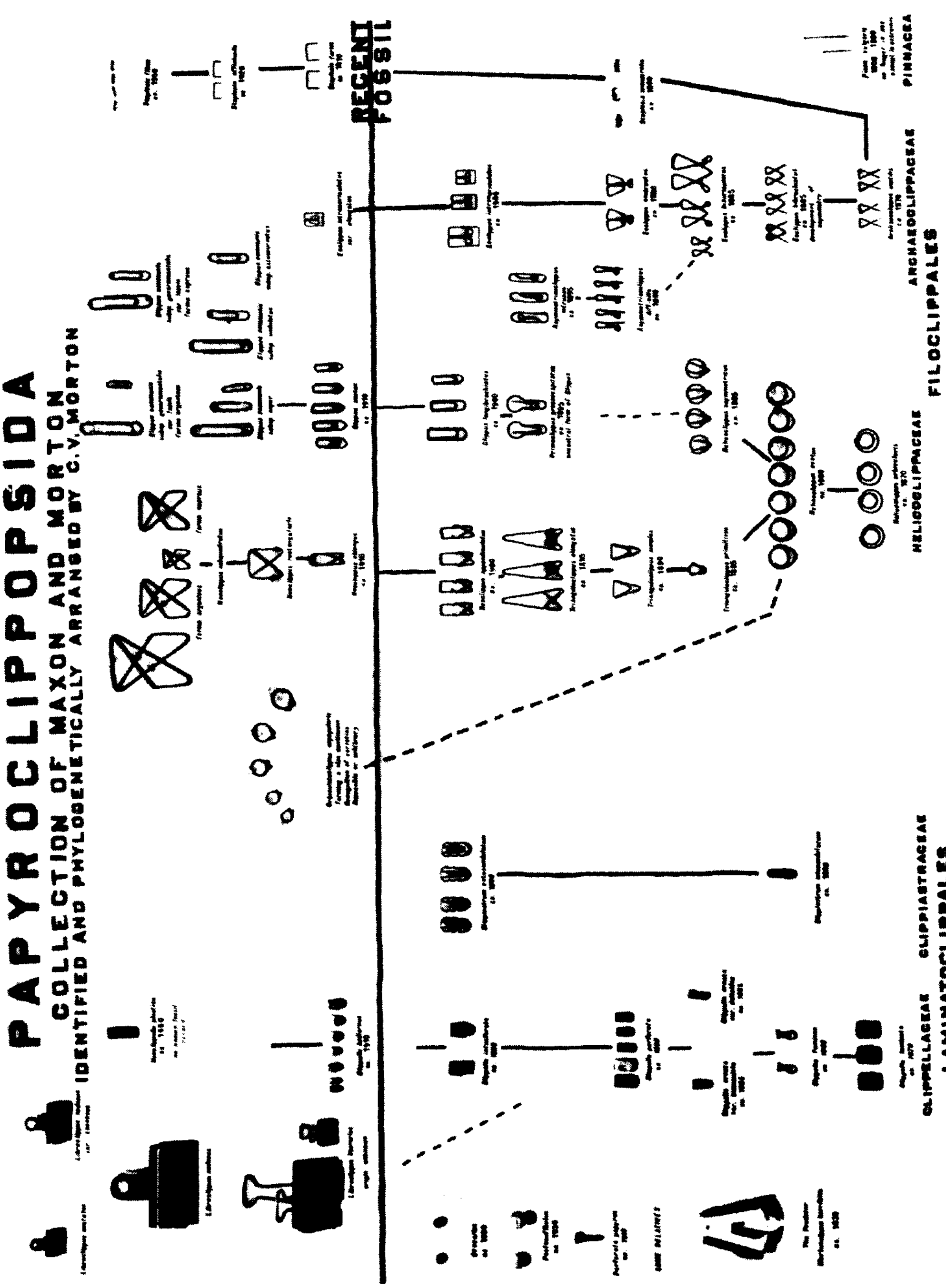

Figure 10.24 "Phylogenetic bush" of the class Papyroclippopsida by C. V. Morton.

principles were championed by P. H. A. Sneath and R. R. Sokol in their work *Numerical Taxonomy* published in 1973.

Proponents of numerical taxonomy emphasized the following seven basic principles: (1) Systematics is no longer viewed as a deductive or interpretive science, but an empirical one. (2) Each character is considered to be of equal weight (*a priori*) with every other character when creating natural taxa. This is done to reduce subjectivity of the data. Some botanists claim that weighting of characters should be allowed because certain characteristics are obviously more important for plant survival than others (e.g., reproductive features are more important than the number of teeth on the margin of a leaf). (3) The greater the number of characters upon which the analysis is based, the better the resulting classification. Usually 100 or more characters are considered a minimum. (4) A function of the similarity of two entities is reflected in their overall similarity. Care must be exercised to be certain that homologous characters are being compared. (5) Distinct taxa are recognized because correlations of characters differ in the taxa being studied. (6) From the character correlations of groups based on particular evolutionary assumptions, phylogenetic relationships can be made. (7) The resulting classifications are based on phenetic similarity.

The basic units of numerical taxonomy are the **Operational Taxonomic Units** or **OTUs.** This is the term given to the lowest ranking taxon in any particular study. The investigator may choose individuals, species, genera, families, or other taxonomic units that are as representative as possible of the unit chosen.

Characters of the OTUs should be chosen from as wide a range of variation as possible: preferably 100 or more are needed to develop a repeatable and reliable classification.

The equally weighted characters selected are coded generally in a simple all-or-none way (+ or - ; or 0 and 1), in which each character is said to exist in only two states. This codification is called a two-state or binary system. For example, leaves may have stipules present or absent, or the corolla with hairs in the throat versus corolla throat glabrous. Other characters are **multistate**, having more than two continuous characters (e.g., corolla blue, orange, red, yellow, or white). A subjective decision must then be made to convert multistate characters into binary characters (e.g., corolla colored versus corolla white). This subjectivity detracts from the objectivity of the taximetric methodology.

The information is then arranged in a similarity or matrix diagram. Here the measurement of similarity (S) is calculated by a computer program that compares each OTU with the attributes of every other OTU. The computer clusters or sorts out the OTUs according to their most similar attributes. This is obtainable by a table of similarity or dissimilarity coefficients. This process is called **cluster analysis**. The resulting visual cluster analysis is portrayed as a **dendrogram** or **phenogram** of phenetic relations (Fig. 10.25). The dendrogram allows for the visualization of the phenetic relationships, in which OTUs that are most similar are linked at higher coefficient levels (e.g., 0.9 or 90%), with less similar OTUs linked at successively lower levels. Arbitrarily fixed coefficient levels of similarity applied to particular taxonomic ranks can be used to objectively classify taxa. This dendrogram (Fig. 10.25) shows that the populations of taxa S. and H. cluster together and are most similar, while the populations of the other taxa are more variable and less similar.

The above discussion has been greatly oversimplified in an attempt to introduce the basic concepts of phenetic classification. The interested student should refer to Sneath and Sokol (1973) for an in-depth discussion of the subject.

The methods of numerical taxonomy have been helpful in providing a refinement of existing classification systems and reclassification above the family level. Taximetrics have been criticized by many systematists who are reluctant to allow a machine to make calculated taxonomic and biological judgments in place of the experience of botanists. On the other hand, the methods of numerical taxonomony are becoming more and more helpful in comparing large sets of data in a precise manner and in computing phylogenetic hypotheses, rates, and trends within similar or between different taxonomic levels.

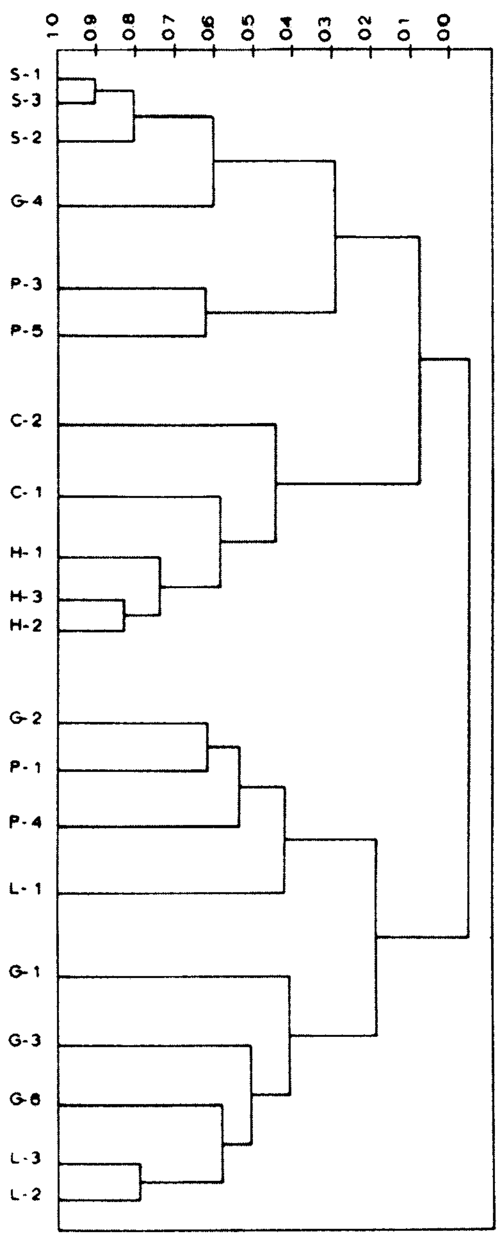

Figure 10.25 Two-dimensional dendrogram showing clustering of biotypes of native North American *Urtica* grown under natural field conditions. Abbreviations: C = U. *californica*, G = U. *gracilis*, H = U. *holosericea*, L = U. *lyallii*, P = U. *procera*, and S = U. *serra*. Numbers with the letters represent populations. The numbers at the top indicate the coefficient levels at which the populations are linked. The vertical lines connecting populations show the closest coefficient of association.

CONTEMPORARY PHYLOGENETIC METHODS

At about the time Sneath and Sokol were developing their phenetic methods of numerical taxonomy, another numerical approach was hypothesized. During the 1950s a German zoologist, Willi Hennig, proposed a new classification method. His new phylogenetic methods differed markedly from other concepts. The methodology, now known as **cladistics**, attempted to objectively analyze phylogenetic data in strict, repeatable methods. Independent of Hennig's work in Europe, the American botanist Warren H. Wagner, Jr. was developing a convergent approach to construct phylogenetic trees, called **groundplan-divergence**. Wagner's effort was an attempt to understand the amount and direction of evolutionary change and the diverse branching portrayed. Both Hennig and Wagner's ideas appeared to be unrelated at first; but after the connection was made in the late 1960s, Wagner's concepts became the basis for the methodology.

Two basic approaches developed from these two philosophies: (1) the principle of parsimony—the most likely evolutionary route is the shortest hypothetical pathway of change that explains the pattern under observation; and (2) **character compatibility** studies—each character is examined to determine the proper sequence of character state changes that take place as evolution progresses. Contemporary cladists determine ancestral and derived states of characters and define evolutionary lineages (or **clades**) by shared derived characters. The analyses can be undertaken within the group studied (called **in-group**) or conducted with outside relatives (**out-group**).

In parsimony and character compatibility methods, **cladists** (biologists who practice the methods of cladistics) consider the similarity used by the pheneticists as not necessarily implying phylogenetic relationship. The classifications emphasize **monophyletic** groups (groups that have arisen through diversification of a simple ancestor) involving **homologous** shared and derived charcters. A **polyphyletic** origin considers groups originating from two or more ancestral tracks and is not recognized by the cladists.

Cladistic relationships are presented in **cladograms**, a type of branching evolutionary diagram or phylogenetic tree. In Figure 10.26, theoretical taxa A-G are all related by having a common ancestor at the stem point X. A different degree of cladistic relationship exists between each taxon. The paired taxa A and B, C and D, and F and G are separated by only one divergence before common ancestries are retraced. Proper interpretation of the cladogram takes into account the number of divergences connecting different branches and the time of origin of one taxon to another. Other methods may also be considered.

An application of cladistic methodology was applied to the relationship of various subgenera within the genus *Rhododendron*, tribe

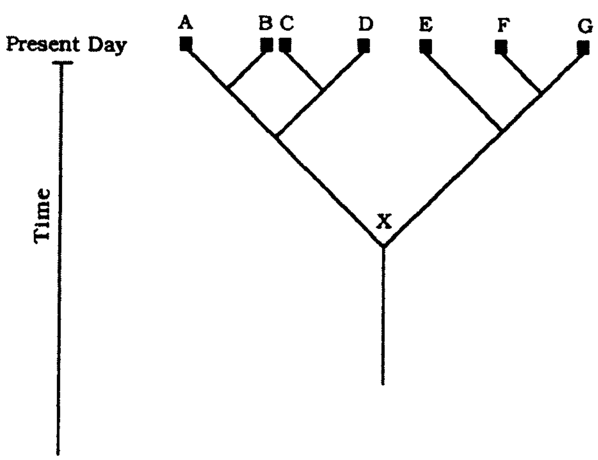

Figure 10.26 Cladogram showing phylogenetic relationships between seven hypothetical taxa.

Rhodoreae, in the family Ericaceae (Kron and Judd, 1990). The resulting cladograms shown in Figure 10.27 support (A) a monophyly of the taxa studied and (D) the polyphyly hypothesis. The numbers on the cladogram are the coded characters used in the analyses.

In the groundplan-divergence methods, Dr. Warren H. Wagner, Jr., the originator of the method, hypothesizes an ancestor for the taxonomic group. Evolutionary modifications from this ancestor are then measured using (1) the number of changes from the ancestral condition,

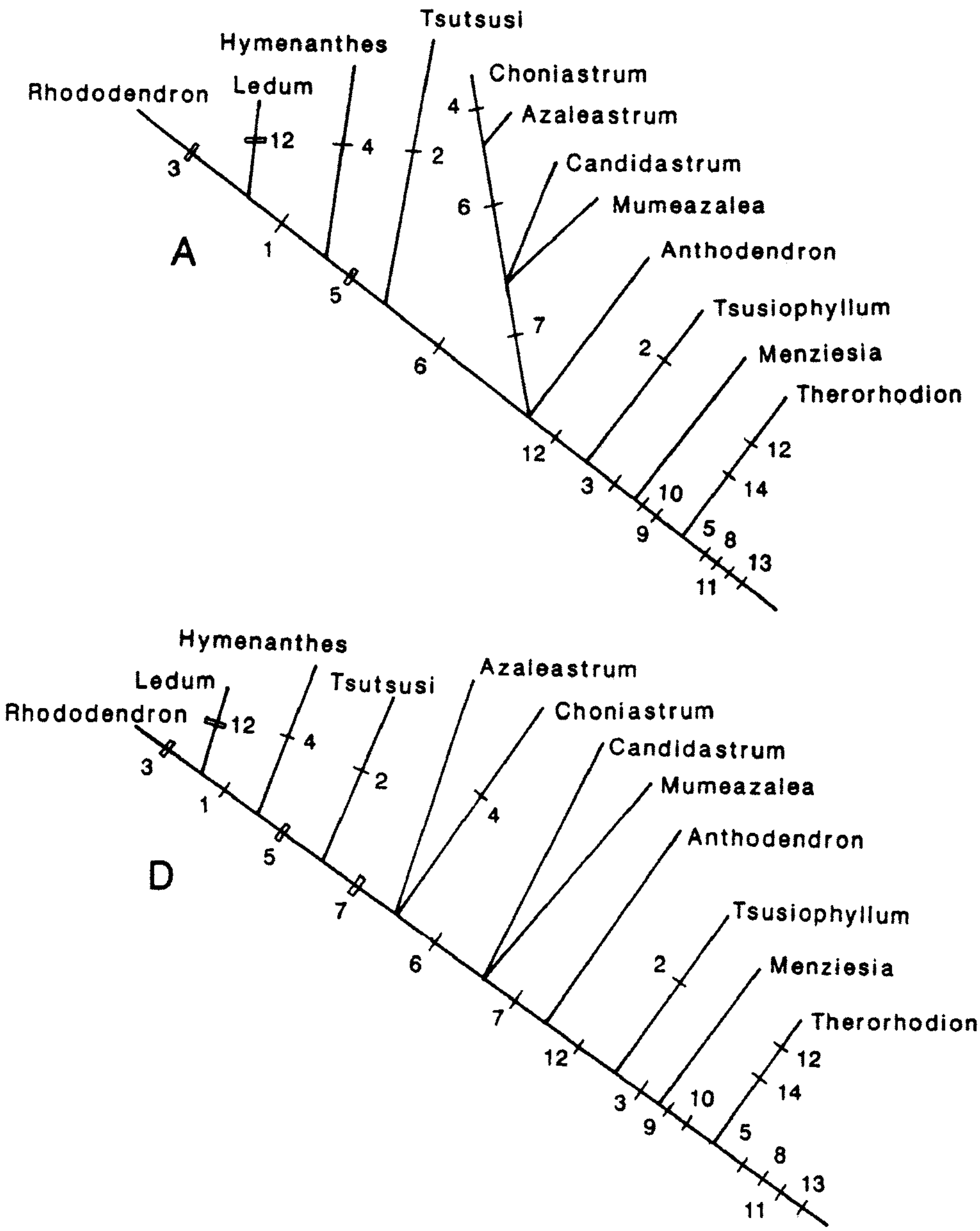

Figure 10.27 Cladograms resulting from analysis of the tribe *Rhodoreae* of the genus *Rhododendron* supporting both monophyly (A) and polyphyly (D).
From Kron and Judd, 1990. Used by permission.

(2) the change of characters from one lineage to another, and (3) the sequences of cladistic branching.

A cladogram in the shape of a bull's eye with concentric rings has phylogenetic relationships plotted on it. The concentric rings represent stages in advancement from the hypothesized ancestor. Dots on the rings represent taxa, with more advanced taxa toward the outer rings. Lines between dots indicate lineages. The number of "advanced" character states (**apomorphy**) evolving with the taxa being studied are reflected in the distance of the taxon from the hypothesized ancestor. Taxa that advance independently show divergence. So-called primitive character states (**plesiomorphy**) may also be recognized.

In Figure 10.28, taxa B, C, D, H, K, and L are the most equally advanced from the hypothetical ancestor, but each has its distinctive characters. Taxon F is less advanced than E, J is less than I, and I is less than H and K. The features of J and I are shared with taxa H and K. Taxa B, C, and L have no ancestor with recognizable features at the level indicated.

During the 1980s and 1990s, cladistic analyses based on evidence from molecular systematics and newly used morphological features (e.g., pollen, chemicals, etc.) have not supported the traditional classification views of flowering plants held by Cronquist, Takhtajan, Thorne, and others. Instead, the traditional groupings of dicots and monocots have been changed considerably. This change has been most recently presented as a group effort, the "Angiosperm Phylogeny Group." This group of botanists published a summary ordinal classification to 462 rearranged families in 40 putatively monophyletic orders, a number of monophyletic "informal higher groups" and a listing of families without any assigned order (APG 1998). These plant groups are the monocots, commelinoids, eudicots, core eudicots, rosids (including eurosids I and II), and asterids (including euasterids I and II) (Fig. 10.29).

A close inspection of the summary scheme quickly reveals that the ordinal names do not have the same naming or grouping of families as earlier classification systems, and that recognition is given mostly to families that are considered monophyletic in origin, while admitting other families are non-monophyletic. The botanists pushing this new clade-based system are attempting to blend the Linnaean classification concepts of paraphyletic taxa with monophyletic ones. This has not gone unnoticed or challenged (see Brummit 1997). The argument is put forth that the clade-based systems are incompatible with traditional Linnaean classifications and nonsensical and disruptive to existing systems and nomenclature. Because of the newness of these ideas, we have not heard the end of this classification controversy, and the botanical debate is sure to carry on through the early parts of the 21st century.

The above contemporary methods are not without criticism on various argumentative

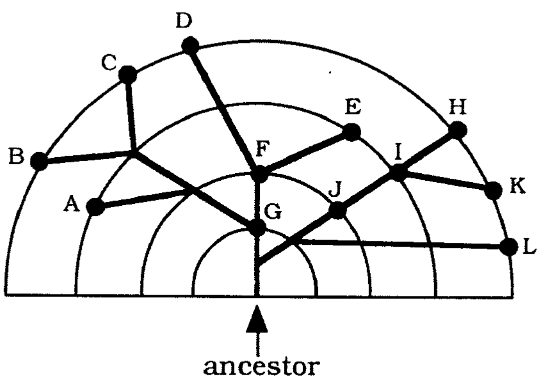

Figure 10.28 Cladogram of a Wagner groundplan-divergence ("Wagner tree") showing the phylogenetic relationship between twelve taxa and the hypothetical ancestor taxon.

points. However, any new method of classification giving insight into a better understanding of evolutionary pathways is worthy of exploration. The student must remember that "...phylogenetic trees are hypotheses, not facts. Our ideas about the relationships among organisms change with increasing understanding" (Wiley et al. 1981).

How well the new ideas will be accepted remains to be seen as it may be too soon to tell; after all, the summary of the new family and ordinal scheme has only been available to the botanical community for a short time. Yet, one systematic text has embraced the new ideas completely and applied them to an instructional level (Judd et al. 1999).

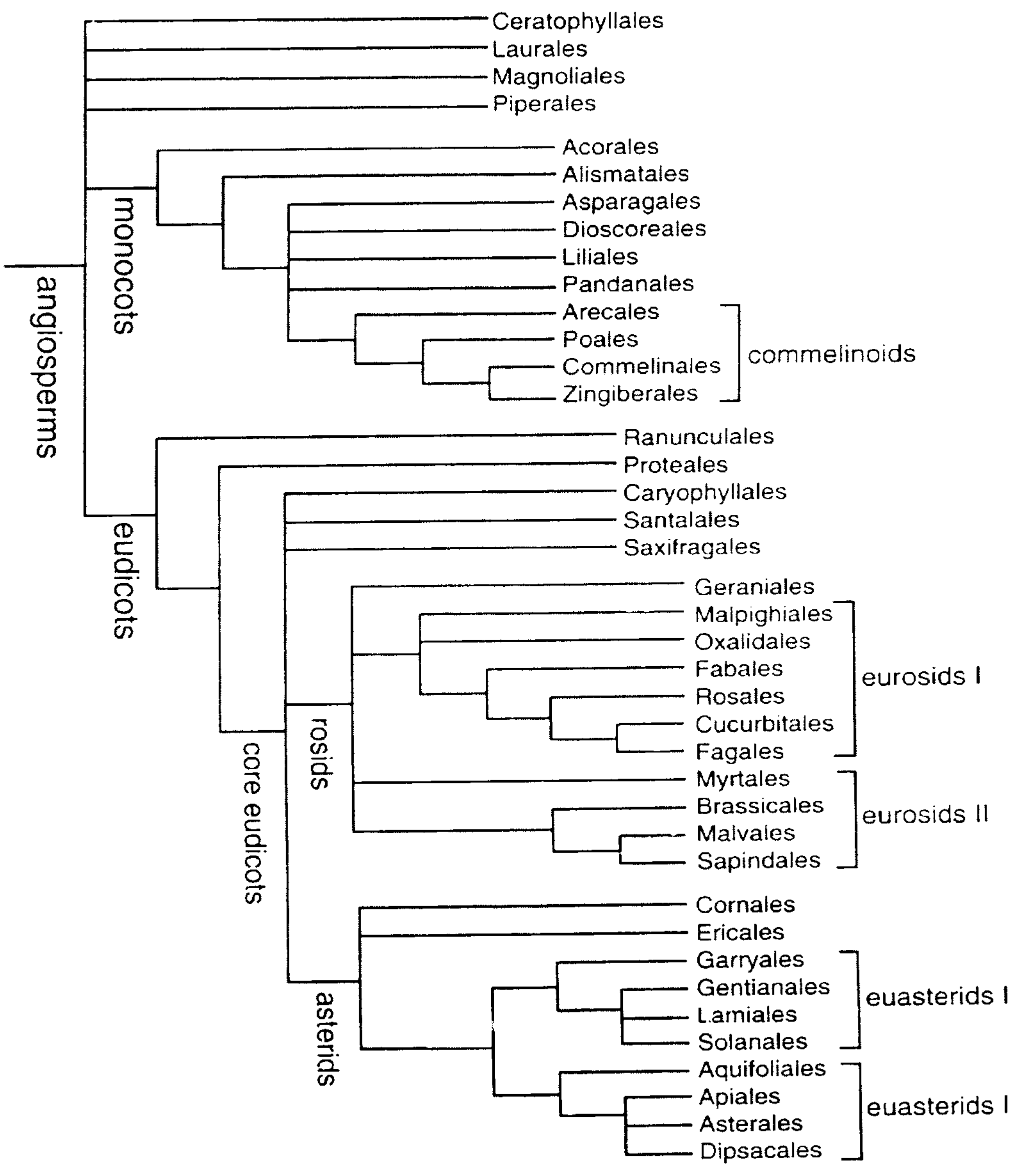

Figure 10.29 An ordinal cladogram classification to 40 putative monophyletic orders of flowering as perceived recently by the "Angiosperm Phylogeny Group."
From APG 1998.