Taxonomy, Classification, and the Debate about Cladistics[1]

Plant taxonomy is the science that deals with the *identification, nomenclature,* and *classification* of plants. The term plant systematics (or systematic botany) is often used synonymously with plant taxonomy (as is done here) but sometimes has the connotation of mainly using recently developed techniques such as chromosomal studies, electron microscopy, or molecular biology to answer questions about plant relationships. From the definition of plant taxonomy, it follows that the primary goals of the discipline are to:

- 1) identify and describe all the various kinds of plants;
- 2) develop a uniform, practical, and stable system of naming plants—one that can be used by both plant taxonomists and others needing a way to precisely communicate information about plants [The naming system for plants follows the International Code of Botanical Nomenclature (Greuter et al. 1994)]; and
- 3) arrange plants with common characteristics into groups that reflect their relationships—in other words, to develop a scheme of classification that is useful. Similar species are thus put into the same genus, similar genera into the same family, etc. (Lawrence 1951; Porter 1967; Radford et al. 1974; Jones & Luchsinger 1986).

Since the time of Darwin, a primary goal of plant taxonomists has been to reflect phylogeny or evolutionary history in the system of plant classification. While this basic premise is agreed on by virtually all botanists, in recent years there has been heated debate between two main schools of taxonomists:

- 1) traditional taxonomists practicing what is sometimes referred to as "Linnaean classification" (Brummitt 1997), a system based on a hierarchy of formal ranks (e.g., family, genus, etc.) and binomial nomenclature (two-part scientific names consisting of a genus name and specific epithet); and
- 2) cladists (whose method of constructing phylogenies is based on the work of the German entomologist Willi Hennig) practicing phylogenetic classification (referred to as cladonomy by Brummitt (1997)). It should be noted that in a clade-based classification system, there are no formal ranks, including the genus, and no binomial nomenclature (de Queiroz & Gauthier 1992; Brummitt 1997; Lidén et al. 1997; Cantino 1998).

In some cases, the classification systems produced by traditional taxonomists and cladists are similar. However, as a result of their different methods, in many instances the classification and nomenclature systems produced are quite different.

Traditional taxonomists, while attempting to have a classification system based on evolutionary relationships, also try to reflect the amount of evolutionary change undergone by groups. They argue that classification is "... more than just branching patterns of evolution" (Stussey 1997). To use an animal example discussed in more detail below, because birds are so different from other vertebrates (e.g., fly, have feathers), they are treated as a different class of animal even though they evolved *from within* the class known as reptiles. Traditional taxonomists also try to incorporate other goals, including practicality and stability, into the classification system (see Brummitt (1997) for a detailed discussion of traditional classification). An example of a classification system produced by a traditional taxonomist can be seen in the work of Cronquist (1981, 1988) whose classification of flowering plants is given (with modifications) in Appendix 2.

The basic goal of cladistics (often referred to as "phylogenetic systematics"), and the only one that is considered important, is that classification should reflect the branching pattern of evolution. Thus one of the central principles of cladistics is that only monophyletic groups (= a common ancestor and all

[1]Reprinted from Diggs et al. (1999).

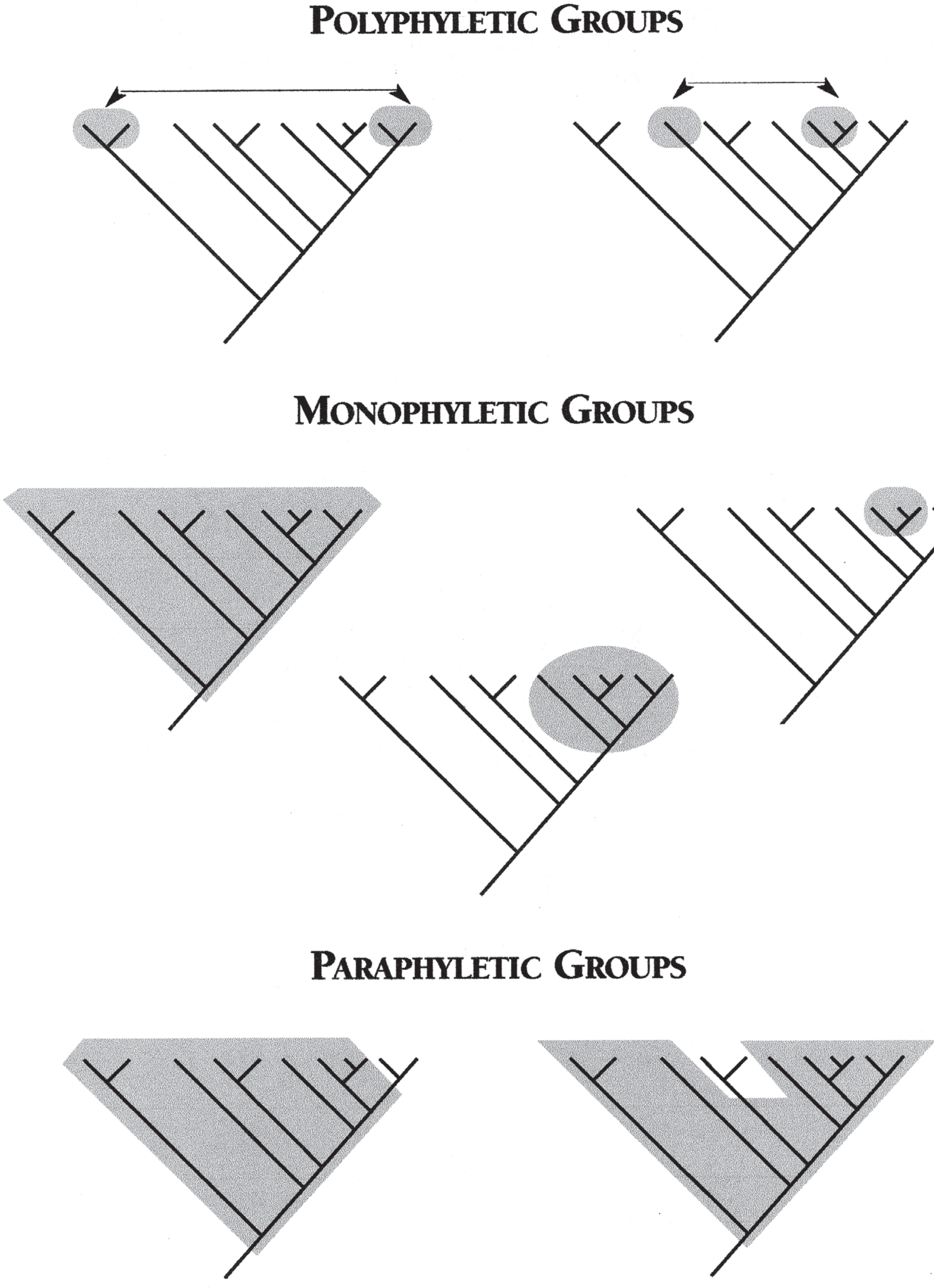

FIG. 176/DIAGRAMMATIC REPRESENTATION OF POLYPHYLETIC, MONOPHYLETIC, AND PARAPHYLETIC GROUPS. FIGURE PRODUCED BY BRIT/AUSTIN COLLEGE; REPRODUCTION OF THIS IMAGE DOES NOT REQUIRE COPYRIGHT PERMISSION.

its descendants) should be given taxonomic recognition (Fig. 176). These groupings should be based on shared derived characteristics or character states, which are referred to as synapomorphies. Every organism is a mosaic of ancestral characteristics (= pleisomorphies) inherited with little or no change from some remote ancestor and derived characteristics (= apomorphies), which reflect more recent evolutionary change (Futuyma 1986). Apomorphies are thus characteristics that have changed evolutionarily and are different from the characteristics of a distant ancestor. All of the species that share an apomorphic characteristic are considered to be derived from a single common ancestor (because they inherited the derived characteristic from that common ancestor). The derived/apomorphic characteristic that they share is referred to as a synapomorphy. Mammals are thus considered a monophyletic group because they share a number of synapomorphies (e.g., produce milk, have hair, are warm-blooded) that were inherited from the common ancestor of the mammals. The unique 4+2 arrangement of stamens in the mustard family is another example of a synapomorphy; this derived characteristic occurred in the ancestor of all the mustards and is shared by, and only by, members of that family. According to cladists, only this type of shared derived characteristic provides evidence of phylogenetic relationships, and therefore only these characteristics should be used in developing a classification system. They say that shared ancestral characteristics—those characteristics two organisms share because they have been retained from a distant common ancestor—do not accurately reflect recent relationships and should therefore not be used. For example, humans and lizards share the ancestral characteristic of four limbs; snakes, however, have no limbs—legs were lost relatively recently in the evolutionary line leading to snakes. Just because humans and lizards have retained the four limbs found in our common vertebrate ancestor does not mean lizards are more closely related to us than lizards are to snakes. In fact, lizards and snakes are closely related (Fig. 177) and have a number of shared derived characteristics that link them.

According to cladists, polyphyletic groups (containing taxa descended from more than one ancestor) and paraphyletic groups (including the common ancestor and some, but not all, of its descendants) should not be recognized (see Fig. 176 for these situations). Further, relationships based on overall similarity (a methodology referred to as phenetics) are not formally recognized—just because two groups appear similar does not necessarily mean they are closely related evolutionarily. For example, the cacti (Cactaceae) and euphorbs (Euphorbiaceae) both have large, desert-adapted, succulent species that are superficially almost indistinguishable but very distantly related evolutionarily. These similarities are due to convergent evolution, a process by which distantly related, or even unrelated, species evolve similar adaptations in the face of similar selection pressures (such as desert-like conditions).

As indicated above, traditional taxonomists since the time of Darwin have attempted to reflect phylogeny in their systems of classification. However, they have used somewhat different methods from cladists—not only shared derived characteristics, but also shared ancestral characteristics have been utilized. Further, in addition to monophyletic groups, paraphyletic groups often have been recognized if they could be defined phenetically. In fact, our current plant classification system contains numerous examples of paraphyletic groups. The evolutionary tree in Figure 178 is a theoretical example of this situation. Species A, B, C, D, and E are all similar morphologically; species F, however, because of adaptation to some extreme environment (e.g., desert), has become very different morphologically. This phenetic difference of species F is reflected in Figure 178 by its distance from the other species. Traditional taxonomists have in general placed species A, B, C, D and E in one genus, and species F in another. Cladists would argue that this is unacceptable because E and F are more closely related than any of the others (they share the most recent common ancestor); the group A, B, C, D, and E is unacceptable because it is paraphyletic. Either A, B, and C have to be put in one genus and D, E, and F in another, or all six have to be put in the same genus. Traditional taxonomists might counter that these solutions do not reflect the tremendous amount of evolutionary change undergone by species F; they in some cases argue that because F is so different phenetically, it should be recognized as a separate group. An actual example can be seen in the case of the Asclepiadaceae (milkweeds) and Apocynaceae (dogbanes), two families recognized by traditional taxonomists (Fig. 179). The milkweeds, like our theoretical species F, are quite distinctive morphologically and, indeed, are widely recognized as monophyletic. However, when cladistic methods are applied, it becomes readily apparent that the Asclepiadaceae are a monophyletic branch derived from within the Apocynaceae, making the dogbane family (with milkweeds excluded) paraphyletic (like our

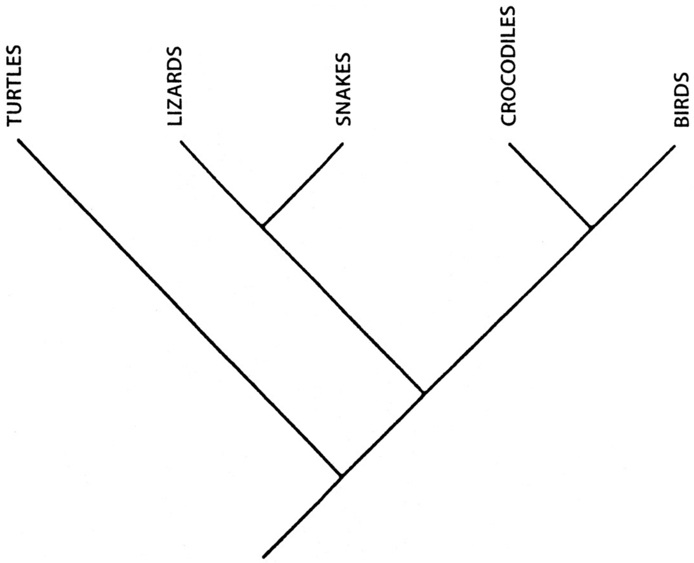

FIG. 177/DENDROGRAM SHOWING RELATIONSHIPS OF SOME VERTEBRATE GROUPS. NOTE THE PARAPHYLETIC NATURE OF THE "REPTILIA." FIGURE PRODUCED BY BRIT/AUSTIN COLLEGE; REPRODUCTION OF THIS IMAGE DOES NOT REQUIRE COPYRIGHT PERMISSION.

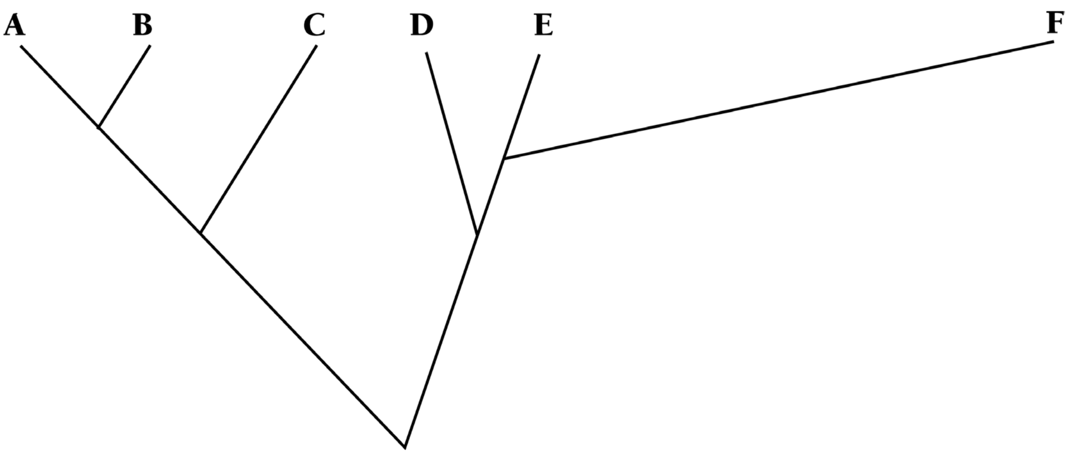

FIG. 178/PHENETIC DISTANCE DIAGRAM; HORIZONTAL DISTANCE BETWEEN SPECIES INDICATES PHENETIC DIFFERENCE. NOTE THAT SPECIES F, WHILE MOST CLOSELY RELATED PHYLOGENETICALLY TO SPECIES E, IS QUITE DIFFERENT IN TERMS OF PHENETICS. FIGURE PRODUCED BY BRIT/AUSTIN COLLEGE; REPRODUCTION OF THIS IMAGE DOES NOT REQUIRE COPYRIGHT PERMISSION.

group A, B, C, D, and E, or like the reptiles with the birds removed). From the cladistic standpoint, the two families thus have to be lumped together into a single more inclusive Apocynaceae (the choice of which name to use is based on the rules of botanical nomenclature) (Judd et al. 1994). To the distress of many traditional taxonomists, the name Apocynaceae is thus used in a very different sense than previously. Traditional taxonomists argue that confusion results from such name changes and that clearly defined and easily recognized groups such as the Asclepiadaceae should be retained. The cladists, on the other hand, emphasize that the methods used by traditional taxonomists result in groups that do not reflect, and in fact actually distort, our understanding of evolutionary history. Cladists further stress that there are specific objective rules by which their characters are chosen and used. Consequently, they consider the results of their analyses repeatable, and in comparison with traditional taxonomy, less subjective.

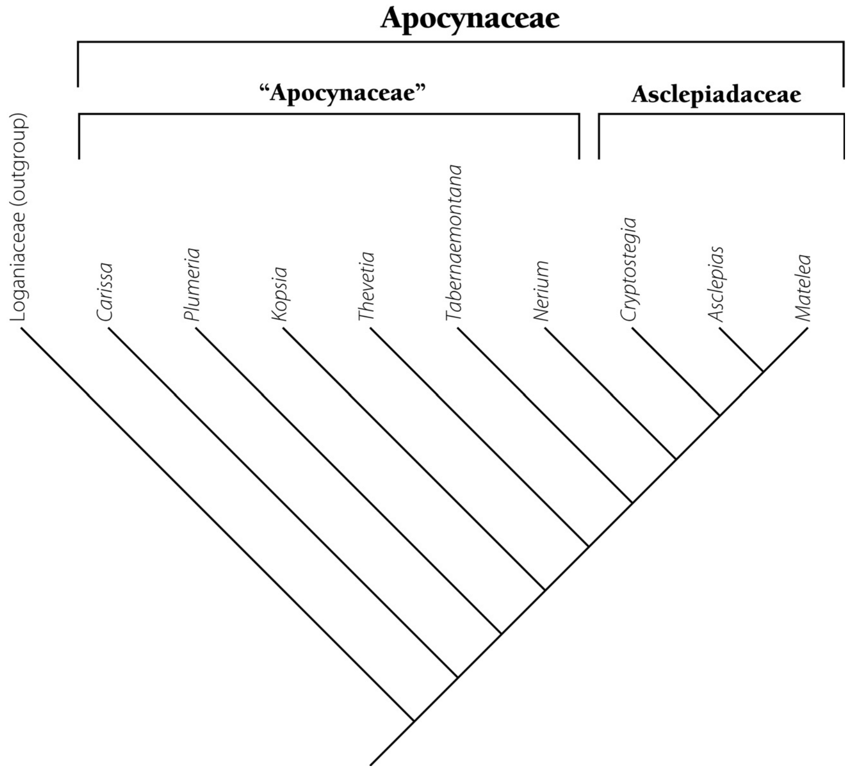

Fig. 179/Dendrogram showing relationship of two closely related families, the "Apocynaceae" and the Asclepiadaceae (modified from Judd et al. (1994); used with permission of the President and Fellows of Harvard College and W.S. Judd).

However, it should be noted that numerous assumptions have to be made in carrying out a cladistic analysis. In particular, because assumptions have to be made as to which character states are derived and which are ancestral, cladistic analyses are subject to various interpretations. Further, in several recent articles (e.g., Brummitt 1997; Sosef 1997) the argument has been made that in a hierarchical system of classification such as that used by plant taxonomists, paraphyletic taxa are inevitable and that a completely cladistic system of classification would be impractical to the point of being nonsensical.

The results of these differing viewpoints are perhaps even more dramatically seen in the case of well known major animal groups. The widely recognized class Reptilia (reptiles) is actually paraphyletic, with turtles representing an early branch and birds arising from within the main body of the group (Fig. 177). Even though birds are very different from other members of the group in many ways (e.g., warm-blooded, have feathers, fly, lack teeth), birds and crocodiles are more closely related to one another than crocodiles are to other reptiles; in other words, from an evolutionary standpoint we should no longer recognize a formal group Reptilia. Some traditional taxonomists argue that the amount of evolutionary change, practicality, stability, and tradition in such cases should override phylogeny, while cladists stress the overwhelming importance of accurately reflecting evolutionary history. In any case, at the very least the recognition of the paraphyletic Reptilia de-emphasizes evolutionary history, such as the close relationship between crocodiles and birds.

This controversy over cladistics is currently very heated, with clearly articulated positions on both sides. Welzen (1997) for example argued that the outdated "Linnaean system" should be abandoned, and de Queiroz (1997) stated, "The Linnaean hierarchy has become obsolete." De Queiroz (1997) also indicated that the "... next stage in the process of evolutionization [of taxonomy] will extend a central role for the principle of descent into the realm of biological nomenclature." Cantino (1998) stated that "Phylogenetic nomenclature is the logical culmination of a revolution that began with Darwin. ..." On the other side of the controversy, Brummitt (1997) and Sosef (1997) argued (as indicated above) that paraphyletic taxa are inevitable and that cladistics is unable to cope with the reticulate evolutionary relationships seen in some groups. They further stated (Brummitt & Sosef 1998) that "... attempts to eliminate paraphyletic taxa from Linnaean classification are logically untenable." For a discussion of some of the methodological, conceptual, and philosophical problems associated with cladistics, see Stuessy (1997); for a discussion of the importance of consistently applying cladistic methods and thus bringing an evolutionary perspective to biological classification and nomenclatural systems, see de Queiroz (1997).

Three things seem clear regarding the controversy:

- 1) This argument over cladistics will not easily or quickly be laid to rest, and thus a clear understanding of cladistic methodology and results is important. Further explanation of cladistics can be found in standard works on plant taxonomy such as Zomlefer (1994), Walters and Keil (1996), and Woodland (1997), or in evolutionary biology texts such as Ridley (1996).
- 2) The implementation of cladistic methodology would result in systems of classification and nomenclature radically different from those currently used; all the implications are not yet clear, but levels in the current hierarchy such as family or genus would no longer have meaning. In fact, if cladistic principles are consistently applied, it will be necessary for the binomial system of nomenclature to be abandoned (de Queiroz & Gauthier 1992; Lidén et al. 1997; Cantino 1998). The potential loss of nomenclatural stability is particularly disturbing to many taxonomists. Detailed discussions of some of the implications can be found in recent articles (e.g., Brummitt 1997; Crane & Kendrick 1997; de Queiroz 1997; Kron 1997; Lidén et al. 1997; Nicolson 1997; Sosef 1997; Stuessy 1997; Welzen 1997; Freudenstein 1998; Backlund & Bremer 1998; Brummitt & Sosef 1998; Cantino 1998; Sanders & Judd 1998; Schander 1998a, 1998b; Welzen 1998).
- 3) Our knowledge of phylogenetic relationships, despite the advances of molecular biology, is still incomplete, and thus all the necessary information for a completely phylogenetic classification system is not yet available. In fact, many groups are poorly known and for some, "... cladistic analysis can yield only the most tentative of hypotheses, subject to drastic change as new relatives are encountered" (Stuessy 1997). There are also methodological problems concerning how the characters used in cladistic analyses are chosen and analyzed (Stuessy 1997). The result can be instability in classification, and more problematically, in nomenclature, if it is linked to a rapidly changing cladistic classification system.

Because of both philosophical and practical implementation problems, Brummitt (1997) pointed out that while the controversy should be debated, it seems unlikely that "Linnaean classification" will soon be abandoned. Brummitt (1997) suggested that both a "Linnaean classification" system and a clade-based phylogeny are desirable because they have different functions. He argued that both be allowed to exist side by side and that the nomenclature of the two should be easily recognized as different (Brummitt 1997). In summarizing his ideas he stated, "... we should not follow traditional practices just because they are traditional, but neither should we adopt new ideas just because they are new. We need to understand the possibilities and appreciate the different objectives and functions of the different options. In the meantime, it seems to me and to many others that the compromise of maintaining Linnaean classification but trying to eliminate paraphyletic taxa is nonsensical and should be abandoned before any more damage is done to existing classifications and nomenclature." Lidén et al. (1997) indicated, "If applied consistently, Phyllis [cladistic methodology] will cause confusion and loss of information content and mnemonic devices, without any substantial scientific or practical advantage. ... any attempts to make Phyllis formal would be disastrous. We can find no conclusive, valid arguments against keeping the body of our current system intact." An interesting point was also made by Stuessy (1997) when he said, "... in this urgent climate of seeking to inventory the world's biota (Anonymous 1994), and requesting funds from the rest of society to do so, it would be highly counterproductive to simultaneously recommend whole-scale change of names of organisms for any reason." While strongly supporting a cladistic system, Welzen (1998) also noted that a compromise between the two types of classification is impossible. He also understood that because of practical reasons it is impossible to abandon Linnaean classification "... because too few cladograms are available to replace the existing system with a complete phylogenetic

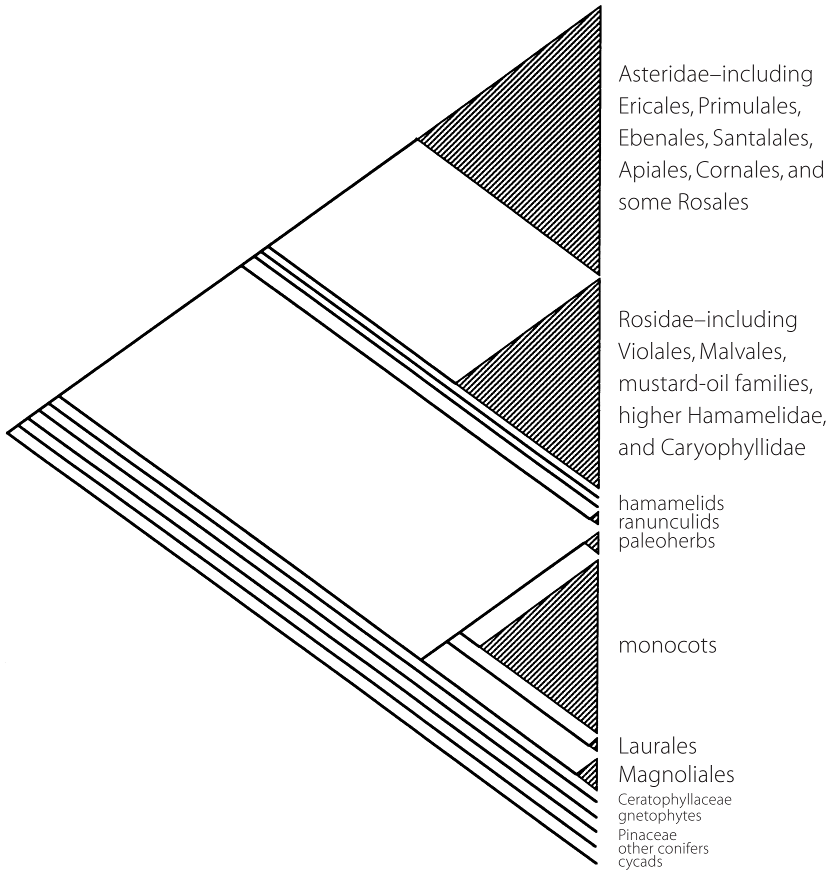

FIG. 180/MAJOR CLADES OF SEED PLANTS BASED ON DNA SEQUENCE DATA (FROM CHASE ET AL. 1993). NOTE THAT THE MONOCOTS ARISE FROM WITHIN THE DICOTS, MAKING THE DICOTS PARAPHYLETIC. USED WITH PERMISSION OF THE MISSOURI BOTANICAL GARDEN PRESS AND M.W. CHASE.

classification. Moreover, quite a few cladograms will not be that trustworthy due to the many homoplasies [result of convergent evolution] that have evolved; they will therefore, provide an unstable classification at best." Welzen (1997) went on to say, "I think, therefore, that the best solution is to choose the second option that Brummitt (1997) provides in his paper, namely, 'retaining Linnaean classification, with paraphyletic taxa, but developing alongside it an independent clade-based dichotomous system with its own separate nomenclature.' "

At present there is no complete, generally accepted, higher level cladistic analysis of the flowering plants; consequently in Appendix 2 we have given family, order, and subclass relationships based largely on the work of Cronquist (1981, 1988). While imperfect from the cladistic standpoint, it is a practical and effective way to organize thinking about plant relationships. Steps are currently being taken toward a new consensus on angiosperm relationships based on both cladistic analyses and much new evidence from molecular systematics; one such scenario is seen in Figure 180. One of the most important implications of this figure is that the monocots appear to be derived from within the dicots, making the dicots paraphyletic and thus—according to cladists—inappropriate for formal recognition. It might also be noted that the placement of the paleoherb families (such as the Aristolochiaceae, Piperaceae, and Nymphaeaceae) as branches off the line leading to monocots makes sense in terms of characteristics such as their unusual 3-merous perianth and androecium.

It is important for students to gain some understanding of the phylogenetic relationships of the various plant families. As a result, we have added notes at the end of many family descriptions (e.g., Asclepiadaceae, Apocynaceae, Brassicaceae, Capparaceae) concerning the implications of cladistics. However, while we believe this understanding is essential, we do not feel it is appropriate or even desirable to undertake a familial rearrangement on cladistic grounds in a largely floristic work such as this; consequently, in most cases traditional family boundaries have been maintained.

CATEGORIES OR RANKS IN THE HIERARCHICAL SYSTEM OF PLANT CLASSIFICATION

The system of classification used by traditional plant taxonomists and reflected in the International Code of Botanical Nomenclature (Greuter et al. 1994) results in the placement of plants into a hierarchical system with the different categories or ranks given such names as class, family, or genus. Every plant species is thus classified in the higher categories. For example, a bluebonnet (*Lupinus texensis*) is in the family Fabaceae (bean family), the subfamily Papilionoideae, the tribe Genisteae, etc. The various categories or ranks are listed below (a number of additional categories can be inserted as needed). Note that not all categories are always used; while every plant species is classified in the categories given below in all capitals (DOMAIN, KINGDOM, CLASS, SUBCLASS, FAMILY, GENUS, and SPECIES), those categories in lower case letters (Subfamily, Tribe, Subspecies, Variety, Form) are often not used.

- **DOMAIN** (sometimes referred to as Superkingdom; all eukaryotic organisms—those with nuclei in their cells—are in Eukaryota; the other two Domains are Archaea and Eubacteria)
  - **KINGDOM** (the Kingdoms include Plantae, Animalia, Fungi, etc.)
    - **DIVISION** (equivalent to Phylum in animal classification; there are nine living divisions of vascular plants; flowering plants are the Division Magnoliophyta)
      - **CLASS** (there are 2 classes of flowering plants: Monocotyledonae & Dicotyledonae)
        - **SUBCLASS** (there are 11 subclasses of flowering plants; see Fig. 173 in Appendix 2)
          - **ORDER** (this level shows relationships between families; it is rarely used by anyone except professional botanists)
            - **FAMILY** (there are ca. 387–685 families of flowering plants, depending on the system of classification used; 202 of these are found in East Texas)
              - **Subfamily** (this level is important for some families such as the Fabaceae; in other families it is not used)
                - **Tribe** (this level is important for some families such as the Asteraceae; in other families it is not used)
                  - **GENUS** (the genus name is the first part of the two-part or binomial scientific name given to each species)
                    - **SPECIES** (the genus name and the specific epithet together make up the scientific name of a species)
                      - **Subspecies** (a subdivision of a species; many species are not divided into subspecies)
                        - **Variety** (many subspecies are not divided into varieties; sometimes varieties are treated in the same sense as subspecies; in other instances the subspecies category is used for grouping varieties within a species)
                          - **Form** (used for minor differences such as flower color)

When studying plants, the most important levels in terms of organizing one's thinking are:

- 1) — Of the nine divisions of vascular plants, is the plant under study a member of Psilophyta (whisk-ferns), Lycophyta (club-mosses), Equisetophyta (Horsetails), Pteridophyta (Ferns), Cycadophyta (Cycads), Ginkgophyta (Ginkgos), Gnetophyta (Joint-firs and relatives), Pinophyta (Conifers), or Magnoliophyta (Flowering plants)?
- 2) **Class** — If a plant is a flowering plant, is it a monocot (in general: herbs, flower parts in 3s, parallel-veined leaves, 1 cotyledon—seed leaf; examples include grasses, lilies, irises, and orchids) or a dicot (in general: herbs to vines, shrubs, or trees, flower parts in 4s or 5s, net-veined leaves, 2 cotyledons; examples include roses, oaks, blueberries, and sunflowers)?

- 3) **Subclass** — According to the Cronquist system (Fig. 173 in Appendix 2), within the dicots there are six subclasses and within the monocots there are five subclasses. These groups can be useful in understanding the relationships among families.
- 4) **Family** — Most botanists consider this the most important level in the classification hierarchy in terms of learning about flowering plants. The first thing a botanist tries to do with an unknown plant is to figure out what family it belongs to. As indicated above, there are ca. 387–685 families of flowering plants depending on the system of classification used (Cronquist 1988; Reveal 1993). Cronquist (1988) recognized 387, while Mabberley (1997) recognized 405. According to the International Code of Botanical Nomenclature (Greuter et al. 1994), with the exception of eight families with long-established names, all families are named after one of the genera in the family and all have the ending -aceae. Even for these eight families, use of alternative names ending in "-aceae" is permitted. These are Compositae (Asteraceae), Cruciferae (Brassicaceae), Gramineae (Poaceae), Guttiferae (Clusiaceae), Labiatae (Lamiaceae), Leguminosae (Fabaceae), Palmae (Arecaceae), and Umbelliferae (Apiaceae).
- 5) **Genus** — Many plants are easily recognized to genus (e.g., oaks—*Quercus*; maples—*Acer*, etc.). The genus name and the specific epithet are always underlined, italicized, or set off in some other manner. Note that the term specific epithet is used for the second part of the binomial referring to the species; the name of a species is a combination of the genus name and the specific epithet. Each binomial is followed by the authority or person who named the plant. For example, the common sunflower was first named botanically by Linnaeus (abbreviated L.) and the full citation of the scientific name includes the genus, specific epithet, and authority: *Helianthus annus* L.

The following is an example of the hierarchical system of classification using *Lupinus texensis*, the Texas bluebonnet. Note that subspecies, variety, and form are not given; not all species are divided below the level of species.

Domain Eukaryota
Kingdom Plantae
Division Magnoliophyta
Class Dicotyledonae
Subclass Rosidae
Order Fabales
Family Fabaceae
Subfamily Papilionoideae
Tribe Genisteae
Genus *Lupinus*
Species *texensis*
Subspecies
Variety
Form