History and Theory in the Development of Phylogenetics in Botany

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This chapter is meant to be a brief intellectual history of cladistic approaches to botanical systematics. As such it focuses on the development of ideas, and the forces constraining them, rather than on biography or bibliography. Botany started from a different place, and went in different directions, than did zoology. The empirical concerns were different, the goals of classification were different, beliefs in the underlying pattern of nature were different, and so on. Even the sociological interactions among botanists were different from those among zoologists. There are still differences in all these things today, although at the end of this chapter I'll suggest some ways they should be resolved and complementary strengths adopted across systematics.

EARLY DIFFERENCES IN THE HISTORY OF BOTANICAL AND ZOOLOGICAL SYSTEMATICS

The deep history of botanical systematics developed differently from zoological systematics in various ways (see the masterful treatment in Stevens 1994). In the earliest days of scientific approaches to systematics, botany had a strongly practical emphasis, because of the uses of plants in medicine that stretches back to the Middle Ages and across all of the world's cultures. Botany was an important subject for a physician; most of the early plant systematists were trained M.D.s. To facilitate uses of herbs in medicine, inventories of plants of a region (floras)

became a strong emphasis in the field. And to make these floras useful for medicine, a premium was placed on providing tools for sure identification. Descriptions emphasized characteristics useful for either recognition or use rather than some deeper theoretical meaning.

This emphasis on floras remains to this day: it represents the majority of research efforts of current plant systematists worldwide. There are major ongoing floristic studies in many regions and states throughout the United States and in most countries of the world. There is little counterpart in the zoological world; relatively few investigators make it their goal to find, describe, and provide identification aids for all the animals of some specific geographic or political area. The effects of this obsession with flora writing and the wealth of specimens that has resulted are both beneficial and limiting to the field of botanical systematics. On the one hand, botanists have a very detailed knowledge of plant distributions, which has resulted in important online databases that have for example become widely used in recent predictive studies of the effects of climate change. On the other hand, a regional approach to systematics, rather than a focus on natural groups throughout their total range, produces many flaws in the resulting taxonomy. The terminal taxa might be correctly distinguished in the local area, but it is often difficult to name them correctlywithout study of additional specimens and types outside the region. Thus it is very difficult to make global comparisons or classifications until a truly worldwide monograph of a group is done, and the number of such studies has been few and declining through the twentieth century given an academic climate that favors publication of more, shorter studies.

Partly because of the emphasis on practical use and identification, in their classifications botanists emphasized the finer-scale units (species and genera). Plants were put together in classifications by criteria allowing easy identification and/or their practical uses, and botanists often didn't worry about theoretical frameworks for higher-level classification. When they did, the conceptual framework or metaphor used was most often conceived of as a map, with higher taxa having direct relationships in many directions (Stevens 1984, 1994, 2000). Botanists spoke of a given family X as approaching family Y at this end of its included variation and approaching family Z at another end. Virtually never was the chosen metaphor a tree.

Free from many of these practical constraints, zoology by contrast had a stronger theoretical bent from the beginning; systematists worried more about the nature of the underlying framework that connected

living things together. Among many theoretical frameworks and metaphors considered (O'Hara 1991), including a divine plan, circles of five, and a great chain of being among others, zoologists most often thought of relationships in terms of a treelike hierarchy rather than a map. Before Darwin this was not an evolutionary tree, of course (with very few exceptions). The hierarchy initially was thought to be due to a divine plan, with higher taxa like phyla being major ideas in the mind of God and progressively lower taxa being smaller elements of the Plan (Agassiz 1859).

The development of the "Natural System" in the late 1700s and early 1800s (as discussed by Stevens 2000; Glimour 1937, 1940) was primarily in botany. In this rejection of the single-character Linnaean approach (which was deemed "unnatural" or "artificial"), taxa were recognized by overall resemblance in many characters. Interestingly the switch to the natural system had already happened before the Darwinian revolution, and since several of Darwin's close friends and correspondents, such as Hooker and Gray, were architects of the natural system, it was part of the intellectual background in which Darwin worked. The demonstration that there is a hierarchy of obvious natural groups in living things was prime evidence for Darwin to present in favor of evolution in the *Origin*.

Thus, as has been noted by many (e.g., de Queiroz 1988), the Darwinian revolution caused no fundamental revolution at the time in systematics in general, and especially in botany. After Darwin there was a shift in the language systematists used: lip service was now given to evolution. Instead of similarities being part of a creator's plan, they were now said to be inherited from common ancestors, but systematists' fundamental approaches remained the same: classification was done by grouping organisms together by overall resemblance ("phenetics"). Zoologists tended to apply the phenetic approach to building their trees, botanists to building their maps.

This same phenetic approach was enhanced by the use of computers in biology in the late 1950s and 1960s (see Sterner this volume). Not surprisingly perhaps, many of the developers of the new objective algorithmic approaches were botanists or bacteriologists (Sneath and Sokal 1962, 1973). Clustering algorithms made it possible to apply the Natural System to many characteristics in a repeatable manner. Initially there was no intent to apply a historical concept of homology, or to interpret the phenetic clusters as lineages (e.g., Sneath and Sokal 1973). However, many workers, especially zoologists, couldn't resist the temptation to consider cluster diagrams as evolutionary trees.

There was a considerable influence of operationalist philosophies of science in the development of numerical phenetics. The supposedly theory-free nature of the endeavor was viewed as an advantage over a competing approach, the so-called evolutionary systematics that developed from the Modern Synthesis of the 1940s. The Modern Synthesis was primarily engineered by zoologists, and in contrast to classical phenetics, classification was not based on overall similarity in *all* characters but rather overall similarity in "evolutionarily important" characters, that is, characters considered to be of adaptive importance. Note that while numerical phenetics and evolutionary systematics did use a different set of characters and considered themselves violently opposing camps philosophically (e.g., Mayr vs. Sokal), they shared the same basic methodology of grouping organisms by overall similarity. Both were fundamentally phenetic approaches; the advent of a truly evolutionary approach awaited Hennig and the cladists (see below).

One impact of the modern synthesis in zoological systematics was a change in focus from higher classification to populations and species. This restriction of focus to the species level, and the relegation of higher taxa to the back burner, brought botanical and zoological thinking together in this particular regard, although many differences remained in how classification was regarded theoretically. Despite differing views of the underlying ontology and appropriate metaphors for representing relationships, botanists and zoologists continued to practice their systematic work as either intuitive or numerical pheneticists.

The distinction between plant and animal studies is probably most glaring on the topic of species; the history of ideas here has never run parallel in botany and zoology. Some botanists, notably the "biosystematists," primarily located in California and England (Clausen, Keck, and Hiesey 1939; Stebbins 1950; Grant 1971), did participate in the development of the Modern Synthesis and absorbed from zoologists an emphasis on the biological species concept. However, even the botanists who ostensibly embraced the BSC tempered their views considerably with considerations of rampant hybridization between species. One gets the impression that some botanists, including Stebbins for instance, only gave lip service to the BSC so they would be accepted by zoologists like Mayr and allowed to join the Modern Synthesis club. The BSC, in its Mayrian state, was not truly favored by any botanists. By far the prevailing view of the nature of species in botany, as clearly laid out by Levin (1979, 2000), was and is as the smallest phenetic clusters

separated by gaps in character variation on all sides. Workers today still commonly refer to "species boundaries"—a holdover of the map metaphor—and decide if an unknown plant is a new species by examining whether it fits within the range of variation of known species. Of course, most zoological advocates of the BSC, including Mayr, applied the same phenetic cluster methodology when describing species rather than doing breeding tests. (Mayr apparently never did a breeding test in his life!) For classification in general, clearly the main distinction between botany and zoology with respect to species is conceptual rather than empirical. It is an interesting feature of the history of science that competing schools of thought can viciously attack each other over ontological issues while differing little over the epistemological methods they apply in day-to-day work (Hull 1988).

THE PICTURE IN BOTANY BY THE 1970S

The situation by the 1970s in systematic botany was dire. Other types of botanists were questioning whether the loose, theory-free, intuitive approach being taken was scientific. Even systematists were not sure: when I started graduate school in the late 1970s, one of my advisers told me that systematics was not a science with objective principles but rather an art acquired over many years of careful apprenticeship. Herbaria were in trouble across the United States: many lost curatorial faculty, and a number were orphaned. The field was teetering on the brink of intellectual extinction. It was perceived as too lacking in rigorous methods and too loosely connected to evolutionary biology.

Phylogenetics came along in the nick of time to save systematic botany, but before turning to that important development, it will be important to understand several attitudes that plagued the field by conspiring against a rigorous phylogenetic approach. To set the stage for the discussion to follow, here is a list of prevailing attitudes of the 1970s that needed to be cleared away for phylogenetic progress to be made.

> *Overconcern about reticulation.* Many botanists of the mid-twentieth century had become so convinced of the prevalence of hybridization that they felt there was no phylogenetic tree of plants to discover. Instead, there was a network (or map!) of genetic relationships going in all directions. Botanists such as Anderson (1949), Stebbins (1950), and Grant (1971) suggested that many angiosperm species were entirely or partly of hybrid origin, which made it more difficult for a phylogenetic tree to be accepted as the

metaphor for classification. Instead, these concerns supported continued use of the traditional map metaphor.

The wrong metaphors. The long tradition of representing relationships in a maplike fashion, where a taxon has "boundaries" in all directions, culminated in this time period. Spectacular two-dimensional diagrams were produced by prominent botanists to show their ideas about relationships of plants (figs. 8.1, 8.2). These were argued to represent cross sections of evolutionary trees, but then of course without being able to see branches, no true phylogenetic relationships could be shown. This lack of specificity was considered a benefit by the authors of these diagrams (it was hard to prove them wrong!), but the lack of explicit hypotheses of relationships and methods to test them was clearly holding the field back.

When phylogeny was attempted, the tendency was to extend the map metaphor back in time and to link up extant taxa in ladderlike series (fig. 8.3). The botanists who took such approaches viewed some taxa as primitive and others as derived progressively along adaptive lines (Bessey 1915; Cronquist 1968). Trends in adaptive value were evaluated a priori and considered to be general—resulting in lists of "dicta" (e.g., Bessey 1915). For example, woodiness is primitive, herbaceous derived; many flower parts is primitive, few flower parts derived, and so on. Again, there was a lack of explicitness in the reasoning process for deciding a priori which characters and taxa are primitive.

Operationalism. Despite the participation of some botanists in the modern synthesis, most plant systematists in England and the United States were enamored with the operationalist philosophy of science fashionable in the 1960s. They were skeptical that one can know evolution (without enough fossils; see below) and thus preferred to produce classifications that are neutral in language and methodology. The most important virtue of a classification under this view is that it be practical—easy to use to identify plants found in the field.

Rejection of a historical concept of homology. Due partly to the philosophical biases mentioned in the previous paragraph in England and the United States and partly to the strong idealistic tradition in plant morphology and anatomy prevalent in Europe (Zimmermann 1931, 1937; Kaplan 2001; see also the chapters by Hamilton and Rieppel in this volume), the treatment of "homology" in botany was quite different from that prevalent in zoology. Either homology was neglected entirely (major works
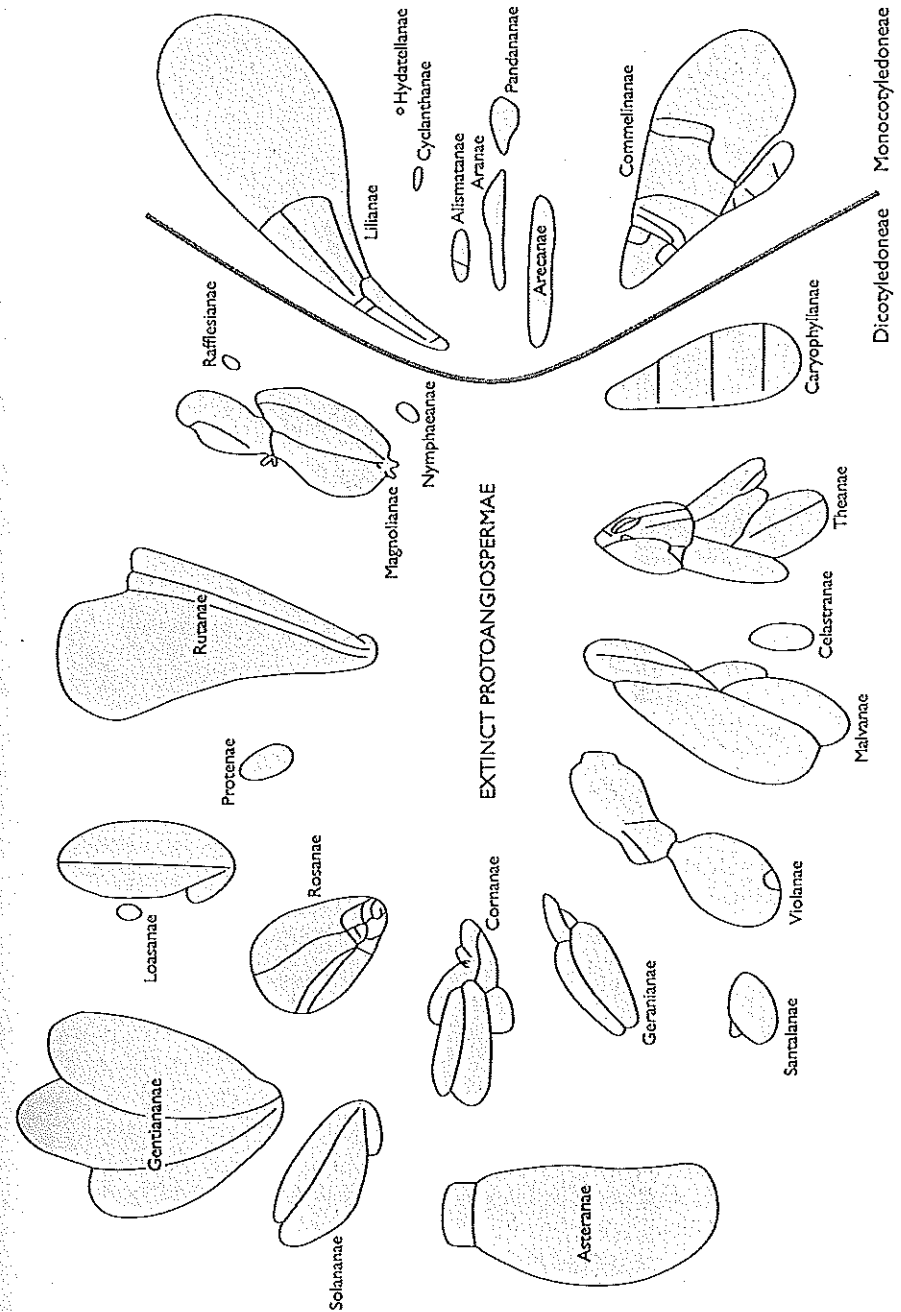

FIGURE 8.1. Phylogenetic shrub of the Angiosperms. Fig. 1, p. 249, in R. F. Thorne, "Classification and Geography of the Flowering Plants," *Botanical Review,* 58 (1992): 225–348. Springer. Used with permission.
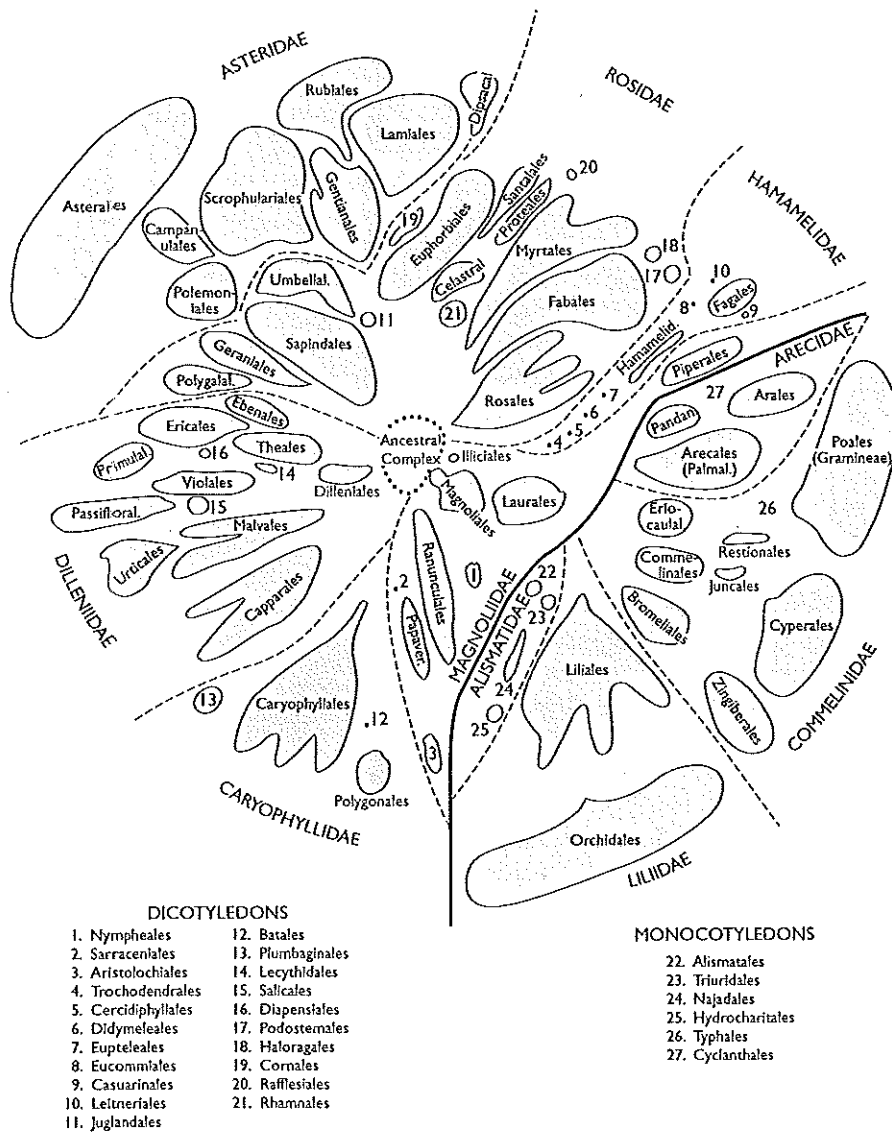
FIGURE 8.2. Diagram showing the relative degree of specialization of the orders of angiosperms. Figure 11–1, p. 247, in G. L. Stebbins, 1974. *Flowering Plants: Evolution above the Species Level* (Cambridge, MA: Belknap Press of Harvard University Press). Used with permission.
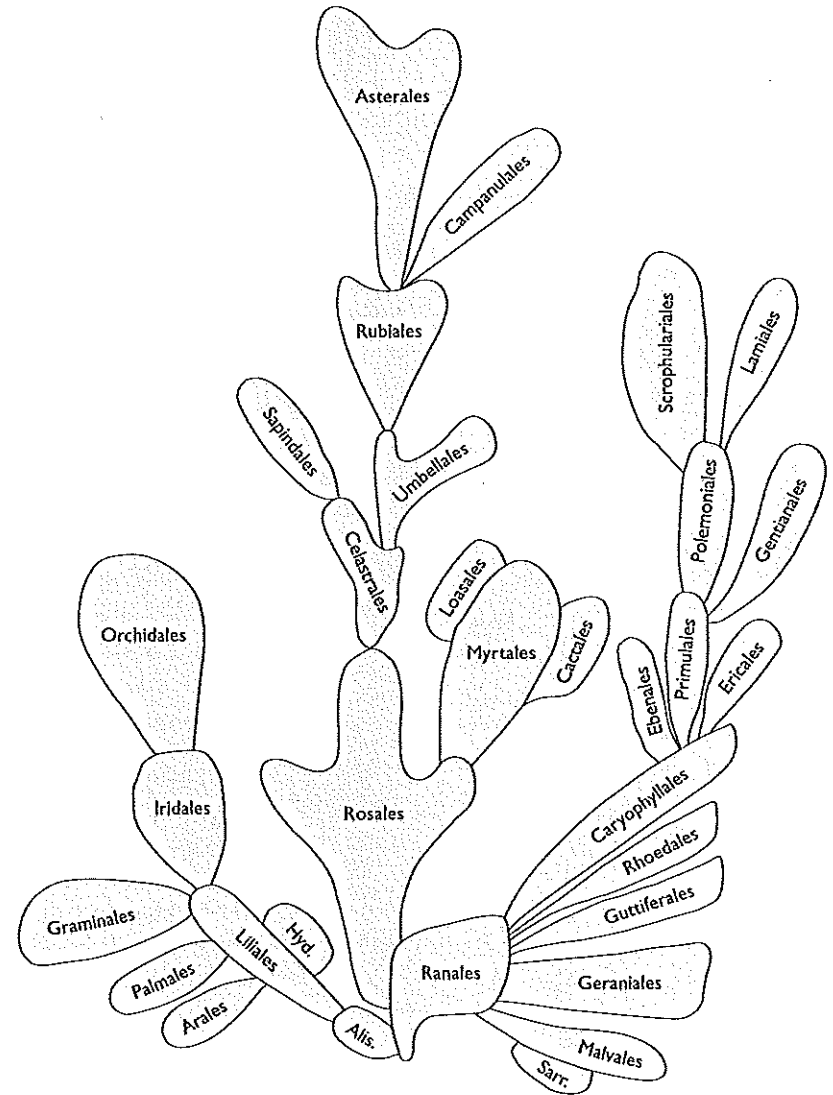
DICOTYLEDONS

1. Nymphaeales	12. Batales
2. Sarraceniales	13. Plumbaginales
3. Aristolochiales	14. Lecythidales
4. Trochodendrales	15. Salicales
5. Cercidiphyllales	16. Diapensiales
6. Didymeleales	17. Podostemales
7. Eupteleales	18. Haloragales
8. Eucommiales	19. Cornales
9. Casuarinales	20. Rafflesiales
10. Leitneriales	21. Rhamnales
11. Juglandales	

MONOCOTYLEDONS

22. Alismatales
23. Triuridales
24. Najadales
25. Hydrocharitales
26. Typhales
27. Cyclanthales

FIGURE 8.3. Bessey's cactus. *Annals of the Missouri Botanical Garden,* 2 (1915): 118.

following the operationalist tradition did not even mention the word), or it was defined based on developmental criteria following the idealistic tradition. In either case, the lack of an appropriate *historical* concept of homology greatly limited phylogenetic reasoning in botany.

Mistaken views on the role of fossils in phylogeny. Because of the lack of a historical concept of homology, botanists were missing out on the powerful phylogenetic evidence to be gained from comparative analysis of modern organisms. Many botanists felt that the fossil record carried all relevant evidence about phylogeny, that only a robust fossil record could give reliable relationships, and that evolution could be directly read from it. However, the methodology for linking fossils was poorly explored or explained: fossils were to be linked into ladders using overall similarity in some intuitive manner. But because there is a sparse fossil record for many plant groups, it was felt that there is no need to develop a rigorous methodology to build phylogenies! This completed a dubious circle of reasoning that kept the study of phylogenetic relationships deeply buried in the background of systematic botany during the 1970s.

EARLY CLADISTICS IN BOTANY

The Hennigian revolution took place in the 1970s to 1980s (Hull 1970, 1988), initially due mainly to the efforts of zoological systematists (Hennig 1965, 1966; Nelson 1973; Wiley 1981; Patterson 1982; Farris 1970, 1983; Kluge 1989). The fundamental conceptual advance was rejecting the use of overall similarity in favor of what Hennig called *special similarity.* Hennig made a distinction between shared derived similarities *(synapomorphies)* that are indicators of shared ancestry at some particular level and shared primitive similarities *(sympleisomorphies)* that are not indicators of shared ancestry (Sober 1988). Hennigian phylogeneticists (or *cladists,* to use a term originally coined as a denigration by Mayr) recognized that the fundamental organizing principle for biological classification should be phylogeny: descent with modification punctuated occasionally by branching of lineages. A strongly historical definition of homology was required (Patterson 1982). Cladists restricted the use of the formal Linnaean system to hypothesized *monophyletic groups* (i.e., groups composed of all and only descendants of a common ancestor), as evidenced by synapomorphies. The fundamental metaphor for classification should be a phylo-

genetic tree. These advances finally completed the Darwinian revolution in systematics (de Queiroz 1988).

The 1970s and 1980s saw the beginning of Hennigan cladistics in botany. The early adopters were young botanists, in many cases graduate students at the time, located in centers where they were exposed to teaching and research by zoological cladists. The first cladistic study in plants was by Timo Koponen (1968), working on mosses in Helsinki, Finland, under the influence of the entomologist Tuomakowsi, himself a colleague of Hennig's. Another early study was on land plant relationships by Lynne Parenti (1980), under the influence of zoological cladists at the American Museum of Natural History. Mishler and Donoghue published early plant cladistic studies with colleagues (Mishler and Churchill 1984, 1985; Doyle and Donoghue 1986) partly because of the influence of the fish systematist William Fink at Harvard. Other examples of early applications of cladistics in botany were Bremer and Wanntorp (1978) in Sweden, Humphries (1979) and Hill and Crane (1982) in England, Funk (1981) in Ohio, and Sluiman (1985) in the Netherlands. A bibliography of early plant cladistic studies can be found in Funk and Wagner (1981).

As was true of cladistics as a whole in that pre-PCR (polymerase chain reaction) era, early studies were solely morphology based and were non-numerical at first. The methodology employed early was manual "Hennigian argumentation": the tree was built by adding one character at a time, basically with pencil and paper. It is important to note that while major advances were soon to come in both sources of data (as molecular characters became available) and numerical analysis methods (as algorithms developed rapidly), the initial relationships discovered using only morphological data, and simple manual data analyses have stood the test of time. Later studies have greatly resolved relationships and added support to the early results, but the major branches in the plant portions of the tree of life were apparent right from the start. Thus the real revolution in plant systematics was caused by theoretical progress. The coming flood of molecular data and the rapid development of computer algorithms were important developments, but they were icing on the cake of the theoretical advances.

I don't want to imply that the young botanists adopting cladistic methods, initially developed by zoologists, were doing so passively. Botanists began to make important contributions to theory and method in cladistics. As befitting the clear biological differences between plants and animals, botanists entered enthusiastically into the debate over how species should be conceptualized in cladistics (e.g., Mishler and Donoghue 1982).

Likewise, botanists insisted that hybridization was real and needed to be studied using cladistic methods (Wagner 1983; Funk 1985; McDade 1990, 1992). Botanists contributed to the development of computer algorithms, particularly those for studying character evolution (Maddison, Donoghue, and Maddison 1984), to assessment of character polarity (Stevens 1980), and to the debates over the role of ontogenetic information in polarization of characters (Mishler 1986, 1988; Blackmore and Crane 1988). Botanists were also heavily involved in working out how fossils should be used in cladistic analyses (Doyle and Donoghue 1987; Donoghue et al. 1989) and in the development of comparative methods to apply cladistics to studies of evolution and ecology (Donoghue 1989; Wanntorp et al. 1990). And of course, botanists were fully involved in considerations of how to apply the newly available DNA sequence data in cladistic analyses (e.g., Mishler et al. 1988).

THE ADVENT OF MOLECULAR PHYLOGENETICS (STARTING IN THE LATE 1980s)

The invention of the polymerase chain reaction and its transfer to systematics labs in easy-to-use protocols in the late 1980s came at a perfect time to reinforce the earlier conceptual advances in phylogenetic reconstruction and further rescue the reputation of systematics that had sunk so low in the 1960s. Combined with rapid advancement in the sophistication of computational techniques, which allowed the use of many more characters in an analysis than was possible by manual techniques, systematics moved from the periphery to the very center of biological research. Phylogenetic research in systematics gave it the full luster of the highest scientific standards of the time; systematists were rigorously testing hypotheses and using cutting-edge laboratory technology. Furthermore, the development of phylogenetic comparative methods (e.g., Donoghue 1989; Funk and Brooks 1990; Wanntorp et al. 1990; Brooks and McLennan 1991; Harvey and Pagel 1991; Miles and Dunham 1993; Martins 1996) and the rapid proliferation of these methods into virtually all areas of biology made phylogenetic expertise a valuable academic skill, enhancing employment opportunities for systematic botanists. The institutions of plant systematics—herbaria and botanical gardens—which provide much-needed resources and expertise for both morphological and molecular studies, underwent a renaissance in status and funding.

Not everything was rosy as systematics developed into the 1990s, however. DNA-based studies were quicker to do than morphology-based

ones, and took much less training. A student could be taught how to PCR and sequence DNA in a few weeks; it took much longer to train a student in techniques of microscopy and anatomy and how to conduct fieldwork and use collections properly. Because DNA-based research was more expensive than traditional "muddy boots" systematics, and regarded as the cutting edge, young faculty naturally concentrated their grant-raising efforts in this area. It was a good route to tenure; large grants could be acquired and publications produced more quickly. The net result of these facts was a tendency to go overboard in the enthusiasm for molecular data and leave out morphology entirely. Too many students were trained in molecular lab skills but not well rounded enough, lacking understanding of the morphology, anatomy, ecology, and systematics of their study group. Too many faculty members felt forced to concentrate on molecular phylogenetics and evolution, to the exclusion of producing systematic results and taxonomic treatments. These trends led to limits on the ability to integrate different kinds of data and synthesize results.

Another difficulty that developed in the early 1990s because of the glut of new data was a lack of coordination across the field. Many genes were being sequenced but from different examplar organisms in different terminal taxa. The morphological studies that were being done often concentrated on yet other taxa. Thus the possibility of compiling large, comparable datasets for multiple genes and morphology was severely limited—the data matrix was full of holes. This situation was brought about because individual labs were working in isolation and even in secrecy until eventual publication, due to worries about being scooped and maintaining competitive advantages in grant seeking. No single lab with a standard National Science Foundation grant could address the big phylogenetic questions that needed to be tackled, and yet there were barriers keeping labs from working collaboratively. The field of systematics needed to make the transition into "big science" much as had previously occurred in physics, astronomy, and molecular biology (particularly genomics)—all areas where the scope of the questions, and the expense and the range of expertise needed to address them, had outstripped the ability of single labs.

The solution to this difficulty clearly lay in broad-scale phylogenetic collaboration, and botanists led the way, taking advantage of a greater degree of existing collaboration and trust among labs than was present in systematic zoology. For example, a large number of labs collaborated in 1993 to produce what was then the largest cladistic analysis ever undertaken, with five hundred taxa of seed plants (Chase et al. 1993).

Most of the botanists working on phylogeny sought ways to collaborate by organizing sampling of standard exemplar taxa for multiple genes with the goal of assembling truly comparable datasets across green plants. The result was the Green Plant Phylogeny Research Coordination Group (known as "Deep Green"), jointly funded by the U.S. National Science Foundation, Department of Energy, and Deptartment of Agriculture. This collaboration began working in 1994 to facilitate interactions among many research labs through a series of workshops, meetings, and sharing of data and information on public websites. This effort culminated at the 1999 International Botanical Congress in St. Louis where the group sponsored eight symposia with seven speakers each, presenting phylogenetic results across the green plants at several nested levels and attracting national media attention. The success of this unusual coordination effort in turn stimulated the formation of two general funding programs by the National Science Foundation: the Research Coordination Network (RCN) program and the Assembling the Tree of Life (AToL) program. Both programs funded a number of further plant collaborations such as the RCN's "Deep Gene" and "Deep Time" and a number of plant AToL grants, as well as many collaborations in animals and microbes.

Thus botanists led the way toward a big science approach to phylogenetics, a trend that has only continued to accelerate. For example, massive collaborative analyses have been done for all green plants (Mishler et al. 1994), liverworts (Forrest et al. 2006), ferns (Pryer et al. 2001), and angiosperms (Qui et al. 2005). There are active research collaborations across most branches of the plant parts of the tree of life today, with botanists increasingly involved in comparative genomics and evolutionary studies that take advantage of the ever more detailed and well supported phylogenetic trees available.

THOUGHTS ON THE FUTURE

Where does systematic botany go from here? In my opinion, it would be good if the traditional differences with systematic zoology became a thing of the past, and we moved forward by adopting complementary concepts and approaches from both sources. Basically, we need to realize plants and animals aren't really that different after all. A common path is needed.

As has been traditional in zoology, the tree of life is the appropriate metaphor for all organisms: animals, plants, and microbes. There is,

however, not a purely diverging tree. Reticulation caused by various processes that result in a horizontal transfer across distinct branches has been clearly shown to be a real phenomenon. Recent work suggests that reticulation, once a concern mostly of botanists, is a potential concern in any group of organisms, and general methods need to be developed to take the possibility of reticulation into account. As has been studied for a long time in plants, reticulation occurs through distinctly different processes (e.g., hybrid speciation, introgression, and horizontal gene transfer). Each of these processes will need distinctly different analytical approaches to sort out and distinguish them from other, nonreticulation processes (such as lineage sorting) that produce similar patterns. And of course, despite misguided arguments to the contrary (Dolittle 1999), phylogenetic methods initially assuming a purely diverging tree are necessary for the discovery of reticulation.

Another area where both plant and animal phylogenetics need to move ahead in parallel is in devoting more effort to selecting data to use for particular questions. There has been an overemphasis on analysis methods; most theoretical work in phylogenetics has been directed toward the issue of how to turn a data matrix into a phylogenetic tree rather than the issue of what kind of data should go into a particular matrix. Phylogenetic analyses at different scales require different datasets, and we need more objective means for selecting the appropriate data. For example, fine-scale "shallow" analyses need rapidly evolving markers but need to pay particular attention to the likelihood of reticulation or other sources of incongruence by using several completely independent data sources. Deep analyses looking for relatively short periods of shared history in the distant past can be confused by artifacts such as long-branch attraction, and handicapped by loss of signal, but are less affected by reticulation. The latter type of analyses needs slowly and episodically evolving markers such as morphological and anatomical characters. Genomic structural data, including, for example, changes in gene order and arrangement, show considerable promise for studies of this type (Mishler 2000, 2005)

Thus the trend toward emphasizing molecular data to the exclusion of morphological data needs to be reversed. We need to reintegrate morphology and molecules into combined matrices for most phylogenetic studies. As detailed in table 8.1, a rigorous morphological character matrix is needed to achieve most of the goals of phylogenetics, including incorporating information from fossils, getting the tree right, and interpreting character evolution rigorously.

TABLE 8.1   TEN REASONS TO INCLUDE OBJECTIVELY ANALYZED
MORPHOLOGICAL DATA IN PHYLOGENETIC DATA MATRICES

1. *The greater complexity of morphological data may often allow better homology assessments.* Unlike DNA sequences, which are one-dimensional strings of data (unless you have secondary or tertiary structure models to use in alignment), morphology is complex and three-dimensional, plus it has a time component (ontogeny).

2. *Morphological data have many potential character states.* An important parameter determining whether data might be subject to "long-branch attraction" problems is the number of potential character states. False reconstructions are only a problem when parallel changes to the same character state occur, a phenomenon that is most frequent with binary data and rare with many available states.

3. *Data can be gathered from many specimens, cheaply and quickly.* A systematist can base his or her conclusions on samples from thousands of semaphoronts.

4. *We need to be able to identify clades easily in the field.* Morphological apomorphies are easier to apply in field keys and in photo ID guides.

5. *We need to objectively determine morphological apomorphies for clades.* A real analysis is needed to show what the apomorphies at a particular level are. It is not rigorous to inspect a purely molecular tree and hang morphological characters onto branches intuitively, although this is unfortunately done frequently.

6. *Morphology gives another independent dataset,* distinct from organellar and nuclear genes. Comparing the topology of morphological datasets to those derived from specific genes can help one discover reticulation, lineage sorting, etc.

7. *Morphological characters might actually help get the best-supported answer!* Even in cases where the topology of the total evidence tree is the same as with the molecules alone, support values such as bootstrap values often go up. And sometimes the total-evidence topology has novel, highly supported branches, synergistically supported by the combined data.

8. *Episodic patterns of change.* Despite common misconceptions to the contrary, clocklike markers are actually undesirable for reconstructing deep, short branches. Such markers continue to click along, changing at a regular rate until all the signal in the deep branch is gone. The best marker for such deep branches is like the marking the deep branch is gone. The best marker for such deep branches is like the clock on the *Titanic:* it ticks once and stops forever. Slow change with long periods of stasis works best for these cases, i.e., the pattern shown by some morphological and anatomical features, as well as by structural features of the genome, such as inversions.

9. *Better sampling of the tree of life.* Good sampling is extremely important for reconstructing the correct phylogenetic tree. We need to break down those long branches. Over 99% of the lineages that have existed on the tree of life are extinct, and the only feasible way to get information about them is by adding fossils, which in turn requires morphology.

10. *Calibrating molecular clocks and dating of lineages.* In order to include fossils, we must have morphological characters in the matrix, and therefore optimized to the cladogram. Fossils do not come with a taxon ID in the fossil record; they simply come with some morphological characters from which we might be able to infer phylogenetic placement and classification. The fossil must therefore be attached to the cladogram based on its characters, then (and only then) can we infer that its sister group is at least as old as the age of the fossil.

A final area where general progress is needed is classification. Classifications are rightly or wrongly used by many people for many purposes, both within and outside biology, including biodiversity inventories, identification guides, conservation planning, ecological models of food webs and community structure, macroevolutionary studies of origination and extinction, predictions of the effect of climate change, coevolutionary studies, and many more. The number of uses is increasing. The availability of comprehensive online databases such as the Paleontology Database, GBIF, and Genbank has greatly increased the ability (and temptation) to conduct broad meta-analyses using taxonomic names as a bridge. The current state of taxonomy is woefully inadequate to support most of these uses: the application of most current taxonomic names found in lists or databases is quite ambiguous. We don't know which names refer to monophyletic clades rather than some paraphyletic or polyphyletic assemblage. Furthermore, even in the best-case scenario where a name does refer to a clade, we don't precisely know which clade (because of a limitation with the current codes of nomenclature) and we can't assume that two clades given the same rank have anything in common, such as age, included diversity, or distinctness in characteristics (de Queiroz and Gauthier 1992, 1994).

In a nutshell, taxonomic practice has not kept up with the recent developments in phylogenetic theory discussed above. We are still using codes of nomenclature that were developed in preevolutionary times to attempt to name evolving entities. The Darwinian revolution may have been completed for systematics by the development of Hennigian cladistics, but it has not yet been completed for taxonomy per se. The developing Phylocode (www.ohio.edu/phylocode/) will attempt to rectify the problems caused by the existing codes in three main ways that will benefit users by making it clear what taxonomic names represent: (1) all taxa named under the Phylocode will be postulated clades; (2) multiple specifiers are used to precisely define the clade being named, unlike the current system, which with only one type specimen does not allow clear specification of an ancestral node; (3) ranks are eliminated, removing the temptation to make inappropriate comparisons. Phylocode names will be hierarchically indexed in a database (REGNUM), along with their associated data, and will allow users to approach their goals appropriately given the modern evolutionary worldview.

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PART THREE

Technology, Concepts, and Practice