

Plant systematics in the next 50 years—re-mapping the new frontier

Kenneth J. Sytsma¹ & J. Chris Pires¹

Summary

Sytsma, K. J. & Pires, J. C.: Plant systematics in the next 50 years—re-mapping the new frontier. – *Taxon* 50: 713–732. 2001. – ISSN 0040-0262.

In the historical context of plant systematics over the last 50 years, systematics is examined in terms of where it is now, where it is headed, where it should be, and how it should get there. Issues and concerns of the past decades are still with us today. Molecular systematics has become the over-arching field in systematics, but each of eight other areas (genome, chromosomes, morphology and anatomy, development, population biology, speciation, floristics and monography, nomenclature and classification) are evaluated. A revolution in systematics is not necessary for the next 50 years in plant systematics. What is needed is a re-mapping of our discipline that involves four elements for the future growth and health of botanical systematics: plant systematics and its utility, dialogue with other disciplines, multi-disciplinary training, and a pluralistic viewpoint.

Keywords: phylogenetics, pluralism, systematics, taxonomy.

Introduction—looking back in order to look forward

“These times were full of new discoveries and new techniques. There was widespread belief that we would soon fully understand the processes of micro-evolution and the origin of higher plant diversity, and be able to express this satisfactorily in our systematic arrangements.”

This optimistic sentiment well summarises the last decade or two in systematic biology, with allusions to the multitude of systematic and evolutionary tools now at our disposal and to the many exciting discoveries in diverse fields ranging from the origin of species (Rieseberg, 1998) to the evolutionary history and rise of angiosperms (Qiu & al., 1999) and even land plants (Qiu & Palmer, 1999; Pryer & al., 2001). It is sobering to realise that this statement was actually made over 30 years ago (Ehrendorfer, 1970). The occasion giving rise to this statement was the XI International Botanical Congress at Seattle and the important set of talks (many of them published in 1970 in this journal, *Taxon*) in the symposium “Biosystematics at the Cross-roads”, and other related symposia. Even more illustrative, perhaps, is that Friedrich Ehrendorfer was **not** referring to the major advances that were then happening in systematic biology during the decades of the 50s and 60s—a time period seemingly appropriate for such comments—but rather he was citing the sentiments of the early 1940s. It is clear that the systematic community has continually and repeatedly experienced cyclical phases of (1) new discovery and techniques, (2) emotions of elation with respect to expected completion of goals for understanding the origin of speciation, uncovering the phylogeny of life, and incorporation of this knowledge into classification, and (3) the inevitable time for re-evaluation of progress and consideration of future directions.

¹Department of Botany, University of Wisconsin, Madison, Wisconsin 53706, U.S.A. E-mail: kjsytsma@facstaff.wisc.edu (author for correspondence); jcpires@facstaff.wisc.edu.

Where are we as a systematic community today? And where are we headed? Is there a revolution occurring in systematics today? Based on the proposed and vociferously argued changes in systematic concepts (e.g., speciation, species definitions, phylogenetics, nomenclature, classification) and in basic systematic techniques and practices (see Sytsma & Hahn, 1996, 2000 for reviews and earlier contributions to this “Jubilee” series to get a taste of these proposals and changes), one might argue that we are indeed witnessing one of the most significant and all-encompassing revolutions in systematics.

Before addressing these questions and examining where plant systematics is today and where it might be headed in the next 50 years, it is perhaps wise to revisit where plant systematics stood several decades ago and where those systematists envisioned the field was headed; see Stevens (2000) for changes and progress in botanical systematics from 1950 to the present. We take a snapshot from a critical time in plant systematics and one that has some parallels with the present time—namely the XI International Botanical Congress held in 1969 in Seattle. At that time, several decades after the so called “evolutionary synthesis” and the rise of biosystematics, the plant systematics community was taking stock of its progress and future. We will mention just four ideas or thoughts that permeate the writings of the period.

1. Ever-present optimism in systematics, but yet the feeling that plant systematics had not accomplished what it thought it could (Ehrendorfer, 1970; see quote above).

2. Ever-present new methods and technologies that act as the “call of the siren”, again with optimism but also with a sense that they have some negative impacts: “Statistical and numerical approaches with the help of computers as well as refined new biochemical methods have led to an unprecedented development of numerical and chemical systematics. No wonder then that many of our students turn to these flourishing fields of activity instead of to biosystematics” (Ehrendorfer, 1970).

3. Ever-present impression that we are borrowing tools from other disciplines, but that systematics or perhaps systematists lag behind in theory or reciprocal impact: “I think that if I have any complaint about the progress and status of systematics, it is that we systematists have been quick to accept new methodologies, but that we are slow to pick up conceptual cues from our sister disciplines” (Ornduff, 1970).

4. Ever-present knowledge that systematics is not integrated: “What goes wrong? The basic evil lies in the fact that we have not sufficiently managed to arrange systematics and biosystematics yet. Their results are hardly correlated; the facts obtained from biosystematics float in thin air, destined rather to land in some curiosity cabinet instead of being integrated into the system” (Merxmüller, 1970).

Where is plant systematics today (and where should it be)?

Are these sentiments still around today, but perhaps in different form and articulated by different people? To begin to answer this, we first need to take a quick look at where systematics is today. We outline here some of the main characteristics (accomplishments, new directions, stalled efforts) of nine areas of botanical systematics. These were selected from a larger list because they represent the range of on-going activity in the field, and because specific papers in this Jubilee Series address them in more detail. We start with “molecular systematics” because it has become the overarching area of botanical systematics that has had or will have the

most impact in the future (rightly or wrongly). The areas are then listed in order from the genome level to that of higher-level classification.

Molecular systematics. — The wave of molecular systematic data is enormous, impossible to avoid, but surprisingly recent in origin—at least for DNA sequencing (see Sytsma & Hahn, 1996, 2000; Crawford, 2000; and Soltis & Soltis, 2001, for reviews). Molecular systematics has not only impacted phylogenetics and perhaps classification, but also most of the other fields surveyed below (Donoghue, 2000). One only needs to follow the work of the “Green Plant Phylogeny Research Coordination Group” [<http://ucjeps.berkeley.edu/bryolab/greenplantpage.html>] to see how molecular systematics (with other approaches) is redefining the way systematics operates. In this case, the technological advances caught up with theory, and the new synergism permitted rapid advances and major surprises. Examples abound of such spectacular advances, ranging from the identification of *Barnadesia* and relatives as sister to all other *Asteraceae* (Jansen & Palmer, 1987), and to the early radiation of flowering plants (Qiu & al., 1999; Barkman & al., 2000; Chase & al., 2000a; Graham & Olmstead, 2000) and vascular land plants (Qiu & Palmer, 1999; Pryer & al., 2001). As discussed below and argued elsewhere (Stevens, 2000; Crawford, 2000), molecular systematics can survive on its own, but it will be most successful when linked with other areas of systematic biology.

Genome level. — We are witnessing an extraordinary time in biology—and no wonder that former U.S.A. President Clinton called the 20th century the “Age of Biology”—where complete plant and animal genomes (nuclear and organellar) have been only recently sequenced. The complete nuclear genome of *Arabidopsis* has just been made available online (*Arabidopsis* Genome Initiative, 2000), with *Oryza* not far behind; this following the publications of numerous chloroplast genome sequences (see Palmer & Delwiche, 1998). Systematics has already borrowed heavily in terms of tools and ideas, as well as basic DNA information, from these efforts on *Arabidopsis* and other ongoing inventories of the rice and maize genomes (Devos & Gale, 2000). The systematic community might well put pressure on funding agencies to see such efforts and money put forward to a few other select and more systematically interesting taxa (*Clarkia*, *Tragopogon*, or *Amborella*, perhaps).

Genomics and bioinformatics are new research areas directly spawned from such herculean endeavours to sequence plant and animal genomes, and systematics has much to gain by embracing and borrowing the tools and ideas that are emerging in these areas (Wendel, 2000). The merging of phylogenetics and genomics (phylogenomics) is now here (Bennetzen, 2000; Heslop-Harrison, 2000; Paterson & al., 2000). A question to ponder, though, is whether phylogenetics is shaping the context and defining the questions that those working in genomics are now formulating. For example, are we as plant systematists doing our job in informing these scientists of the phylogenetic backdrop of *Arabidopsis* (Fig. 1) (or of *Oryza* and *Zea*); that *Arabidopsis thaliana* is more closely related to other genera than to some species of *Arabidopsis* (Koch & al., 1999); that its family is now placed in a larger, more diverse, and evolutionarily far more interesting family comprising both *Brassicaceae* and *Capparaceae* (Hall & Sytsma, 2000); and that this group is a small, but derived

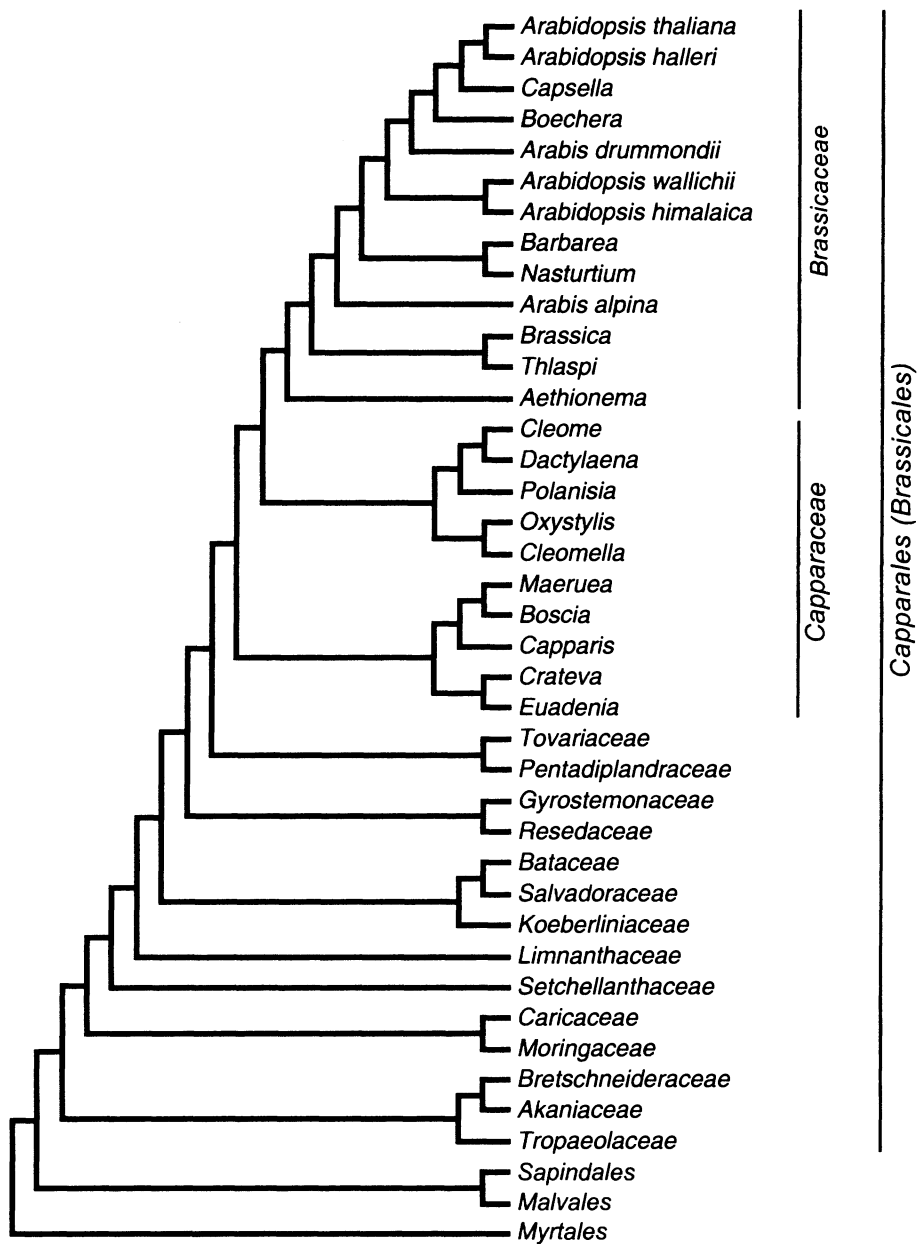


Fig. 1. Composite phylogenetic perspective of *Arabidopsis*, *Brassicaceae*, and related families in *Capparales* (*Brassicales*) based on molecular phylogenetic work of Rodman & al. (1998), Koch & al. (1999), and Hall & Sytsma (2000).

portion of a large and morphologically diverse mustard oil clade (Rodman & al., 1998)? Surely these phylogenetic perspectives on *Arabidopsis* can have profound impacts on what and how genomics is addressed in the future.

Chromosomes. — The time-consuming, difficult, and less rewarding business of counting chromosomes and examining their gross structural changes is little done these days [see lucid reviews by Heslop-Harrison (2000) and Stace (2000)]. A sobering thought is that only 25% of angiosperms have any chromosome number reported (Bennett, 1998); even more somber is the realisation that although the flora of Iceland has been 100% covered, less than 1% of the species in many tropical areas have been counted (Stace, 2000). One approach is to take previous chromosome counts and simply “map” them onto new phylogenies (Knox & Kowal, 1993; Roalson & al., 2001). More integrated approaches involve looking at fewer taxa in more detail as in recent studies of hybridisation and polyploidisation (Husband & Schemske, 1998; Rieseberg & al., 2000; Soltis & Soltis, 2000; Wendel, 2000).

It is interesting to see that the systematics community is again revisiting the chromosome level—perhaps to stay, although now with a new set of questions and tools involving *in situ* hybridisation (ISH) (Jiang & Gill, 1994; Schwarzachner & Heslop-Harrison, 2000). The ability to track individual genomes via genome *in situ* hybridisation (GISH) might well revolutionise some biosystematic areas of research (reviewed in Stace & Bailey, 1999). These techniques are being used now most successfully by biologists working on cultivated plants, but will be increasingly used in powerful ways to better understand chromosome evolution, as well as documenting hybridisation and polyploid speciation (Stace, 2000). Recent systematic applications of fluorescent *in situ* hybridisation (FISH) in *Paeonia* (Zhang & Sang, 1999), *Nicotiana* (Lim & al., 2000), and *Tragopogon* (Pires & al., in press) have already demonstrated the utility of this approach using specific DNA segments as probes. At a fundamental level, issues of homoeology as they relate to chromosomes could be significantly lessened with these *in situ* approaches (Lim & al., 2000).

Morphology and anatomy. — Comparative plant structure, morphology, and anatomy have formed the backbone of systematic botany (see Endress & al., 2000 for review of 50 years of progress and future challenges). Although morphological data sets have been shown to possess more homoplasy than equivalent sampled DNA data sets (Givnish & Sytsma, 1997b, c), the emerging picture is that when combined with molecular data sets, the phylogenetic results are generally more robust than with either data set alone (Endress & al., 2000; Sytsma & Hahn, 2000). Thus, both approaches to phylogenetic estimation are intimately intertwined. It has been noted that many of the “surprises” uncovered with molecular phylogenetic studies actually were suggested decades earlier (although largely ignored or misinterpreted by others) based on morphological evidence (Endress & al., 2000). However, considering the large number of diverse and opposing hypotheses, based on morphological evidence, for certain systematic issues (e.g., early vascular plants, early angiosperms, or early *Asteraceae*), it would be indeed surprising if none of these hypotheses were congruent to some degree with molecular data.

What these spectacular examples do indicate is the need to assess the evolution of morphological characters that both fit and do not fit (in a character congruence sense) the emerging phylogenetic hypotheses obtained with both molecular and morphological data. Of particular importance and urgency is the need to examine morphology and its evolution in the context of ecological conditions (Givnish &

Sytsma, 1997c; Les & al., 1997; Givnish & al., 1999; Givnish & Patterson, 2000; Nyffeler & Baum, 2000; Schwarzbach & Ricklefs, 2000; Whitlock & al., 2001).

Evolutionary development. — The exciting area interfacing genomics and development, popularly nicknamed “evodevo”, is still in its infancy but already redirecting systematic investigations with new questions and new answers (Meyerowitz, 1994; Kellogg, 2000; Soltis & al., in press). Although the tools and concepts associated with the field (such as the “ABC” model of floral development) are best applied still to model organisms (Doebley & Wang, 1997; Baum, 1998), the apparent ubiquitous nature of these genetic developmental programs has already permitted the exploration of the uses of this field to other, arguably more evolutionarily interesting, plant groups (Albert & al., 1998; Friedman & Floyd, 2001). Perhaps for the first time, homology issues in various morphological features can be addressed near their genetic source. However, as we are learning more about the black box between genes and their phenotypic effects (such as the role of heterotopic changes in macroevolutionary changes in *Poaceae* (Kellogg, 2000) and signal transduction systems), we will need to proceed with caution.

Population biology. — The convergence of population biology with plant systematics is marked by different conceptual frameworks (Schaal & al., 1998; Schaal & Olsen, 2000; Schaal & Leverich, 2001). The genetic structuring of populations and their future as independent evolutionary lineages is strongly influenced not only by the present or future pattern of gene flow within and between populations but also by historical patterns of relationships of these populations. Thus, although considerable progress has been advanced in the traditional approaches to the study of genetic structuring and differentiation within and among species, especially with the aid of new molecular markers (Wolfe & Liston, 1998), issues of phylogeography and coalescence are also now part of this biosystematic endeavour. In the nearly 15 years since phylogeography has been part of the systematic landscape (Avice & al., 1987), relatively few explicitly phylogeographic studies in plants versus animals have been published (e.g., Abbott & al., 2000). Schaal & al. (1998) argue that this paucity of plant studies exists not because phylogeography is less applicable or useful in plants, but rather a lack of useful genetic variation applicable to phylogeographic analyses. A major focus for the next decades should be the search for more useful molecular markers in and among plant populations, in order to remedy this problem. Two other issues will need to be addressed as well. First, the emerging ecological arena of metapopulation research (Husband & Barrett, 1996; Barrett & Pannell, 1999) will need to be interfaced with systematics in order to better understand the dynamic forces operating on populations within species that are largely *ahistorical* in nature. Barrett & Pannell (1999) specifically address the prospects that metapopulation studies will help inform systematic and evolutionary studies of plants, and conclude that they will, once difficulty in measuring extinction, colonisation and migration is overcome. Second, issues arise related to “tree thinking” (O’Hara, 1992, 1993) as a language of not only phylogenetics but also now with those interested in phylogeography. Taking this complex tree pattern, as shown in Fig. 2, and recognising taxonomic entities will be no easy task as the conceptual frameworks used by practitioners at

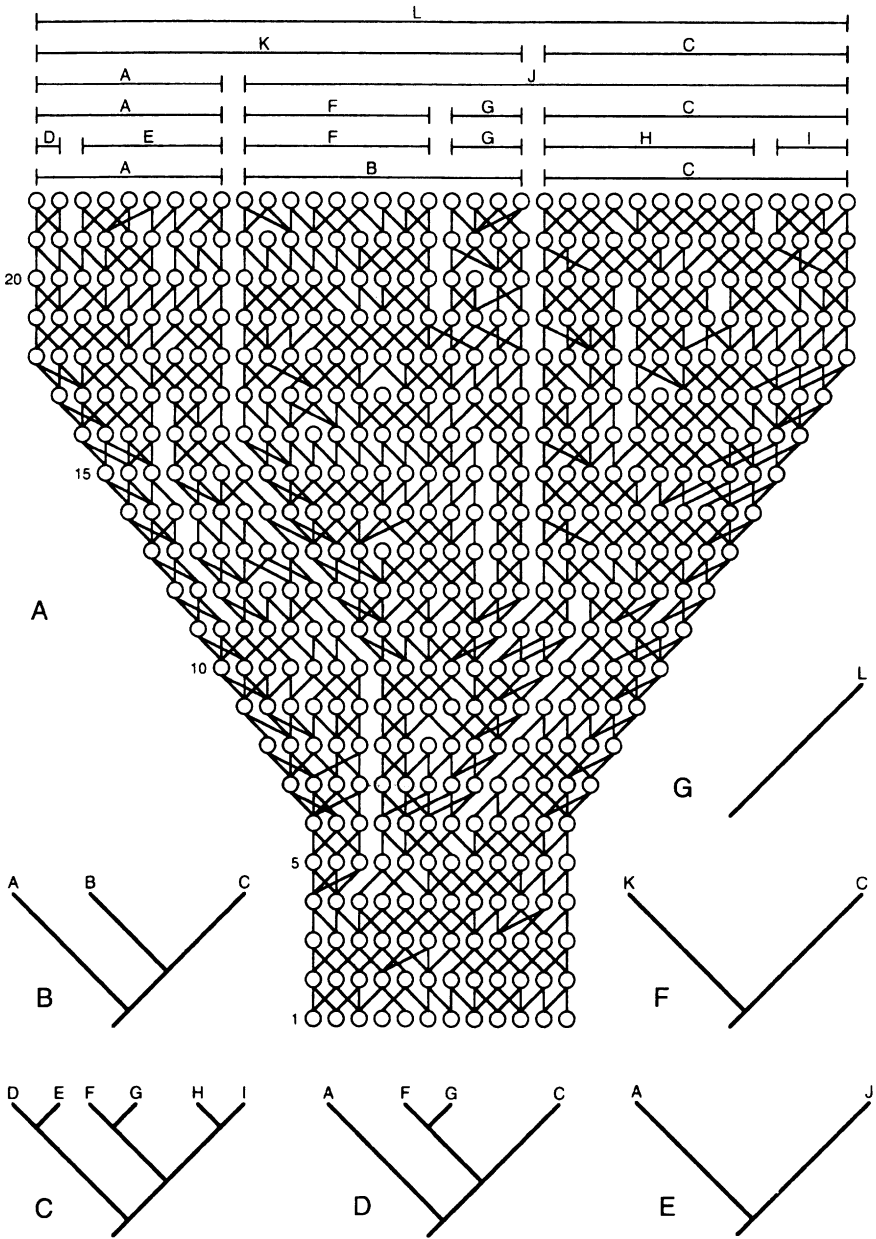


Fig. 2. An hypothetical evolutionary chronicle (A) and six different generalisations of that chronicle (B–G) depending on different perspectives used to interpret gaps in the “fabric of relationships”. Adapted from O’Hara (1993, Fig. 6).

this level—those working from below and those working from above—can be at odds, and we need continued dialogue, interaction, and clear presentation of assumptions in order to sort these issues out.

Speciation. — At the level of speciation in plants, there has been much progress made in understanding both pattern and processes operating (e.g., entire 7th issue of *Trends in Ecology and Evolution*, vol. 16). Much of this work has been done with adaptive radiations on island settings, both continental and oceanic (Wagner & Funk, 1995; Givnish & Sytsma, 1997a; Givnish, 1998; Grant, 1998). Some of the most exciting work has been done in the area of hybrid and polyploid speciation (Rieseberg, 1997, 2001; Cook & al., 1998; Wolfe & al., 1998; Rieseberg & al., 2000). One of the most promising areas for future work, where broadly trained systematists can make a major impact, is the study of pollination biology, floral evolution, and genetic analysis of floral differences. The emerging realisation that many closely related species diverge dramatically in floral form and pollinator specificity (e.g., *Platanthera*, Hapeman & Inouye, 1997), and that the underlying genetic differences responsible for such changes are often minor (e.g., *Mimulus*, Bradshaw & al., 1998; Schemske & Bradshaw, 1999), opens a myriad of research paths that systematists can and should travel.

Floristics and monography. — How many species of plants are there? As one of the fundamental and most basic duties of systematics, it is with some guilt that we do not really know the answer to this question. Inventorying (and naming of species) certainly has taken a back seat to other areas in systematics: “Excited by the many new and rapidly growing fields of investigation associated with modern biology, we sometimes forget that it is the actual plants, their ranges and other features, and their status that we need to investigate first. Without the continuous acquisition of such knowledge, so fundamental for everything else; without the ability to recognize and distinguish the kinds of organisms; without the careful documentation of what we learn in biological collections, nothing else in systematic or evolutionary biology is possible” (Raven, 1995). As Donoghue & Alverson (2000) have convincingly argued that we are in a “New Age of Discovery”, it is imperative that the systematic community ensure that this basic systematic endeavour continue with strong emphasis and funding. This information is more than just a species list. Donoghue & Alverson (2000) document findings from a recent Ph.D. dissertation of 15 tropical plant genera in which more than a third of the species are known from a single herbarium specimen, and well over 60% are known from three or fewer. We know little of geographic ranges and/or variation in a large proportion of the tropical flora. It is perhaps in vogue and satisfying to talk about the “Age of Phylogeny” (Donoghue, 2000) from the comfort of the office chair or lab bench, but “phylogeny” is only as good as the investment made in getting off these chairs and into the field throughout geographical ranges of described and undescribed (and even uncollected) species. “Expeditionary biology is fundamental to modern biology” (V. Funk, pers. comm.).

A detailed look at the issues surrounding floristic and monographic projects is provided by Heywood (2001), and the specific issue of incorporating phylogenetic results into floristic treatments is increasingly being examined (Sanders & Judd, 2000). It is worthwhile looking at one aspect of this problem. The tendency to let flounder, stop, or not even initiate floristic (or monographic) works is telling perhaps of our society’s (and funding agencies) need for immediate results. But it is also telling of the unrealistic expectations on the part of our discipline in mandating

100% completion and coverage with all the “i”s dotted and “t”s crossed before the information sees the light of day. These projects need not be open-ended enterprises, but surely with the advent of the electronic age, they could be provided in different, “user-friendly” formats (Ribeiro & al., 1999; Heywood, 2001), or updated and enlarged through time (Kartesz, 2000; Miller & Arriagada, 2000). Wilson (2001) argues that increasingly the digital format will be the archival copy or perhaps the only copy.

The Flora North America project had its own symposium back at the XI International Botanical Congress at Seattle in 1969—“The Flora North America Project” chaired by R. Thorne. As several of the participants at the XI IBC in Seattle argued and it is increasingly true today, most field biology is done by non-Ph.D. plant systematists, and there are real issues and concerns that we (including our herbaria) have not and are not meeting the needs of the majority of the users of (and taxpayers who have largely paid for) this systematic information. Recent floras such as Hawaii (Wagner & al., 1990) and the Venezuelan Guayana Highlands (Steyermark & al., 1995) are success stories of how such floras can still be done in timely fashion. After these floristic databases are digitised, the next step is to link them to phylogenetic databases. Perhaps what we need besides “TreeBASE” (<http://phylogeny.harvard.edu/treebase>) and the “Tree of Life” (<http://phylogeny.arizona.edu/tree/phylogeny.html>) is the “TreeShrubHerb BASE” with updatable information on keys, distributions, and descriptions of the world’s flora. As a starter, the further development and use of descriptive, but multi-purpose, databases such as DELTA (Dallwitz & al., 1993, 2000) are needed.

Nomenclature/classification. — The issue of nomenclature and classification, at least as we define them here as domains within taxonomy (Stuessy, 1990), encompasses three distinct but linked problems: species definitions or recognition, naming of these species, and grouping species in clades or categories. In the area of species definitions we have made significant strides (or circles perhaps), but has this field progressed largely one-sided and become increasingly so out of touch with reality that we are alienating not only the non-professional users of “species” but many of our colleagues in related fields as well? We will get back later to the issue of “pattern” and “process” and pluralism and what they bode for the future of species definitions, but this quote from one of our more astute evolutionary ecologists has some ring of truth: “We should reject the idea that pattern-based species concepts are superior to the BSC, or at least limit the number of new proposals to one per century. When combined with phylogenetic information, the BSC provides a powerful framework for studying the process of speciation in a wide variety of organisms” (Schemske, 2000). We are not advocating the biological species concept per se, but applaud the idea of testing and/or modelling species concepts instead of insisting on one concept out of principle (see discussion of “pluralism” below).

In similar vein, McNeill’s (2000) overview of nomenclatural issues (at least the traditional ones) raises similar tensions of what might be needed and what some of us perhaps are insisting on. We professional systematists, who are a small minority of users, need to seriously entertain bionomenclatural stability and tradition. The historic tendency in nomenclature to improve its rules by a continual process of “tinkering” with the Code does need to give way to the recognition that stability and

simplicity in names and web-based lists of names will be crucial and necessary for providing this taxonomic information to its main “users.” In the words of McNeill (2000), “what we need are more and more authoritative lists, readily available to users, which, as they become more and more complete and hence more valuable will, like Linnaeus’ binomials, become *de facto* and then inevitably *de jure* standards for plant nomenclature.” Greuter (2000) paints a dismal view of the future of taxonomy (in the narrow sense) if we fail to see that nomenclature at present is itself a major impediment to the progress of taxonomy and we throw away the “taxonomists’ chance of a lifetime” (the possessive is here changed to the plural). Changes in technology, in systematic endeavours, and in the users of this information will lead to changes in nomenclatural needs in the next 50 years. If so, “Names in Current Use” proposals will have to be accepted by botanists, as have been accepted—at least in part—by bacteriologists (since 1980) and zoologists (Ride & al., 1999). Despite how one reacts to the changes in classification (above the species level) endorsed by *PhyloCode* advocates [see Nixon & Carpenter (2000) and Stevens (2000) for such well-argued reactions], the real friction will be in how species names will be used. While the phylogenetic method would increase explicitness and universality regarding the application of names, it may do so at the expense of taxonomic flexibility and circumscriptional stability (Moore, 1998). While many views exist among *PhyloCode* advocates on how to name species (Cantino, 1998; Cantino & al., 1999), we predict that the success (and acceptance) of phylogenetic nomenclature in general will be dependent on the final decision whether or not to have species names reflect as closely as possible the present binomial system, and thus possess “historical” information and connotations readily grasped by most of the users of systematic information. Suggestions are provided on how a code of nomenclature could be designed so as to accommodate both systems (Moore, 1998), and the systematic community would be wise to consider them.

Perhaps the one area that really has identified and placed its stamp on the field of systematics in the last two decades of the 20th century is phylogenetics and the knowledge gained of relationships above the species level with resulting new classifications. The forecast of Raven (1995) of what would happen in one decade is perhaps too conservative: “We are clearly living in the most exciting period ever for the study of plant phylogeny, a period in which we shall understand well for the first time the phylogenetic structures of individual families, the relationships of families, and the evolutionary history of phyla and kingdoms of organisms. Within no more than a decade, we shall have achieved a relatively complete solution to problems that have preoccupied botanists for centuries, and a vision of plant evolution that will exceed anything we can imagine now”. Molecular systematics (see above) has been pivotal in the proliferation of new, and often updateable, classification systems of all green plants. This plethora of phylogenetic information, both morphological and molecular, is increasingly being used to make changes in classification systems at all levels (APG, 1998; Chase & al., 2000a, b).

Again we systematists must heed Raven (1995): “Although we are all deeply and properly impressed with the power of cladistic methods of analysis, and with the exciting new information that is becoming available as result of macromolecular comparisons, as well as with the importance of information retrieval, it is ultimately

the scientific process of classification—of grouping organisms into meaningful units—that makes possible everything else in systematic, evolutionary, and environmental biology, and which ultimately gives meaning to all of biology”. The emerging controversies fall along two issues: principles of grouping—for example, should we allow paraphyletic groups (Brummitt & Sosef, 1998), and principles of naming—for example, should we use phylogenetic or rankless systems (de Queiroz & Gauthier, 1990, 1992; Withgott, 2000). Careful attention is required to the wider impact of these changes on the majority of users of systematic information (Stevens, 1998, 2000), and to what is gained/lost (Moore, 1998; Bremer, 2000). We predict that portions of the *PhyloCode* pertaining to issues above the species level will be incorporated into the rudiments of the Linnaean system; an example of such an attempt is seen in Bremer (2000).

Where do we go from here, and how do we get there?

In summary of where systematics is now, it should be clear it has advanced very fast along some of these fronts, and very slowly along others. This is, of course, to be expected based on the emergence of novel ideas, tools, fields, and funding which drive systematics. Where we go from here and how we get there as a discipline has been examined somewhat in the previous section, and are similarly discussed as seven goals for systematic botany in the 21st century by Nordenstam & Ehrendorfer (2000). We highlight four critical issues below.

Plant systematics and its utility. — We need to make plant systematics useful to the rest of the world (inventory, nomenclature, classification, geographic ranges, conservation status, phylogenetic relationships)—we are, after all, just a small minority of those actually using this information. Heywood (2001) emphasises this point based on the three key missions as outlined in *Systematics Agenda 2000* (Anonymous, 1994). Ecologists, for example, have done more to build bridges with policy-making people and organisations than have systematists (Allen & al., 2001).

Dialogue with other disciplines. — Many of the previous papers in this Jubilee Series call for closer ties of systematics to emerging areas in genomics, bioinformatics, ecology, to name a few. Systematists need to continue dialogue with other disciplines—not just in terms of borrowing tools, but using our model systems and approaches to help refine and elaborate these emerging areas with a decisively systematic tenor. Much of this new work is being done very well in horticultural/agronomy settings, but the systematic perspective and thus broader and more interesting questions have not yet been woven into the fabric of these approaches.

Multi-disciplinary training. — The field of systematics needs to go back to truly multi-disciplinary Ph.D. (and post-doc) training. We are losing our broadly trained systematists, as more and more students simply get trained in phylogenetics, with field and herbarium work comprising increasingly smaller sections of Ph.D. theses. Is it not uncommon to receive reviews for U.S.A. National Science Foundation proposals that criticise or at least question the requests for travel and field expenses when it is generally assumed that one could simply mine the genetic information from specimens in the herbaria? Perhaps the systematic community should insist on

linkage of federal grant funds with truly multi-disciplinary studies incorporating at least some amount of field work [see Landrum (2001) for a commentary on this issue]. Perhaps we need to insist on a reward structure for those willing to invest in long term (and multi-disciplinary research) that is not typical of today's systematic grant funding—i.e., where results of long-term investment clearly outweighs the loss of short-term profits (papers). Raven (1995) has already stressed this point: "Although investigations of this sort [long-term biosystematic studies] are not suitable for doctoral dissertations, people who have long-term employment and access to the necessary field space might appropriately plan such experiments and carry them out. Doing so would enhance our knowledge of patterns of variation and evolution of some very different groups of California plants greatly, and assist in the development of a synthetic theory of plant evolution". Perhaps the systematic community should insist on some amount of funding for long-term systematic studies; ecologists have their LTER (Long-Term Ecological Research) sites, do we not need as systematists our LTSR (Long-Term Systematic Research) projects? As it has been argued for ecology (Allen & al., 2001), multi-disciplinary projects should desire to be self-reflective and therefore should include collaborations and training for the history, philosophy, and sociology of our discipline.

Integration/synthesis (pluralism).— As the field of systematics begins a new millenium of endeavour, one adjective probably more than any other describes the field—divided. Systematics needs to consider other assumptions and approaches without reifying one particular view. How do we produce synthesis or integration in systematics? What is synthesis? Why do we need **one** synthesis? Why not have a pluralistic view? Let's look at two examples:

"Ultimately, we envisage a future in which we worry primarily about managing the vast wealth of systematic data available to us....**Clearly our biggest problems are not methodological or theoretical.** They are instead mundane and unexciting and consist of how we document, manage, and communicate the vast amounts of systematic information that we are set up to produce and need to integrate" (Savolainen & al., 2000). While we agree with Savolainen & al. that analyzing large data sets can be easier and faster than constructing the appendices of vouchers and GENBANK numbers that accompany such publications, we disagree in that we think there remain many large and exciting methodological and theoretical issues. We need to look at methods of analysis and theory—what Doyle (1993) has so appropriately called the soft underbelly of systematics. Both "*to produce*" and "*to integrate*" are so dependent on methodology and theory used!

Second, much of our present debates in systematics are based on taking narrow or partial views of important but complex or dualistic issues. For example, the debates that centre on "pattern" vs. "process" and its many manifestations such as classification and the species concept issue are inherently the result of reifying one or the other of the two faces of evolution. Darwin's (1859) definition of evolution is "**descent with modification**"—evolution is thus inherently dualistic [see Knox (1998) for further discussion on this topic]. As Stebbins (1970) so cogently stated, "Among botanists who are concerned with classifying and understanding relationships between plants, there are some who think only in terms of the end products of evolution and others who are primarily concerned with its processes. Both kinds of

approach to the problem of evolutionary diversity are legitimate and important, but a distinction must be made between them”. Cladistics, for example, although powerful is thus limited as it gives primacy only to “descent” and increasingly, at least, refuses to acknowledge “modification” as coequal with “descent” [see further review of this issue by Knox (1998)]. Likewise, in species definitions, are we placing too much emphasis on “pattern” and not on “process”—as Schemske (2000) and Stebbins (1970) were suggesting?

Depicted in Fig. 3 is the view from Lyman Benson’s (1962) classic textbook showing the interrelationships of disciplines. Note how the various disciplines can take their turn in the centre. Today we have moved “phylogeny” into the centre and largely excluded the others from participating in the centre as a focal viewpoint. Do we need just “phylogenetic background”—that is, just “tree thinking”—despite how

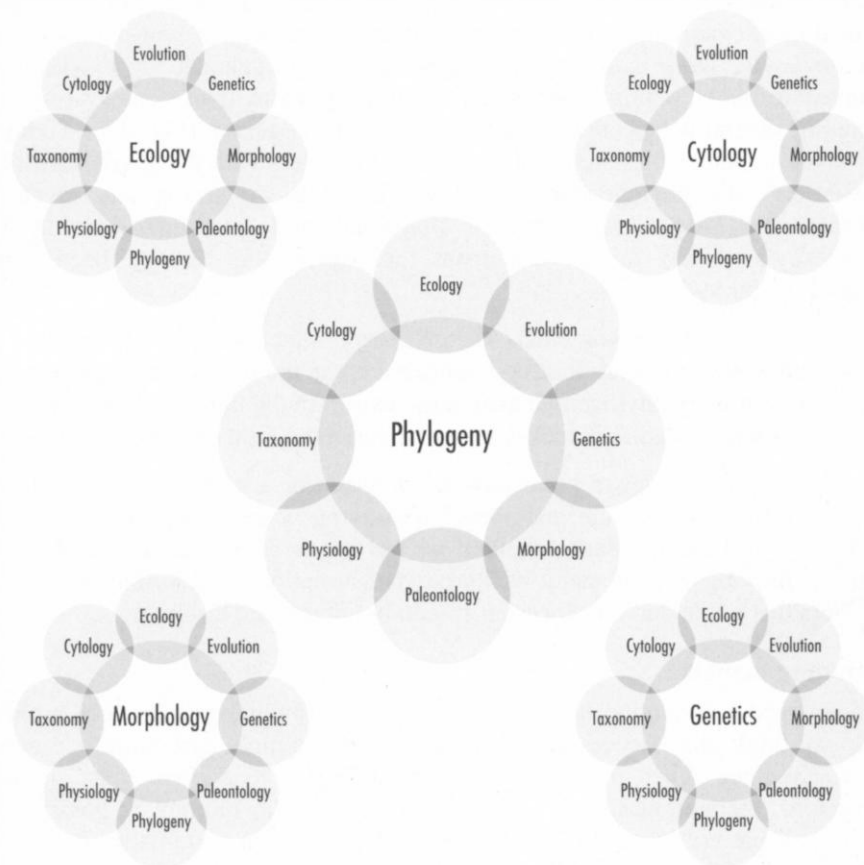


Fig. 3. Inter-relationships of biological systematic fields [adapted from Benson (1962, Figs. 8–1)]. Each field is characterised by its special objective when placed in the centre, but with contributing perspectives or circles. “Phylogenetics in the centre” is increasingly becoming the paradigm of modern systematics.

powerful this approach is? Is there always only one thing in the middle (e.g., phylogeny), or can we place different items in the middle as the occasion dictates? For example, “ecology” is a big black hole that would be useful to explore as an item in the “middle”—for issues of canalisation, phylogenetic constraint, niche conservatism, concerted homoplasy, for starters. Pluralism we would argue, not a single world view, is necessary and healthy in systematics. Are not the current debates on monophyly, species definitions, *PhyloCode*, for example, just an attempt to find the “one best system”? But is there one system, let alone one best system? Perhaps we need a “system of systems”, a “hierarchy of hierarchies” —in the words of Small (1989): “It is ironic that specialists in biological classification have failed to provide a clear systematization and clear nomenclature for their own field and its components”.

The biosystematic work of Clausen & al. (1940) might be illustrative of where we are going and perhaps what we are losing. The work of this group of systematists and ecologists was an explicit attempt at being pluralistic in world views. Their work on *Layia*, *Viola*, and other plant groups was summarised by diagrams that attempted to show multiple perspectives: showing more than “one history” and illustrating several perspectives of the evolution of the genera (Fig. 4A). Today we have largely replaced these icons of the biosystematic era with the **single icon** of the cladistic era—the phylogenetic tree (Fig. 4B). Are we seeing now even this important, but single, icon further simplified and reduced? Starting with Dobzhansky’s (1973) famous statement, has systematic biology been further collapsed by this syllogism?:

Nothing in biology makes sense except in the light of evolution
 Nothing in evolution makes sense except in the light of phylogeny
 Nothing in phylogeny makes sense except in the light of cladistics
 Nothing in cladistics makes sense except in the light of total evidence

We ask, is this syllogism a narrative of progress or a narrative of reduction of historical sciences to computer programs? We obviously are not opposed to the light shed by any of these approaches; rather, we are opposed to systematic biology that insists on reifying one of many background assumptions and verbal models and metaphors that guide our very (or what should be) pluralistic discipline.

Concluding thoughts

Do we need a revolution in systematics? No, we do not argue for such a change nor do we think one is necessary. Revolutions often simply cast aside one narrow view for another, when in fact a pluralistic approach to a diverse set of ideas, assumptions, technologies, and approaches in systematic biology is possible and necessary. What we do need is a careful rethinking of what systematics is all about and a thoughtful look both at the road already well traveled and at the road map ahead; it is re-mapping and connecting the multiple directions we take—not the singular revolution we do—with what we have received from the past, have added in the last few years, and what we are willing to deal with in the future that will largely define how successful plant systematics will be in the next 50 years. In the

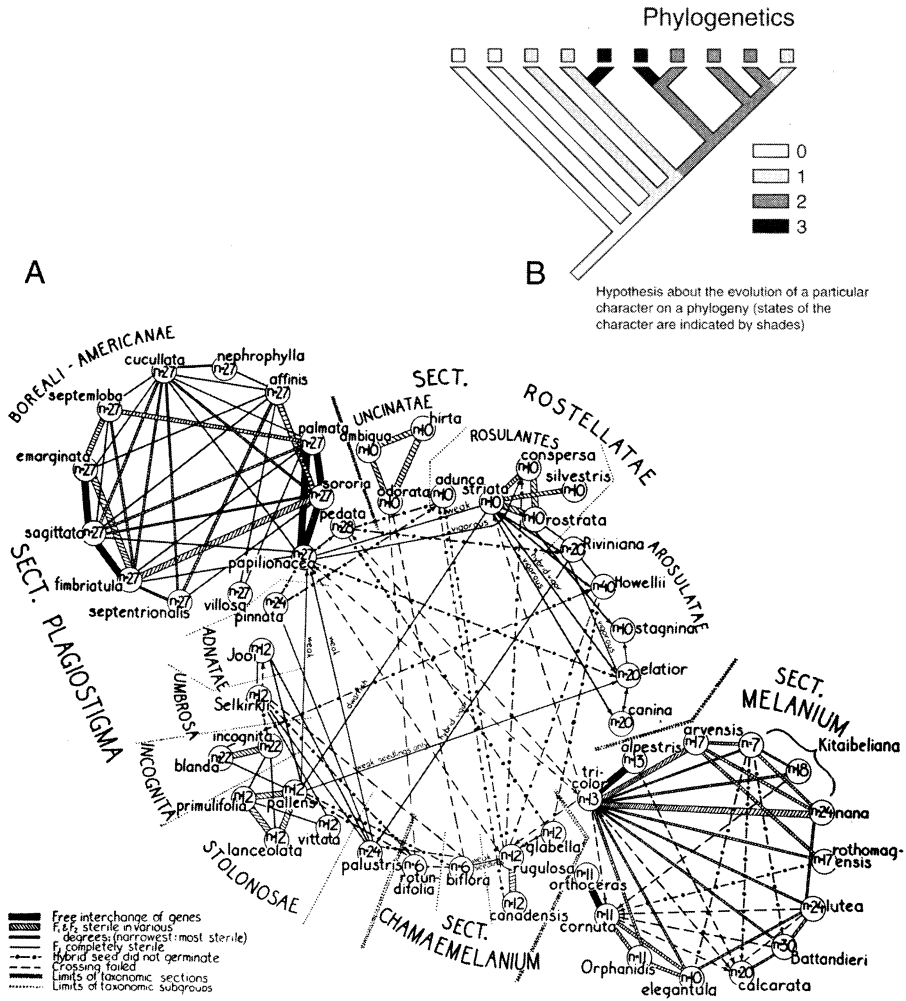


Fig. 4. Interrelationships of species from a pluralistic biosystematic viewpoint [A; adapted from Clausen (1951, Fig. 64)] in contrast with that solely from the phylogenetic viewpoint (B).

words of Ralph Waldo Emerson (1893) in “The American Scholar”—“this time, like all times, is a very good one, if we but know what to do with it”.

Literature cited

Abbott, R. J., Smith, L. C., Milne, R. I., Crawford, R. M. M., Wolff, K. & Balfour, J. 2000. Molecular analysis of plant migration and refugia in the Arctic. *Science* 289: 1343–1346.

Albert, V. A., Gustaffson, M. H. G. & DiLaurenzio, L. 1998. Ontogenetic systematics, molecular developmental genetics, and the angiosperm petal. Pp. 349–374 in: Soltis, D. E., Soltis, P. S. & Doyle, J. J. (eds.), *Molecular systematics of plants II: DNA sequencing*. Norwell, Massachusetts.

Allen, T. F., Tainter, J. A., Pires, J. C. & Hoekstra, T. W. 2001. Dragnet ecology—“Just the facts, ma’am,” a privilege of science in a post-modern world. *BioScience* 51: 475–485.

- Anonymous. 1994. *Systematic agenda 2000: charting the biosphere*. New York.
- APG [The Angiosperm Phylogeny Group]. 1998. An ordinal classification for the families of flowering plants. *Ann. Missouri Bot. Gard.* 85: 531–553.
- Arabidopsis Genome Initiative. 2000. Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana*. *Nature* 408: 796–815.
- Avise, J. C., Arnold, J., Ball, R. M., Bermingham, E., Lamb, T., Neigel, J. E., Reeb, C. A. & Saunders, N. C. 1987. Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annual Rev. Ecol. Syst.* 18: 489–522.
- Barkman, T. J., Chenery, G., McNeal, J. R., Lyons-Weiler, J., Ellisens, W. J., Moore, G., Wolfe, A. D. & dePamphilis, C. W. 2000. Independent and combined analyses of sequences from all three genomic compartments converge on the root of flowering plant phylogeny. *Proc. Natl. Acad. Sci. U.S.A.* 97: 13166–1317.
- Barrett, S. C. H. & Pannell, J. R. 1999. Metapopulation dynamics and mating-system evolution in plants. Pp. 74–100 in: Hollingsworth, P. M., Bateman, R. M. & Gornall, R. J. (eds.), *Molecular systematics and plant evolution*. London.
- Baum, D. A. 1998. The evolution of plant development. *Curr. Opin. Pl. Biol.* 1: 79–86.
- Bennett, M. D. 1998. Plant genome values: how much do we know? *Proc. Natl. Acad. Sci. U.S.A.* 95: 2011–2016.
- Bennetzen, J. L. 2000. Comparative sequence analysis of plant nuclear genomes: microlinearity and its many exceptions. *Pl. Cell* 12: 1021–1029.
- Benson, L. 1962. *Plant taxonomy*. New York.
- Bradshaw, H. D., Otto, K. G., Frewen, B. E., McKay, J. K. & Schemske, D. W. 1998. Quantitative trait loci affecting differences in floral morphology between two species of monkeyflower (*Mimulus*). *Genetics* 149: 367–382.
- Bremer, K. 2000. Phylogenetic nomenclature and the ordinal system of the angiosperms. Pp. 125–133 in: Nordenstam, B., El-Ghazaly, G. & Kassas, M. (eds.), *Plant systematics for the 21st century*. London.
- Brummitt, R. K. & Sosef, M. S. M. 1998. Paraphyletic taxa are inherent in Linnaean classification —a reply to Freudenstein. *Taxon* 47: 411–412.
- Cantino, P. D. 1998. Binomials, hyphenated uninomials, and phylogenetic nomenclature. *Taxon* 47: 425–429.
- , Bryant, H. N., de Queiroz, K., Donoghue, M. J., Eriksson, T., Hillis, D. M. & Lee, M. S. Y. 1999. Species names in phylogenetic nomenclature. *Syst. Biol.* 48: 790–807.
- Chase, M. W., Fay, M. F. & Savolainen, V. 2000a. Higher-level classification in the angiosperms: new insights from the perspective of DNA sequence data. *Taxon* 49: 685–704.
- , Soltis, D. E., Soltis, P. S., Rudall, P. J., Fay, M. F., Hahn, W. H., Sullivan, S., Joseph, J., Molvray, M., Kores, P. J., Givnish, T. J., Sytsma, K. J. & Pires, J. C. 2000b. Higher-level systematics of the monocotyledons: an assessment of current knowledge and a new classification. Pp. 3–16 in: Wilson, K. L. & Morrison, D. A. (eds.), *Monocots: systematics and evolution*. Sydney.
- Clausen, J. 1951. *Stages in the evolution of plant species*. Ithaca, New York.
- , Keck, D. D. & Hiesey, W. M. 1940. *Experimental studies on the nature of species*. Washington, D.C.
- Cook, L. M., Soltis, P. S., Brunfeld, S. J. & Soltis, D. E. 1998. Multiple independent formations of *Tragopogon* tetraploids (*Asteraceae*): evidence from RAPD markers. *Molec. Ecol.* 7: 1293–1302.
- Crawford, D. J. 2000. Plant macromolecular systematics in the past 50 years: one view. *Taxon* 49: 479–501.
- Dallwitz, M. J., Paine, T. A. & Zurcher, E. J. 1993. *User's guide to the DELTA system: a general system for processing taxonomic descriptions*. [<http://biodiversity.uno.edu/delta/>].
- , – & – 2000. *Principles of interactive keys*. [<http://biodiversity.uno.edu/delta/>].
- Darwin, C. 1859. *The origin of species by means of natural selection*. London.
- de Queiroz, K. & Gauthier, J. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. *Syst. Zool.* 39: 307–322.

- & – 1992. Phylogenetic taxonomy. *Annual Rev. Ecol. Syst.* 23: 449–480.
- Devos, K. M. & Gale, M. D. 2000. Genome relationships: the grass model in current research. *Plant Cell* 12: 637–646.
- Dobzhansky, T. G. 1973. Nothing in biology makes sense except in the light of evolution. *Amer. Biol. Teacher* 35: 125–129.
- Doebley, J. & Wang, R. L. 1997. Genetics and the evolution of plant form: an example from maize. *Cold Spring Harbor Symp. Quant. Biol.* 62: 361–367.
- Donoghue, M. J. 2000. Frontiers in phylogenetic biology. *Amer. J. Bot.* 87 (6, suppl.): 2. [Abstr.]
- & Alverson, W. S. 2000. A new age of discovery. *Ann. Missouri Bot. Gard.* 87: 110–126.
- Doyle, J. J. 1993. DNA, phylogeny, and the flowering of plant systematics. *BioScience* 43: 380–389.
- Ehrendorfer, F. 1970. Introduction. Biosystematics at the crossroads. Proceedings of a symposium held at the XI International Botanical Congress, Seattle—1969. *Taxon* 19: 137–139.
- Emerson, R. W. 1893. *The American scholar. Self-reliance. Compensation.* New York.
- Endress, P. K., Baas, P. & Gregory, M. 2000. Systematic plant morphology and anatomy—50 years of progress. *Taxon* 49: 401–434.
- Friedman, W. E. & Floyd, S. K. 2001. Perspective: the origin of flowering plants and their reproductive biology—a tale of two phylogenies. *Evolution* 55: 217–231.
- Givnish, T. J. 1998. Adaptive radiation of plants on oceanic islands: classical patterns, molecular data, new insights. Pp. 281–304 in: Grant, P. (ed.), *Evolution on islands*. Oxford.
- , Evans, T. M., Pires, J. C. & Sytsma, K. J. 1999. Polyphyly and convergent morphological evolution in *Commelinales* and *Commelinidae*: evidence from *rbcl* sequence data. *Molec. Phyl. Evol.* 12: 60–385.
- & Patterson, T. B. 2000. Adaptive radiation: concerted convergence and the crucial contribution of molecular systematics. Pp. 97–110 in: Iwatsuki, K. (ed.), *IIAS international symposium on biodiversity*. Kyoto.
- & Sytsma, K. J. (eds.). 1997a. *Molecular evolution and adaptive radiation*. New York.
- & – 1997b. Homoplasy in molecular vs. morphological data: the likelihood of correct phylogenetic inference. Pp. 55–101 in: Givnish, T. J. & Sytsma, K. J. (eds.), *Molecular evolution and adaptive radiation*. New York.
- & – 1997c. Consistency, characters, and the likelihood of correct phylogenetic inference. *Molec. Phyl. Evol.* 7: 320–333.
- Graham, S. W. & Olmstead, R. G. 2000. Utility of 17 chloroplast genes for inferring the phylogeny of the basal angiosperms. *Amer. J. Bot.* 87: 1712–1730.
- Grant, P. 1998. *Evolution on islands*. Oxford.
- Greuter, W. 2000. Botanical nomenclature today and tomorrow. Pp. 135–141 in: Nordenstam, B., El-Ghazaly, G. & Kassas, M. (eds.), *Plant systematics for the 21st century*. London.
- Hall, J. C. & Sytsma, K. J. 2000. Solving the riddle of Californian Cuisine: phylogenetic relationships of capers and mustards. *Amer. J. Bot.* 87 (6, suppl.): 132. [Abstr.]
- Hapeman, J. R. & Inouye, K. 1997. Plant-pollinator interactions and floral radiation in *Platanthera* (*Orchidaceae*). Pp. 433–454 in: Givnish, T. J. & Sytsma, K. J. (eds.), *Molecular evolution and adaptive radiation*. New York.
- Heslop-Harrison, J. S. 2000. Comparative genome organization in plants: from sequence and markers to chromatin and chromosomes. *Pl. Cell* 12: 617–635.
- Heywood, V. 2001. Floristics and monography—an uncertain future? *Taxon* 50: 361–380.
- Husband, B. C. & Barrett, S. C. H. 1996. A metapopulation perspective in plant population biology. *J. Ecol.* 84: 461–469.
- & Schemske, D. W. 1998. Cytotype distribution at a diploid-tetraploid contact zone in *Chamerion* (*Epilobium*) *angustifolium* (*Onagraceae*). *Amer. J. Bot.* 85: 1688–1694.
- Jansen, R. K. & Palmer, J. D. 1987. A chloroplast DNA inversion marks an ancient evolutionary split in the sunflower family (*Asteraceae*). *Proc. Natl. Acad. Sci. U.S.A.* 84: 5818–5822.
- Jiang, J. & Gill, B. S. 1994. Nonisotopic in situ hybridization and plant genome mapping: the first 10 years. *Genome* 37: 717–725.

- Kartesz, J. T. 2000. Prospects for a digital flora of North America. Pp. 121–127 in: Lipscomb, B. L., Pipoly III, J. J. & Sanders, R. W. (eds.), *Floristics in the new millennium: proceedings of the Flora of the Southeast US Symposium*. Fort Worth.
- Kellogg, E. A. 2000. Genetics of character evolution. *Amer. J. Bot.* 87 (6, suppl.): 104. [Abstr.]
- Knox, E. B. 1998. The use of hierarchies as organizational models in systematics. *Biol. J. Linn. Soc.* 63: 1–49.
- & Kowal, R. R. 1993. Chromosome-numbers of the East-African giant senecios and giant lobelias and their evolutionary significance. *Amer. J. Bot.* 80: 847–853.
- Koch, M., Bishop, J. & Mitchell-Olds, T. 1999. Molecular systematics and evolution of *Arabidopsis* and *Arabis*. *Pl. Biol.* 1: 529–537.
- Landrum, L. R. 2001. What has happened to descriptive systematics? What would make it thrive? *Syst. Bot.* 26: 438–442.
- Les, D. H., Cleland, M. A. & Waycott, M. 1997. Phylogenetic studies in *Alismatidae*, II—evolution of marine angiosperms (seagrasses) and hydrophily. *Syst. Bot.* 22: 443–463.
- Lim, K. Y., Matyasek, R., Lichtenstein, C. P. & Leitch, A. R. 2000. Molecular cytogenetic analyses and phylogenetic studies in the *Nicotiana* section *Tomentosae*. *Chromosoma* 109: 245–258.
- McNeill, J. 2000. Naming the groups: developing a stable and efficient nomenclature. *Taxon* 49: 705–720.
- Merxmüller, H. 1970. Provocation of biosystematics. Biosystematics at the cross-roads. Proceedings of a symposium held at the XI International Botanical Congress, Seattle—1969. *Taxon* 19: 140–145.
- Meyerowitz, E. M. 1994. Flower development and evolution—new answers and new questions. *Proc. Natl. Acad. Sci. U.S.A.* 91: 5735–5737.
- Miller, N. G. & Arriagada, J. E. 2000. Web site and unpublished data sets for the southeast flora. Pp. 83–96 in: Lipscomb, B. L., Pipoly III, J. J. & Sanders, R. W. (eds.), *Floristics in the new millennium: proceedings of the Flora of the Southeast US Symposium*. Fort Worth.
- Moore, G. 1998. A comparison of traditional and phylogenetic nomenclature. *Taxon* 47: 561–579.
- Nixon, K. C. & Carpenter, J. M. 2000. On the other “phylogenetic systematics”. *Cladistics* 16: 298–318.
- Nordenstam, B. & Ehrendorfer, F. 2000. Future of systematic botany—results of a panel discussion. Pp. 345–356 in: Nordenstam, B., El-Ghazaly, G. & Kassas, M. (eds.), *Plant systematics for the 21st century*. London.
- Nyffeler, R. & Baum, D. A. 2000. Phylogenetic relationships of the durians (*Bombacaceae-Durioneae* or *Malvaceae/Helicteroideae/Durioneae*) based on chloroplast and nuclear ribosomal DNA sequences. *Pl. Syst. Evol.* 224: 55–82.
- O’Hara, R. J. 1992. Telling the tree: narrative representation and the study of evolutionary history. *Biol. Philos.* 7: 135–160.
- 1993. Systematic generalisation, historical fate, and the species problem. *Syst. Biol.* 42: 231–246.
- Ornduff, 1970. Discussion. Biosystematics at the crossroads. Proceedings of a symposium held at the XI International Botanical Congress, Seattle—1969. *Taxon* 19: 202–204.
- Palmer, J. D. & Delwiche, C. F. 1998. The origin and evolution of plastids and their genomes. Pp. 375–409 in: Soltis, D. E., Soltis, P. S. & Doyle, J. J. (eds.), *Molecular systematics of plants II: DNA sequencing*. Norwell, Massachusetts.
- Paterson, A. H., Bowers, J. E., Burow, M. D., Draye, X., Elsik, C. G., Jiang, C.-X., Katsar, C. S., Lan, T.-H., Lin, Y.-R., Ming, R. & Wright, R. J. 2000. Comparative genomics of plant chromosomes. *Pl. Cell* 12: 1523–1539.
- Pires, J. C., Sherwood, A. M., Lim, K. Y., Leitch, A. R., Leitch, I. J., Bennett, M. D., Soltis, P. S. & Soltis, D. E. In press. Integrating molecular cytogenetics and phylogenetics: genome evolution in diploid and polyploid *Tragopogon* (*Asteraceae*). *Amer. J. Bot.* 88 (6, suppl.). [Abstr.]

- Pryer, K. M., Schneider, H., Smith, A. R., Cranfill, R., Wolf, P. G., Hunt, J. S. & Sipes, S. D. 2001. Horsetails and ferns are a monophyletic group and the closest living relatives to seed plants. *Nature* 409: 618–622.
- Qui, Y.-L. & Palmer, J. D. 1999. Phylogeny of early land plants: insights from genes and genomes. *Trends Pl. Science* 4: 26–30.
- , Lee, J. H., Bernasconi-Quadroni, F., Soltis, D. E., Soltis, P. S., Zanis, M., Zimmer, E. A., Chen, Z. D., Savolainen, V. & Chase, M. W. 1999. The earliest angiosperms: evidence from mitochondrial, plastid and nuclear genomes. *Nature* 402: 404–407.
- Raven, P. H. 1995. The university, the state, and the loss of plant diversity. *Madroño* 42: 295–306.
- Ribeiro, J. E. L., Hopkins, M. J. G., Vicentini, A., Sothers, C. A., Costa, M. A., Brito, J. M., Souza, M. A. D., Martins, L. H. P., Lohmann, L. G., Assunção, P. A., Pereira, E., Silva, C. F., Mesquita, M. R. & Procópio, L. C. 1999. *Flora da Reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônia Central*. Manaus.
- Ride, W. D. L., Cogger, H. G., Dupuis, C., Kraus, O., Minelli, A., Thompson, F. C. & Tubbs, P. K. (eds.). 1999. *International code of zoological nomenclature*, ed. 4. London.
- Rieseberg, L. H. 1997. Hybrid origins of plant species. *Annual Rev. Ecol. Syst.* 28: 359–389.
- 1998. Genetic mapping as a tool for studying speciation. Pp. 458–487 in: Soltis, D. E., Soltis, P. S. & Doyle, J. J. (eds.), *Molecular systematics of plants II: DNA sequencing*. Norwell, Massachusetts.
- 2001. Chromosomal rearrangements and speciation. *Trends Ecol. Evol.* 16: 351–58.
- , Baird, S. J. E. & Gardner, K. A. 2000. Hybridization, introgression, and linkage evolution. *Pl. Molec. Biol.* 42: 205–224.
- Roalson, E. H., Columbus, J. T. & E. A. Friar. 2001. Phylogenetic relationships in *Cariceae* (*Cyperaceae*) based on ITS (nrDNA) and *trnT-L-F* (cpDNA) region sequences: assessment of subgeneric and sectional relationships in *Carex* with emphasis on section *Acrocystis*. *Syst. Bot.* 26: 318–341.
- Rodman, J. E., Soltis, P. S., Soltis, D. E., Sytsma, K. J. & Karol, K. G. 1998. Parallel evolution of glucosinolate biosynthesis inferred from congruent nuclear and plastid gene phylogenies. *Amer. J. Bot.* 85: 997–1006.
- Sanders, R. W. & Judd, W. S. 2000. Incorporating phylogenetic results into floristic treatments. Pp. 97–112 in: Lipscomb, B. L., Pipoly III, J. J. & Sanders, R. W. (eds.), *Floristics in the new millennium: proceedings of the Flora of the Southeast US Symposium*. Fort Worth.
- Savolainen, V., Chase, M. W., Hoot, S. B., Morton, C. M., Soltis, D. E., Bayer, C., Fay, M. F., De Bruijn, A. Y., Sullivan, S. & Qiu, Y. L. 2000. Phylogenetics of flowering plants based on combined analysis of plastid *atpB* and *rbcl* gene sequences. *Syst. Biol.* 49: 306–362.
- Schaal, B. A., Hayworth, D. A., Olsen, K. M., Rauscher, J. T. & Smith, W. A. 1998. Phylogenetic studies in plants: problems and prospects. *Molec. Ecol.* 7: 465–474.
- & Leverich, W. J. 2001. Plant population biology and systematics. *Taxon* 50: 679–695.
- & Olsen, K. M. 2000. Gene genealogies and population variation in plants. *Proc. Natl. Acad. Sci. U.S.A.* 97: 7024–7029.
- Schemske, D. W. 2000. Endless forms (book review). *Evolution* 54: 1069–1073.
- & Bradshaw, H. D. 1999. Pollinator preference and the evolution of floral traits in monkeyflowers (*Mimulus*). *Proc. Natl. Acad. Sci. U.S.A.* 96: 11910–11915.
- Schwarzacher, T. & Heslop-Harrison, J. S. 2000. *Practical in situ hybridization*. Oxford.
- Schwarzbach, A. E. & Ricklefs, R. E. 2000. Systematic affinities of *Rhizophoraceae* and *Anisophylleaceae*, and intergeneric relationships within *Rhizophoraceae*, based on chloroplast DNA, nuclear ribosomal DNA, and morphology. *Amer. J. Bot.* 87: 547–564.
- Small, E. 1989. Systematics of biological systematics (or, taxonomy of taxonomy). *Taxon* 38: 335–356.
- Soltis, D. E., Soltis, P. S., Albert, V. A., Oppenheimer, D., dePamphilis, C. W., Ma, H., Frolich, M. W. & Theissen, G. In press. Missing links: the genetic architecture of the flower and floral diversification. *Trends Pl. Sci.* 6.
- Soltis, P. S. & Soltis, D. E. 2000. The role of genetic and genomic attributes in the success of polyploids. *Proc. Natl. Acad. Sci. U.S.A.* 97: 7051–7057.

- & – 2001. Molecular systematics: assembling and using the Tree of Life. *Taxon* 50: 663–677.
- Stace, C. A. 2000. Cytology and cytogenetics as a fundamental taxonomic resource for the 20th and 21st centuries. *Taxon* 49: 451–477.
- & Bailey, J. P. 1999. The value of genomic *in situ* hybridization (GISH) in plant taxonomic and evolutionary studies. Pp. 199–210 in: Hollingsworth, P. M., Bateman, R. M. & Gornall, R. J. (eds.), *Molecular systematics and plant evolution*. London.
- Stebbins, G. L. 1970. Biosystematics: an avenue towards understanding evolution. Biosystematics at the cross-roads. Proceedings of a symposium held at the XI International Botanical Congress, Seattle—1969. *Taxon* 19: 205–214.
- Stevens, P. F. 1998. What kind of classification should the practicing taxonomist use to be saved? Pp. 295–319 in: Dransfield, J., Coode, M. J. E. & Simpson, D. A. (eds.), *Plant diversity in Malesia III: proceedings of the third international Flora Malesiana symposium, 1995*. Kew.
- 2000. Botanical systematics 1950–2000: change, progress, or both? *Taxon* 49: 635–659.
- Steyermark, J. A., Berry, P. E. & Holst, B. K. (eds.). 1995. *Flora of the Venezuelan Guayana*. St. Louis.
- Stuessy, T. F. 1990. *Plant taxonomy: the systematic evaluation of comparative data*. New York.
- Sytsma, K. J. & Hahn, W. J. 1996. Molecular systematics: 1994–1995. *Progr. Bot.* 58: 470–499.
- & – 2000. Molecular systematics: 1997–1999. *Progr. Bot.* 62: 307–339.
- Wagner, W. L. & Funk, V. A. 1995. *Hawaiian biogeography, evolution on a hot spot archipelago*. Washington, D.C.
- , Herbst, D. R. & Sohmer, S. H. 1990. *Manual of the flowering plants of Hawai'i*. Honolulu.
- Wendel, J. F. 2000. Genome evolution in polyploids. *Pl. Molec. Biol.* 42: 225–249.
- Whitlock, B. A., Bayer, C. & Baum, D. A. 2001. Phylogenetic relationships and floral evolution of the *Byttnerioideae* (“*Sterculiaceae*” or *Malvaceae* s.l.) based on sequences of the chloroplast gene, *ndhF*. *Syst. Bot.* 26: 420–437.
- Wilson, H. D. 2001. Informatics: new media and paths of data flow. *Taxon* 50: 381–387.
- Withgott, J. 2000. Is it “So Long, Linnaeus”? *BioScience* 50: 646–651.
- Wolfe, A. D. & Liston, A. 1998. Contributions of PCR-based methods to plant systematics and evolutionary biology. Pp. 43–86 in: Soltis, D. E., Soltis, P. S. & Doyle, J. J. (eds.), *Molecular systematics of plants II: DNA sequencing*. Norwell, Massachusetts.
- , Xiang, Q.-X. & Kephart, S. R. 1998. Diploid hybrid speciation in *Penstemon* (*Scrophulariaceae*). *Proc. Natl. Acad. Sci. U.S.A.* 95: 5112–5115.
- Zhang, D. & Sang, T. 1999. Physical mapping of ribosomal RNA genes in peonies (*Paeonia*, *Paeoniaceae*) by fluorescent *in situ* hybridization: implications for phylogeny and concerted evolution. *Amer. J. Bot.* 86: 735–740.