Botanical systematics 1950–2000: change, progress, or both?

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Summary

Stevens, P. F.: Botanical systematics, 1950–2000: change, progress, or both? – Taxon 49: 635–659. 2000. – ISSN 0040-0262.

Biosystematics, the study of variation patterns and evolution at the species level and below, flourished In the 1950s. Higher evolutionary level studies, however, were stalled because there was no convincing way of hypothesising relationships. Phenetic systematics developed in the late 1950s as a critique of both the goals and methods of evolutionary systematics, its own goals being those earlier stated by Gilmour (1940: 472, emphasis in original): "A natural classification is that grouping which endeavours to utilise *all* the attributes of the individuals under consideration, and hence is useful for a very wide range of purposes". Phenetic computer-assisted analyses of data became popular. Nevertheless, many systematists were specifically interested in phylogenies. By the late 1970s several methods that produced hypotheses of phylogeny were in use; they emphasised the possession of shared, derived characters. Since then variants of parsimony-based Hennigan analyses have remained popular. With the influx of molecular data—a flood after 1990— and the development of methods that estimated aspects of support for branches of phylogenetic trees, a radical overhaul of higher-level relationships got underway. Analyses of species-level patterns of variation were less popular during much of this period, and the process of description of species has remained largely unchanged. However, computer-based interactive keys and multi-purpose descriptive databases may fundamentally affect this area of our business. During the last 50 years some kinds of systematic work have become highly cooperative and systematics as a whole is a much more unified discipline, even as some more traditional areas of botanical systematics seem largely static if not in regress.

Keywords: evolutionary systematics, cladistics, phenetics, species.

Introduction

The three following quotations summarise some of the main developments in systematics over the last sixty years. "...[W]hat place is left for phylogeny? If the lineage concept of phylogenetic relationship is accepted, then a phylogenetic classification must be regarded as a subsidiary classification, useful for the special purpose of studying the relationship between genealogy and other attributes" (Gilmour, 1940: 473). "Mission [of Systematics Agenda 2000] 2: To analyse and synthesise the information derived from this global discovery effort into a predictive classification system that reflects the history of life...to determine the phylogenetic relationships among the major groups of organisms...of groups of species that are critical for applied biology,....of groups of species that are of critical importance for the basic biological sciences" (Anonymous, 1994: 19, 21). "...[M]ost systematic innovation in the last 30 years has revolved around the development of more and better computer methods of phylogeny reconstruction and better understanding of the mathematics and theory underlying them" (Winston, 1999: 442).

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The last fifty years have seen arguably the most far-reaching developments in systematics in the last 300 years. The prioritisation of the aims of systematics has changed, and phylogeny reconstruction, deemed unimportant and/or nigh-on impossible in the 1950s, is now accepted without question as being a major goal for systematics. Gilmour's ideas helped spark this change, even if he himself was not optimistic as to the possibility of reconstructing phylogeny, and he is much cited in systematic textbooks in the latter part of the twentieth century (e.g., Davis & Heywood, 1963; Sokal & Sneath, 1963; Stuessy, 1990; Briggs & Walters, 1997). There are new sources of data and new—both conceptually and technically—ways of analysing these data; Winston's quotation emphasises how important computer technology has been. Finally, the very structure of the discipline of systematics is changing, and parts of it are now unified in a way that they have not been for a very long time.

Any attempt to review developments in systematics over this period in a brief article such as this must fail, if only because of incompleteness; developments in the last ten years alone have been particularly extensive, and few important issues are now restricted to botanical systematics alone. It must also fail if compared to Johnson's (1968) trenchant analyses of systematic practice or Hull's *Science as a Process* (Hull, 1988), although there is necessarily some overlap. I have not attempted to capture the dynamics of botanical systematics in Europe and America in the 1960s and 1980s—the arguments, the shouting, studied exits and entrances, and the confessions of belief. Furthermore, I have been selective; I take most of my examples from flowering plants, and my own interests inevitably affect the issues I consider important. However, an article that simply chronicled seriatim some of the major (how to judge? largest?) articles appearing over the course of the last half century would be of little interest either to write or to read.

Background

In the 1950s higher-level studies of phylogeny were at something of an impasse, largely because there was no accepted method of producing phylogenies. As a student in the 1960s, I first learned families following Hutchinson (1959) and Rendle (1930–1938), but I soon found that there were several other systems, each with its supporters and detractors. Even up to the 1970s, much development in higher-level botanical systematics seemed to be marked largely by the introduction of new kinds of data, each successively touted as being *the* answer to the problems facing systematics (Constance, 1958). Thus in the 1960s chemosystematics was a very dynamic area of systematics, and with the clarification of hybridisation in *Baptisia* (Alston & Turner, 1963) and *Asplenium* (Smith & Levin, 1963) and the potential phylogenetic significance of phenolics (Bate-Smith, 1954, 1962), there was much promise. However, problems developed. For instance, the same compound might be produced by different pathways, or a compound that accumulated in one plant was part of a pathway that in a related plant led to the formation of a quite different substance.

Not only did the new data fail to supply the answer, but there was no agreed-upon way to analyse the data. Innumerable papers in the last fifty years have examined developmental features, wood anatomy, cytology, chemicals, etc., using the data

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presented to understand relationships. However, if I were given a dollar for each paper in which the author confidently stated that particular relationships were excluded or more or less mandated by the observations presented—assertions that would find little current support—I would be distinctly richer. Despite the brave talk of systematics being pre-eminently a discipline that synthesised data (e.g., Constance, 1964), similarity and affinity turned out to be elusive concepts when it came to evaluating relationships. The data themselves were not really readily accessible (Heywood, 1973), and simply too many data had accumulated over the previous two centuries for a single mind to comprehend fully, still less analyse (Johnson, 1968). In systems such as those of Cronquist (1981), Takhtajan (1997) and Thorne (1999) new data have influenced the structure of older systems even as the detailed relationship of any particular set of data to the system remained largely obscure. Exceptions—particularly clear in Cronquist's *magnum opus*—are in cases of doubt: families are assigned to higher taxa because a single character is heavily weighted. It is in this area that there have been the most profound changes of the last fifty years.

In the 1950s and 1960s the field of biosystematics, where emphasis was placed on the evolution of patterns of variation at and below the species level, was very active and attracted many students. In 1950 Stebbins's magisterial *Variation and Evolution in Plants* appeared, a book that more than any one other marked the integration of botany with the evolutionary synthesis (Mayr, 1980; Stebbins, 1980). The biological species concept seemed to some to be applicable to both plants and animals (Grant, 1971; cf. Raven, 1972), and plant speciation was an area of active research. I learned about the work of Stebbins, Gregor, Marsden-Jones, Turrill, Turesson, Danser, Müntzing and their likes, and read Heslop-Harrison's *New Concepts in Flowering-Plant Taxonomy* (Heslop-Harrison, 1953)—it was all about species-level variation. However, since the 1960s, the field has been in decline (Coyne, 1996; Schemske, 2000), the focus of interest switching to studies on population-level variation and processes often without any immediate systematic implications and, more recently and more comprehensively, to studies of higher-level relationships.

Phenetics and cladistics

Here I focus on how phenetics and cladistics, two methods of data analysis informed by rather different philosophies, affected botanists studying higher-level relationships; Hull (1970) provides a contemporary analysis of the philosophical issues involved. Developments in this area mark the period after 1960, although only when molecular data began to be widely used in the last decade was the full potential of some of the new methods of data analysis apparent. By the later 1960s, phenetics or, more broadly, numerical taxonomy, had become well established. Sokal & Sneath (1963) and Sneath & Sokal (1973: see Hull, 1988; Vernon, 1988; Sneath, 1995, for historical background) were two of the main proponents of this approach, and they did what they thought was a demolition job (but which others, such as Rollins, 1965, saw as a straw man argument) on then-current evolutionary taxonomy, emphasising the repeatability and objectivity of the new techniques as compared to the circularity, imprecision, speculative nature, and what seemed anti-scientific approach of evolutionary systematics. Simpson's (1961: 123) mention of

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artistic judgment in systematics seemed a particularly egregious example of the latter.

Phenetics in its twentieth-century guise was made possible by developing computer technology, and Sokal & Sneath (1963) show the taxonomist sitting at the console of a computer that would easily fill my office. A major emphasis was on operationality, and phenetics attempted to demystify and codify what taxonomists did when they went about their daily business (e.g., Cain & Harrison, 1958; Sokal & Rohlf, 1980); the inability of orthodox systematists to say exactly what they were doing and why they were doing it made its defense difficult (Throckmorton, 1965). By making systematists think about how they evaluated relationships, attention also turned to the characters being used to determine relationships (e.g., Kendrick & Proctor, 1964; Kendrick & Weresub, 1966).

Phenetics was often seen as being anti-evolutionary, and although Sneath (1995) claimed that this was not really true, it is certainly accurate to say that phylogeny detection did not come across as an issue of major concern (but cf. Camin & Sokal, 1965). Following Gilmour (e.g., 1940, 1951, 1961; Winsor, 1995, for background), Sokal & Sneath (1963) aimed for a "natural" classification based on as many characters as possible that would *ex ipso facto* be of great general use. Phylogenetic inferences could be made, but only by inspection of phenetic trees, and it seemed possible to Sokal & Sneath that a redefinition of monophyletic might even be "most natural in a phenetic sense". Certainly, given the absence of fossils, understanding phylogeny directly seemed unlikely (Sokal & Sneath, 1963)[2]. In general, early phenetic literature emphasised producing classifications without reference to theories in general, and that of evolution in particular; it could be summarised or caricatured as look, see, infer, code, cluster—or just look, see, code, cluster (Hull, 1970). Johnson (1968), in his criticisms of Gilmour's principles (Gilmour & Walters, 1963), had noted that there was no way of agreeing or testing whether a classification should be changed or not, and in many respects phenetics represented Gilmour's philosophy of classification made operational. Phenetics could, indeed, arbitrarily assign a limit for, say, genera, which were then objectively definable and exactly comparable across the study. One source of interminable argument would have been removed—or at least it would have been if different methods of analysis of the same data had given the same tree.

But many systematists were interested in phylogenetic relationships, whether between species or at higher levels. General-purpose classifications were beside the point; what was needed was a phylogeny. Evolutionary studies gave systematics "meaning, stature and excitement" (Thorne, 1963: 290), while the interest in biochemical systematics in the 1960s owed much to its promise in helping to understand phylogenetic questions (Alston, 1967). As Throckmorton (1965: 222) observed, "Before we can investigate method we must determine its objective...the production of a classification that reflects phylogeny, ...the first thing a taxonomist must do is produce phylogeny", and an emphasis on operationalism (Rollins, 1965), on methods without the goal being clearly articulated, seemed strange.

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[2]Reactions to this paragraph vary. Some have thought it is too mild, others have wondered how phenetics could ever be interpreted as being anti-evolutionary.

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Willi Hennig, an entomologist, had in 1950 already proposed a way to detect phylogenies, although Sokal & Sneath (1963) found Hennig's idea of reciprocal illumination little different from the circularity they saw as damning evolutionary systematics, and most of his other proposals were also found wanting. In any case, phylogenetic systematics remained largely outside the consciousness of botanical systematists. However, what is now called Wagner parsimony, a much-used option in phylogenetic systematics, started a gradual ascent to prominence at about this time. It began inconspicuously in a diagram showing relationships in *Diellia*, a genus of ferns (Wagner, 1952, his Fig. 31; see Fig. 1).
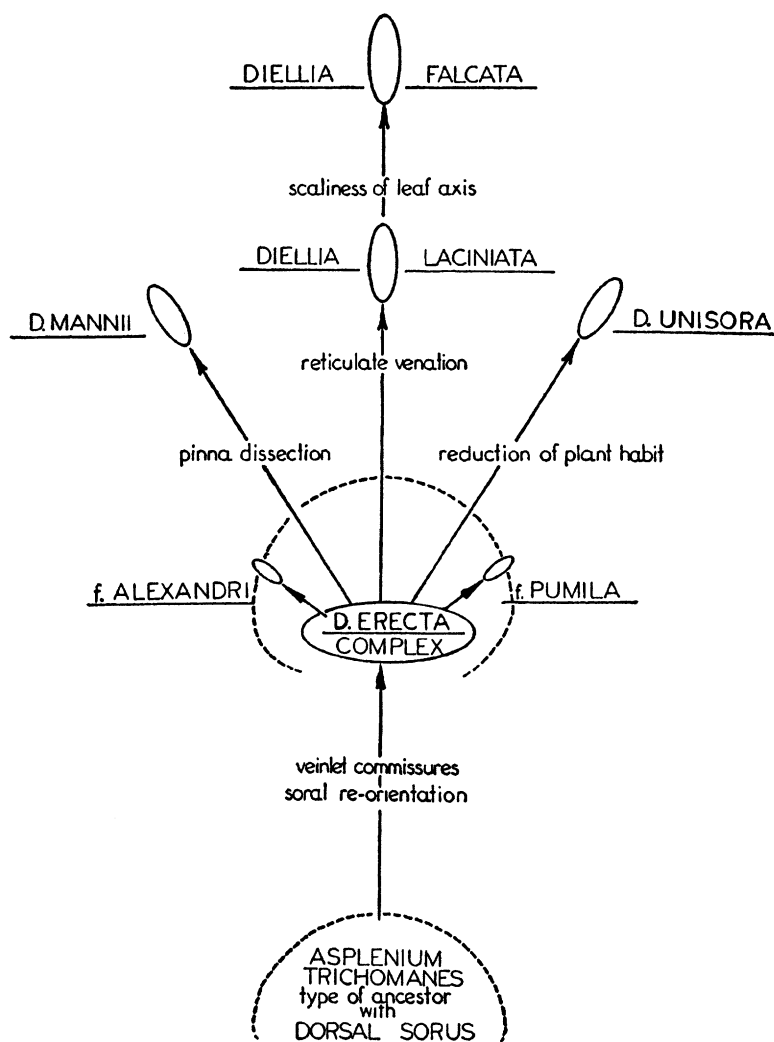

Fig. 1. Relationships in the fern genus *Diellia* (Wagner, 1952).

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In its emphasis on ancestors (Wagner, 1953, even found a herbarium specimen of what he thought was the ancestor of *Diellia*; it is now apparently extinct) and on amount of change, this diagram is conceptually similar to many evolutionary and pre-evolutionary trees (Cuerrier & al., 1996). Wagner (1952) paid considerable attention to derived character states, and his general approach to phylogeny reconstruction was quite widely used over the ensuing quarter of a century, up to four papers per year (in 1963) using his method (see Wagner, 1980). As the method became more formalised (see also Wagner, 1961), the emphasis on ancestors and amount of divergence remained (Wagner, 1980). Adapted for use in computers, it gave rise to Wagner Trees (Kluge & Farris, 1969), although these were based on absolute differences in character states between taxa (i. e., Manhattan distance) rather than synapomorphies (Stuessy, 1990). At that time it was still considered necessary to modify the computer programs for manual use (e.g., Whiffin & Bierner, 1972).

Nevertheless, in the mid 1970s there was relatively little methodological discussion in botany, and the bulk of systematic work remained unaffected by phenetics or by Wagner trees. In 1975 an issue of the *Annals of the Missouri Botanical Garden* was devoted to articles discussing the bases of angiosperm phylogeny, while a year later a symposium in Hamburg addressed problems in higher-level angiosperm classification. The papers in the former were largely reviews of characters, and the problems of what taxa should be compared and why relationships suggested by one set of data should be preferred over those suggested by another. The papers in the Hamburg symposium also suffered from similar problems, although several papers contained phenetic analyses of one sort or another; despite this, Kubitzki (1977: 22) ruefully observed "few people are really aware of just how vacillating the phylogenetic basis of recent systems of classification really is!". Although systematists were interested in the correlation of characters as a way of deciding how valuable they were (see Sporne, 1956, for a widely cited approach), this was a very uncertain affair. As Cronquist (1980: 17) observed, "Like so many other things, [a character] works when it works, and doesn't work when it doesn't" (but cf. Cronquist, 1990). Unfortunately, there was still no way of knowing why a character worked (or didn't), and this, along with the selection of the characters used, was a problem with phenetic analyses such as that by Young & Watson (1970) that attempted to delimit major groupings in dicotyledons. Kendrick & Weresub (1966: 325) also recognised this latter problem as they explained how, in their phenetic study of basidiomycetes, they had recapitulated the whole history of mycology as they experimented with the delimitation and weighting of characters. They concluded "What, after all, is a character? Unless we know this, it seems to us, no technique, however cleverly devised, can be of use to us".

But in the Hamburg symposium in particular there was discussion about several characters—old, old and redefined, and new—that turned out to be very important in understanding higher level relationships (see below). And in Missouri, the authors of the review on chemotaxonomy saw writing on the wall. Zuckerkandl & Pauling (1965) had suggested that variation in amino acid sequences in proteins allowed a reconstruction of their phylogenetic history (see also Crick, 1958). For Fairbrothers

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& al. (1975: 786), this approach "permits the reconstruction of a precise, quantitative, and objective topology of relationships", and despite that they recognised that a gene phylogeny was being produced, they were encouraged to think that an organismal phylogeny was represented because of the successes that zoologists had already achieved. A mitochondrial cytochrome c gene tree of fourteen plants produced by Boulter & al. (1972), was "remarkably similar to more traditionally derived trees based primarily on morphological considerations" (Fairbrothers & al., 1975: 788, his Fig. 13; see Fig. 2), although it is difficult to know which traditionally-derived tree they might have been thinking about. The main drawback with the analysis of amino acids seemed to be that of assembling enough data; how best to analyse such data was not discussed. Later, reviewing plant
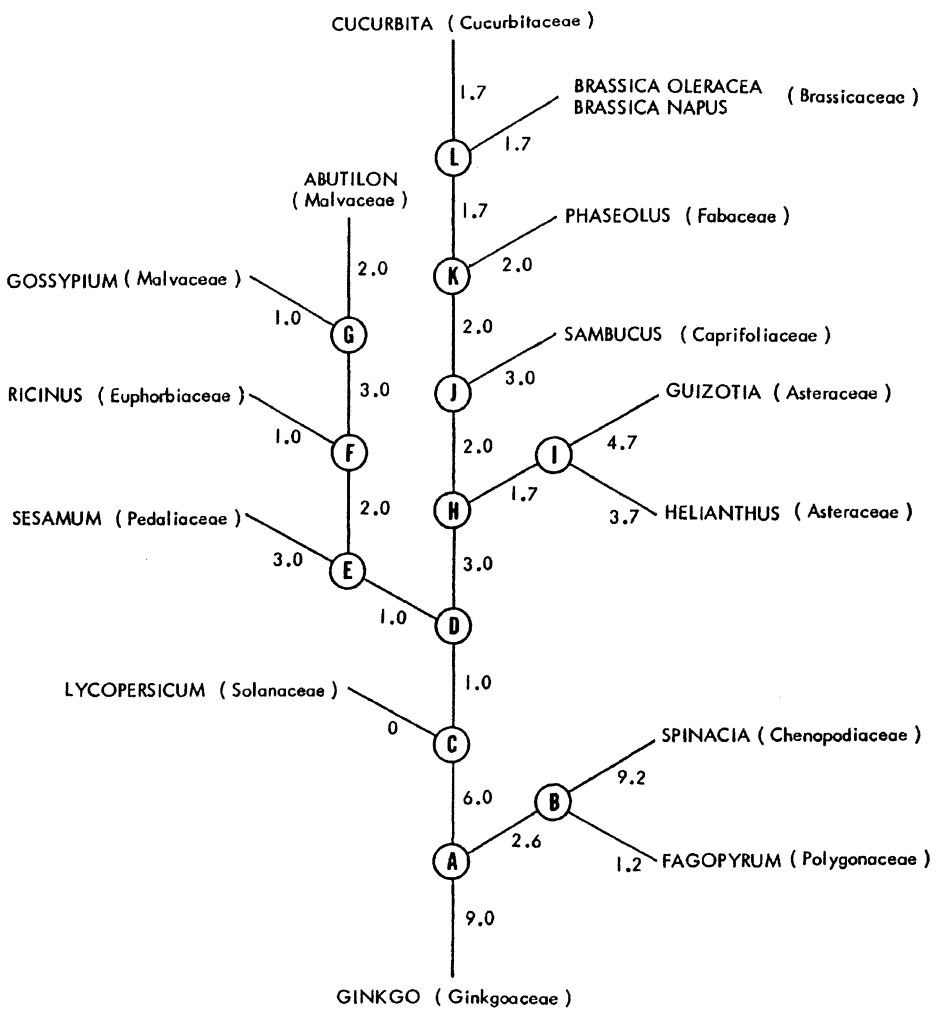

Fig. 2. Relationships among some flowering plants based on amino acid sequences of mitochondrial cytochrome c (Fairbrothers & al., 1975).

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secondary chemicals, Gershenzon & Mabry (1983)—the latter one of the co-authors of Fairbrothers & al.—pointed to two papers, Bate-Smith & al. (1975) and Humphries & Richardson (1980), in which more critical approaches to data analyses were adopted. The former attempted to compute advancement indices—not a novel approach—for *Cornaceae* based on iridoids using (partly) biosynthetic evidence—that is, attempting to get at the idea of similarity from a chemical point of view. The latter was an early example of the use of Hennigian methodology in botany.

It was not until 1978 that Bremer & Wanntorp were able to fix botanists' attention on the work of Hennig (1950, since 1966 available in English). They emphasised that the methods used in Hennigian phylogenetic systematics were repeatable and the results falsifiable—that is, it was "truly part of science according to Popper" (Bremer & Wanntorp, 1978: 322). The bulk of their paper was taken up in discussing the impact of phylogenetic thinking on the circumscription of plant taxa, and they saw change here as necessary because "It is exactly their [traditional classifications] dual foundation on both phenetic and cladistic information which makes them, however, totally unsuitable for such [evolutionary] considerations" (Bremer & Wanntorp, 1978: 328)—and, not so incidentally, made it difficult to understand the whys and wherefores of particular relationships. Of course, given the attempts by pheneticists to clarify just what it was that systematists thought they were doing and to make systematics scientific, it must have seemed somewhat galling to hear cladistics being lauded as finally making systematics a "truly empirical science" (Funk & Brooks, 1981: vi).

Hennig's ideas had impact in phylogenies produced by Bremer (1976) and by Humphries (in Ehrendorfer & al., 1977), and Hennig was mentioned in a study using character compatability (Gardner & La Duke, 1978), another cladistic approach formulated about this time [see Estabrook, 1972 (Hennig is cited here, too); Estabrook & al., 1976]. Numerous specifically Hennigian phylogenetic studies soon appeared, two in particular taking the bull by the horns. Parenti (1980), an ichthyologist, produced the first cladistics-based phylogeny of the land plants, although it occasioned much criticism over the characters used. Her tree suggested that charophytes were sister to land plants. Young (1981) questioned the belief that angiosperms were primitively vesselless and found it wanting; this, he emphasised, affected our search for the ancestral angiosperm. The work of Dahlgren, active in this period, is particularly interesting. "Dahlgrenograms" were initially conceived as a way of presenting data in the context of an implied phylogeny, a transection of an evolutionary tree (Dahlgren, 1975), while Heywood (1978) even saw the value of such diagrams as allowing characters to be interpreted from a largely phenetic point of view. However, Dahlgren was focusing on distinctive and probably derived characters and soon moved to producing cladogram-like "models of evolution" (e.g., Dahlgren & al., 1985) before his untimely death in 1987.

After 1980 there was what can only be called a massive development of phylogenetic systematics (Winston & Metzger, 1998), especially as the use of computers became commonplace and algorithms for analysing data improved. Producing phylogenies became a generally accepted goal for systematists, and in many parts of North America and Europe they are now a necessary part of any systematist's thesis. Gone are the days when floristic accounts were deemed

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adequate to fulfill the research requirements for a doctorate. It fairly quickly became apparent that phylogenies were integral to answering questions that evolutionary biologists in general were asking, or had wanted to ask, but did not know how to answer. The development of the comparative method in evolutionary biology (Harvey & Pagel, 1991) to address evolutionary questions, although perhaps not a development of systematic theory *per se*, meant that one of the major products of late twentieth century systematics, phylogenetic trees, became an integral part of comparative biology; indeed, these trees made comparative biology possible.

Phylogenetic systematics particularly flourished with the development of new sources of data, specifically, data derived from various ways of analysing DNA. A trend in systematics particularly from the 1950s onward has been a shift from data taken from looking directly at plants or their parts to data taken indirectly—data that represent peaks in a chromatogram and the like (Heywood, 1973). This trend has been accentuated by the development of molecular systematics, to the great distress of some. (Of course, any claim that direct observation of the organism is *ex ipso facto* best cannot be maintained.) The impact of molecular systematics was initially quite slow, yet the whole field of molecular systematics as a subdiscipline is less than twenty years old (for references, see Giannasi & Crawford, 1986). Atchison & al. (1976) and Vedel & al. (1976) early explored the use of restriction endo-nucleases; these, by recognising four to six base pair palindromic sequences of chloroplast DNA and cutting the DNA only when there was an exact match, sampled the DNA sequence of the organisms. However, it was not until studies of *Brassica*, *Lycopersicon*, *Triticum*, and *Faboideae* in the early 1980s and the use of phylogenetic methods for analysing the data that the field took off, with over 30 laboratories using the technique in 1988 (reviewed in Palmer & al., 1988). The finding that an inversion in the chloroplast DNA divided up *Asteraceae* in an unexpected way (Jansen & Palmer, 1987), confirming morphological work (Bremer, 1987), was a stimulus both for morphological and molecular phylogenetics. However, in all combined molecular/morphological studies, it is unclear how or how much ideas of relationships developed in molecular work affect how morphologists choose and delimit character states.

Sequencing of contiguous stretches of DNA (e.g., Zurawski & al., 1984) initially was quite time consuming. A thousand base pairs might be analysed per laboratory per week *after* cloning of the fragment, if conditions were favourable. The development of the polymerase chain reaction by Mullis in 1986, however, completely changed this approach—and the face of systematics. By allowing easy amplification of DNA it facilitated sequencing (the latter was quickly highly automated) while grant-awarding bodies like the National Science Foundation (N.S.F.) threw their support behind molecular studies (Chase & Albert, 1998). Since 1990 DNA sequencing has been the molecular technique of choice (Winston & Metzger, 1998), and a milestone was the paper by Chase & al. (1993), by far the largest molecular analysis attempted at that date; subsequent work on higher-level relationships within flowering plants has used this as a benchmark.

Massive amounts of data quickly became available, and it seemed that analytical tools would be unable to cope. The sheer size of the data set in Chase & al. (1993) was such that the analysis was never completed, and it has since been criticised on a

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number of grounds (e.g., Rice & al., 1997—another analysis that was not completed). But not only were more powerful analytical algorithms soon developed, but our preconceptions about how large data sets would behave turned out to be in part incorrect. Large data sets with hundreds of taxa and characters are now almost commonplace (Savolainen & al., 2000; Soltis & al., 2000), and emphasis is placed more on support for branches in trees than on details of the topology of the most parsimonious tree. Heywood in 1974 saw the combination of data from the scanning electron microscope (SEM) and from biochemical systematics interacting with computer technology to change systematics. Although the SEM has not had such a major effect yet, the combination of biochemical systematics (sequence analysis) and computers has proved explosive.

Although it is often easier to obtain molecular than morphological data, and certainly the documentation of the latter is often poorer, there has been a major infusion of new morphological data over the last fifty years. Papers presented at the 1975 Hamburg symposium discuss many characters that have proven to be particularly interesting at high levels, e.g., sieve tube plastids and dilated cisternae in the endoplasmic reticulum (Behnke, 1977), ovule morphology (Philipson, 1977), and numerous features including starchy endosperm and iridoids (Dahlgren, 1977). Philipson (1977) thought unitegmic groups included both sympetalous and polypetalous taxa, but our understanding of this character has been changed by developmental studies (Erbar, 1991); Philipson's sympetalous and polypetalous taxa represent extremes of sympetalous development. Ultrastructural data, including those of the genome, have been particularly valuable in teasing apart relationships at the base of the land plant lineage (e.g., Pickett-Heaps, 1969; Pickett Heaps & Marchant, 1972; Moestrup 1974; Manhart & Palmer, 1990). Systematic palynology has flourished during this last half-century, the name of Erdtman being closely linked with its development (e.g., Erdtman, 1952), and it, too, has profited from the accessibility of the SEM, also developed over this period. Valuable treatments of plant anatomy, and particularly the embryology and morphology of individual groups, continue to appear. These include studies of floral morphology and development using SEM (e.g., Endress & Stumpf, 1991), although one should not forget Payer's remarkable work of almost a century before *Taxon* began (Payer, 1857), of embryological details in monocots (e.g., Rudall & Linder, 1988), and seed coat anatomy (e.g., Corner, 1976; see also Danilova, 1996, and earlier volumes). As E. A. Kellogg (pers. comm.) suggests, the SEM allows botanists without any particular technical skills to make good morphological observations; such obervations could be made in the nineteenth century, but only by highly skilled craftsmen.

Some major phylogenetic studies have used morphological data (e.g., Hufford, 1992; Nandi & al., 1998, in part). However, it is interesting how little morphological information there often is, even of common, widespread taxa like *Platanus*, let alone more restricted but phylogenetically critical taxa like *Physena*, *Simmondsia* and *Asteropeia* (to mention just three examples from *Caryophyllales*). Characters from embryology and chemistry that are deemed important in higher-level classification are often very poorly sampled—a complaint of the first major numerical attempt to detect higher level relationships (Young & Watson, 1970). Older literature can be

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difficult to understand because of the changing use of terms. Finally, the reification of botanical terms has been both pervasive and pernicious. Indeed, although botanists have been using morphological data for hundreds of years, its use in phylogenetic analysis (and elsewhere in systematics) is decidedly less straight-forward than one might have expected (Watson, 1971; Stevens, 2000). The argument as to how effective morphological data are or can be in detecting relationships seems far from being resolved.

In the late 1970s I thought that development might come to play a key role in systematics, but it was soon sidelined. Now, however, close attention to develop-ment is clarifying our interpretation of several important morphological characters, as with corolla type above (see also Floyd & al., 1999, for endosperm; Hermann & Palser, 2000, for anther wall). At the level of gene expression and organ identity the excitement is only just beginning as we struggle to understand the relationship between the reproductive organs of angiosperms and those of gymnosperms, and between the flowers of monocots and those of core eudicots (e.g., Hasebe, 1997; Kramer & Irish, 1999); however, the evolutionary and developmental relationships between the vascular system of the majority of seed plants and that of the monocots remain as inscrutable as ever.

It is surprisingly difficult to evaluate how much change in our understanding of relationships of higher taxa—genus and above—there has been over the last fifty years, and in particular over the last ten years. The "progress" in my title is almost as hard to judge in science as it is in evolution or society. Does the removal of the odd genus from *Euphorbiaceae,* however delimited, really change our understanding of that family? Are adding *Vochysiaceae* to *Myrtales*, *Biebersteiniaceae* to *Sapindales*, or *Scytopetalaceae* to *Lecythidaceae* significant changes? It is certainly hard to downplay the significance of such recent hypotheses as to the composition of *Ericales* (Morton & al., 1997), *Saxifragales* (Soltis & Soltis, 1997), the basal embryophyte lineages and their relatives (Graham, 1985; Mishler & Churchill, 1984; Mishler & al., 1994), and of basal angiosperm lineages (e.g., Mathews & Donoghue, 1999), as well as of the relationships between angiosperms and gymnosperms (e.g., Winter & al., 1999). But even if the circumscription of taxa remains unchanged, having these taxa displayed in the context of a phylogenetic tree for which one can evaluate the support, completely changes our understanding of relationships and evolution. Indeed, that some "new" relationships have been suggested in the past is not quite to the point; now there is a way of evaluating evidence to choose between alternative hypotheses of relationship, and the choice is no longer simply having stood the test of time (interestingly, a test used also by Sokal & al., 1965). Teaching today is certainly quite different from what it was a decade ago. As Reinaldo Aguilar F. (pers. comm.) mentioned when finding out about recent ideas of relationships, it had never been satisfactory simply being *told* that genera in the old *Malvales* belonged to a particular family. It was a relief to him to find out that there was in fact no support for these families (*Malvaceae* s.str. in part excepted; e.g., Alverson & al., 1999); a broad *Malvaceae* was a satisfactory concept to learn, as was a *Putranjivaceae* removed from *Euphorbiaceae*.

Interestingly, Davis (1978) thought that it was phylogenetic speculation that contributed to the confusion in ordinal and supraordinal levels of classification, and

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he saw a long battle ahead over groupings at this level. He also noted rather sadly the impending total divorce between classification and identification. Developments since 1978 have quite changed the nature of the problems as he saw them, although it should be noted that systematists since Lamarck (1778) have noted that identification and the recognition of "natural" relationships were quite different problems.

Of course, not all is sweetness and light. Major arguments about methodology, and which methodology has appropriate philosophical support, persist, and for many Popper remains the philosopher of choice when browbeating opponents. Kuhn (1962) suggested that philosophical issues came to the fore in periods of "paradigm" shift in a discipline, but systematists have long grappled with fundamental philosophical issues such as nominalism versus realism, essentialism, and the like, even if all too often in the cause of polemics. There has been prolonged discussion over whether evolutionary assumptions should or should not underly the methods of phylogenetic analysis used (see Hull, 1988). This issue has resurfaced in the sometimes bitter debate over whether the application of such assumptions invalidates the use of maximum likelihood analyses (Edwards, 1996; Siddall & Kluge, 1997; Brower, 2000).

But perhaps *the* issue that still divides practising botanists is the relationship between a classification and a phylogenetic tree (see also Hull, 1970). Can phenetic (or patristic) *and* cladistic information be combined in a single classification? This issue, too, is of long standing; some evolutionarily-inclined systematists balked at the rigid conversion of dendrograms into classifications (Sokal & Michener, 1967). Phylogenetic systematists would reply to Mayr's (1974: 94) question "Cladistic analysis or cladistic classification?" with "not either/or, but both!", while evolutionary systematists have for the most part come to say "yes" to cladistic analysis, but still say an emphatic "no!" to cladistic classification (see also Hennig, 1975). The differences between the proponents of an evolutionary classification and of a classification based on monophyly are fundamental, and the papers by Bremer & Wanntorp (1978) and Wagner (1980) represent incompatible philosophies.

Compared to this, differences between the proponents of the *PhyloCode* (Cantino & al., 1999) and those who prefer to keep a more or less formalised "Linnaean" hierarchy of monophyletic groups perhaps smack more of book-keeping. Both groups agree that only monophyletic groups should be named, and it has long been evident that the Linnaean hierarchy faced problems (e.g., Hull, 1965; Johnson, 1968). The development of complex phylogenies make these problems unavoidable, but there seems to be no agreement as to how to distinguish babies and bathwater. There is a real danger that arguments over naming will simply reinforce one longstanding (about 250 years!) public stereotype that botanists are people who argue about names.

Species

At lower levels, phenetic methods in general and multivariate statistical techniques in particular have become an integral part of the armamentarium of systematists attempting to understand details of patterns of variation (e.g., Rohlf, 1993), although this is not to say that those using such techniques follow Sokal &

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Crovello's (1970) much-discussed phenetic species concept (e.g., Hull, 1970, for a criticism). However, debates at the species level have had a rather different focus than the phenetics/cladistics controversy. It is not that the specter of phenetics has not sometimes been raised to discount an opponent's species concept, but, by and large, most taxonomists, at least until recently, seem to have thought that species were somehow or other "out there" and were some sort of basic unit in evolution (e.g., Davis, 1978). Even some of those who downplayed the importance of evolution in higher-level classifications allowed for the possibility of directly investigating evolutionary processes below the level of species (Gilmour & Heslop-Harrison, 1954).

Despite the slowdown in studies of variation patterns at the species level and below, over the last twenty years such studies have been revolutionised by molecular data of various sorts, first by the study of isozymes and later by sequence analysis. This has allowed phenomena like introgression and hybridisation to be reinvestigated in a new light. Anderson's (1949) idea that there had been introgression between *Iris fulva* and *I. hexagona* was confirmed (Arnold & al., 1990); on the other hand, an almost equally famous example, that between *Helianthus anuus* and *H. bolanderi* (Heiser, 1949) was not (Rieseberg & al., 1988). Indeed, it seems that morphology, secondary chemistry and ecology alike may be poor indicators of hybridisation and introgression (e.g., Rieseberg & al., 1990). Although phylogeography (Avise, 2000) has not been so popular in botany as in zoology, partly because of the untoward behaviour of the plant mitochondrial genome, phylogeographic studies (e.g., Soltis & al., 1997) show how our under-standing of infraspecific patterns of variation can be enhanced. Apparent conflict between relationships suggested by different parts of the plant genome will greatly clarify the evolutionary history of taxa (Wendel & Doyle, 1998).

Some of the disagreement at the level of species stems from different interests; those who are interested in processes have tended to have different concerns than those whose primary interest is pattern. Within the old biosystematic community there was tension between those like Camp & Gilly (e.g., 1943) who were perhaps more interested in delimitation and categorisation, and those like Clausen, Keck and Hiesey (e.g., Clausen, 1951), more evolutionary in their approach and concerned with processes rather than end products (Valentine, 1961). Could such studies check the morphological systematist's work, would they help to discover ancestors, or were they largely independent of systematics? Gilmour (1958) even suggested that the findings of experimental taxonomy necessitated the abandonment of lower ranks of the hierarchy, including that of species (see Winsor, 2000, for Gilmour and the deme). Such tensions persist, although in somewhat different contexts.

Independent origins of what is arguably now the one species or of different species from the same parents (e.g., Ogihara & Tsunewaki, 1982) should be grist to the mill of those who theorise about species. There has been a great deal of discussion during the last 15 years in particular over the nature of species (Mishler & Donoghue 1982 is an interesting early paper), with five books on species in the last five years (e.g., Wilson, 1999). It has become clear that many species concepts are criteria used to delimit species and have more to do with epistemology than ontology. In addition, a conceptual resolution of part of the problem may be in sight

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in the form of the general lineage concept of species (de Queiroz, 1998; see also O'Hara, 1993), with different species concepts emphasising different aspects of the various processes or stages of lineage individuation—although this hardly helps systematists to decide on what to call a species. Moreover, working through the arguments of the proponents of different species concepts can be difficult, in part because they are what can be called "argument-by-demonisation". If the opposing concept can be labelled essentialist, typological, nominalist (Hull, 1970), Platonist, or phenetic, or a concern about breeding barriers be demonstrated and linked to a discredited biological species concept, valuable points can be scored.

In any event, it is notable that discussions about species concepts have generally had little effect on those actually describing species (Heywood, 1974; McDade, 1995); those who write about species and those who describe them seem for the most part to be living in separate worlds. (The most obvious exception is the replacement of the biological species concept in ornithology that is leading to a substantial increase in the number of species recognised.) Indeed, taxonomists' right to delimit species in whichever way they feel (the word is carefully chosen) is considered nigh-on inalienable, as any subscriber to TAXACOM will appreciate. General systematic practice at the species level—herbarium taxonomy, floristic and monographic work—has changed little over the last fifty years, or even over the last century (see also Ehrlich, 1961; Sokal & Camin, 1965). Species descriptions may be getting longer, geographic coordinates are often given for localities, and some sort of phylogeny included, but that is about all; multivariate analyses and morphometric techniques other than simple measurement are not generally used when delimiting species. That being said, remarkable monographic studies are being produced (e.g., Barneby, 1977) that are classical in the best sense of the term.

McDade (1995) found that for 81% of the 1790 species she analysed there were no indications of notable difficulties in species delimitation. However, since there was generally little discussion as to how data were being analysed, this scarcely converts to a vote of confidence for the soundness of the species delimited. In at least parts of the tropical flora differences in how taxonomists study the same plants may lead to very different estimates of the numbers of species. In 1962 Leenhouts recognised 14 species of *Fagraea* (*Loganiaceae*) growing in Borneo, with three species endemic to that island. In 1996 these numbers increased to 42 and 24 respectively (Wong & Sugau, 1996), yet material of all except for about 5 of those 42 species had been available to Leenhouts. It would be naive to suppose that because Leenhouts saw those specimens, he should have recognised species; indeed, an outsider could be forgiven for seeing both treatments as making similar poorly-documented assertions about the limits of species.

Indeed, how do systematists recognise the discontinuities they use to delimit species? Characters that can be used as apomorphies, or make a cluster of organisms diagnosable, or provide them with unique combination of characters, do not come conveniently labeled; the systematist has to find them. In this context, the relationship between monographic and local studies from the point of view of how pattern is perceived and analysed (e.g., Gentry, 1990) is critical, yet generally underemphasised. This issue will not go away in a rank-free classification (Mishler, 1999) and is far more than a matter of lumping *versus* splitting. Even if students

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follow current literature on species concepts, it is doubtful if how they actually delimit species has changed much, if at all, whatever the species concept ostensibly used—so this "how" is little better than a black box. Close attention to the relationship between species concepts and carefully analysed patterns of variation may help clarify a very confused area (e.g., Burtt, 1970), that of the infraspecific hierarchy.

Such issues have far-reaching implications for diversity assessment and conservation. One wonders if our much more sophisticated knowledge of the process of lineage individuation or speciation will translate at the community level to some agreement as to the ultimate units that are generally given names, or if systematists with differing species concepts will make conflicting conservation recommendations (May, 1995; Wheeler & Meier, 2000).

The description of species is closely linked with flora writing. We continue to produce floras, the bigger floras taking a century or more to finish—about 400 years at the current contribution rate for treatments is the estimate for *Flora Neotropica*, 190 years for *Flora Malesiana* (Prance & Campbell, 1988; Polhill, 1990), while even those with the backing of a substantial systematics force such as the *Flora of North America* are likely to take 30 years to finish. Flora-writing is thoroughly institutionalised, yet it remains a common complaint that many floras, especially those of tropical countries, are written by and for specialists in herbaria (e.g., Heywood, 1983). Few copies of the flora may be available, let alone used, in the countries whose flora they describe. Furthermore, progress towards standardisation of practice in the many areas of species description where this is possible has been slow, although publications like the monumental *Taxonomic Literature* (Stafleu & Cowan, 1976–1988; Stafleu & Mennega, 1992–2000)—invaluable for botanists and a truly remarkable bibliographic achievement in its own right—is stabilising use in some areas.

Nevertheless, some recent developments bid fair to change how biologists and others access systematic data in general and botanical data in particular, and how systematists present data, although they are taking place with little fanfare. These are the production of computer-based interactive keys, and, more generally the development of multi-purpose descriptive databases such as DELTA (DEscriptive Language for TAxonomy; Dallwitz, 1980; Dallwitz & al., 1993, 2000), from which descriptions (with a little effort, in more than one language), a variety of identification aids, and analyses of relationships can all be derived. Sokal & Sneath (1963: 279) had charmingly suggested that larger museums might have "a computer wholly employed as a machine for identification of specimens, to be fed with specified characters on punched cards"—an early example of a punched card key is that of Hansen & Rahn (1969). Recent developments show the power of the descendants of such stacks of punched cards—interactive keys (see Dallwitz & al., 2000, for the principles of such keys)—especially when linked to glossaries, illustrations, photographs of specimens, distribution maps, and the like (e.g., Watson & Dallwitz, 1998; Hyland & al., 1999), and of other "public interfaces" using the digital medium (e.g., Kartesz & Meacham, 1999). A local flora such as that of the Reserva Ducke in Brasil (Ribeiro & al., 1999; interestingly, the authors include an ecologist, students with bachelor's degrees, undergraduates, and foresters, but no conventional

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systematist), with its over 20,000 photographs for 2200 species, is not conventional, but very effective.

Epilogue—the discipline of systematics

Phenetics in the 1960s represented a major change in how systematics was practiced. Phenetics was about computers, but more about questioning how systematists went about their business, and about methods. However, pheneticists could rightly be charged as being naive in their analysis of how systematists observed the world (Hull, 1970). This naivity was, however, widespread, witness the oft-repeated claims of systematists to be observing nature directly, of the value of having seen many families in the field when it came to understanding their relationships, and the like. Cladists in their turn emphasised the need to find appropriate methods and to make appropriate observations for answering one particularly important question systematists asked—what are the phylogenetic relationships within and between groups of organisms? And problems evident in phenetic studies, such as whether the matches symptote and non-specificity hypotheses (Sneath & Sokal, 1962) held, have their descendants in cladistic studies in attempts to develop statistics for tree support and arguments over the combinability of different kinds of data. The main change in higher-level systematics comparing 1950 to 2000 is that there are now well-documented hypotheses of phylogeny whose support can be estimated and that were produced by a methodology that attempts to be explicit.

But botanical systematics, or systematics as a whole, does not develop in a vacuum, and there is a larger context in which to view the last fifty years. Systematics is now unified in a way that it has not been for a very long time, although this is perhaps more evident in academia than in museums and herbaria. Sokal & Sneath (1963) bewailed the compartmentalisation within systematics, and indeed developments in both phenetics and cladistics have been followed by systematists of all persuasions. However, discussions at the Numerical Taxonomy Conference in 1979 were bitterly polarised between the competing schools of systematics—it should not be forgotten that Kuhn's *The Structure of Scientific Revolutions* appeared in 1962, and some protagonists in the discussions then (and since) saw themselves as being revolutionaries. The need was felt for the foundation of a new society, but again, both botanical and zoological systematics were represented at the inauguration of the Willi Hennig Society in Kansas in 1980. The change in name of the journal *Systematic Zoology* to *Systematic Biology* in 1992 also in part reflects this shift towards unification, as do proposals like the *BioCode* and *PhyloCode*, both of which include all organisms. However, the unification is that of a monoculture, as a glance at the first volume of *Taxon* with its articles in a variety of languages makes clear.

Another important change has been brought about by the technologies now used in systematics. The computer programs developed over the last decade are immensely powerful and can analyse massive amounts of data. Furthermore, sequences become freely available when they are deposited in *GenBank*. If new systems are to be developed or major phylogenetic questions answered, collaboration and coordination of effort will remain the order of the day (Alston,

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1967; Clegg & Zurawski, 1992; Chase & Albert, 1998; Endersby, in press). It is relatively uncommon for a molecular paper to have a single author, although Chase & al. (1993), with its 43 contributors, is exceptional. (One hopes the number of authors appended to formal plant names will not show a similar increase.) There are also more formal collaborations, such as the very successful *Green Plant Phylogeny Research Coordination Group* that was convened to study the basal branches in the lineage of which land plants are a part.

Some aspects of systematics, such as deciding on terms to be used when describing plants and group names that will be used in general communication, are largely matters of convention, and conventions entail general acceptance—again, collaboration is called for. An early effort along these lines was a meeting that resulted in the acceptance of terms used to describe leaf shape (Systematics Association Committee, 1962), and such efforts continue, e.g., the clarification of terms used in wood anatomy (Wheeler & al., 1989). (Note, however, that although such consensuses are indispensable in helping botanists to communicate, their value in recording basic information for phylogenetic problems is less obvious.) Recent years have seen welcome (my bias shows) attempts to establish consensus classifications, as of *Cactaceae* (ongoing since 1984: Hunt, 1996 et seq., 1998), *Poaceae* (Grass Phylogeny Working Group, 2000), and of the major groups of flowering plants (APG, 1998).

The health of systematics depends in part on how it is seen by other branches of biology, other scientists, those who administer grant programs or make budgets, or those who are simply donors. Systematic activity has increased in some countries (J. Parnell, pers. comm.) and there may have been a brief resurgence in Europe in the early 1970s (Heywood, 1983). Graphs extracted from an analysis of BIOSIS over the period 1969–1996 (Winston & Metzger, 1998) suggest that taxonomic articles (both botanical and zoological) seem to have been proportionally increasing. There was a particularly sharp increase about 1985, with something of a plateau more recently; papers in which new taxa are described have almost quadrupled.

However, systematics—or at least more classical aspects of it—is currently seen as being threatened in much of Europe and North America where historically systematists have been very active (Claridge & Ingrouille, 1992), the linkage of taxonomy with human destiny (May, 1990) notwithstanding. In the United States, successive reports paint a dim picture of systematics (e.g., Steere, 1971; Stuessy & Thompson, 1981), although there is little in the way of documentation of long-term trends. Stuessy & Thompson (1981) noted that only 30% of the systematists in United States herbaria were under 40. In the British Isles, the systematic population is similarly aging (May, 1992; Claridge & Ingrouille, 1992), and over 60% of the institutions surveyed by the latter authors offered no instruction in systematics at any level. Although phylogenetic studies—which will almost certainly remain heavily molecular, although incorporating morphological components—are now firmly established as a *sine qua non* for all interested in comparative biological questions, there is little evidence that basic revisionary work in poorly studied groups—i.e., nearly the entire tropical and much of the temperate flora—is really high on most administrators' and fund-givers' agendas. However, initiatives like the American National Science Foundation-funded PEET grants (Partnerships for the

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Enhancement of Expertise in Taxonomy) have focused on monographic studies, especially those of less well-studied organisms.

The changing social climate, with its emphasis on accountability, information management, and cost-effectiveness and utility, as well as the growing demands of conservation, challenge the heart of the systematic enterprise. However, many observers see the systematic community in general and the botanical community in particular as being fragmented at various levels, including that of the institution. Individual systematists are fiercely protective of what they see as their right to name and describe, making the discipline as a whole, or at least that part involved in species description, seem at best behind the times and at worst reactionary and haggling over names. There has been little guidance from professional societies over directions systematics might take [Stuessy & Thompson (1981) suggested that a Federation of Systematic Biologists was needed]. However, consensus is needed for the development of a rational nomenclature, of standards for databasing and data management, and of conventions to streamline species descriptions. Progress in these areas been very slow. It is in such contexts that initiatives like *Species 2000*, the *Global Biodiversity Information Facility* (GBIF), the *Global Taxonomic Initiative* (GTI), internet freely accessible databases such as the *International Plant Names Index* (IPNI), and nomenclatural issues such as the *BioCode* and the *PhyloCode* are to be seen. Some of these will turn out to be twentieth- or even nineteenth-century issues and products merely repackaged for the next century, some may take botanical systematics in directions it should not go, but others will turn out to be absolutely necessary. It is how matters such as these are handled, almost as much as the developments of new or improved techniques to detect relationships and evaluate patterns, that will affect both what botanists do and how they are seen by other scientists and by the public in the twenty-first century.

Acknowledgements

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