TAXONOMY AND PHYLOGENY RECONSTRUCTION: TWO DISTINCT RESEARCH AGENDAS IN SYSTEMATICS

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The state of systematics, a vital biological discipline investigating fundamental questions about the earth's biological diversity, is currently the subject of concern amongst the UK scientific and political communities. The scope of this complex field is redefined in terms of a number of linked agendas. Currently, key areas of research can be divided into the reconstruction of phylogeny and taxonomy, here defined as the description, delimitation and inventory of species. Molecular data have great potential to elucidate the relationships between taxa and, together with recent methodological advances, have instigated a resurgence of interest in phylogeny reconstruction. A literature survey indicates a decline in interest and investment in taxonomy, as defined above, an activity for which morphological data supply most information. We highlight the need to restore the balance in activity and profile between phylogeny reconstruction and morphology-based taxonomy, to redress the plight of systematics and dependent biological research.

Keywords. Biodiversity, molecular systematics, morphology, species inventory, tree of life.

INTRODUCTION

Systematics plays a fundamental role in describing, naming, classifying and determining relationships among the earth's biota (Prance, 1995). Methodological advances such as cladistics (Hennig, 1966) and new sources of data such as nucleotide sequences (Clegg & Zurawski, 1992; Wolfe & Liston, 1998) have greatly increased the rigour, credibility and appeal of systematics over recent years (Davis, 1995). The resulting heightened interest in systematics has been predominantly associated with reconstructing phylogenetic relationships, such as those among land plants (e.g. Pryer *et al.*, 2001), seed plants (e.g. Chase *et al.*, 1993; Chaw *et al.*, 2000) and angiosperms (e.g. Palmer *et al.*, 1988; Qiu *et al.*, 1999).

Other traditionally substantial elements of systematics research, such as the description, delimitation and inventory of species, now trail behind phylogeny reconstruction in both scientific interest and funding. Concern has therefore been growing over the state of systematics research in the UK for at least a decade (Gaston & May, 1992). This was highlighted in a report by the House of Lords Select Committee

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on Science and Technology (House of Lords, 1992). Subsequently there have been several national, European and global initiatives aimed at enhancing systematics research. These include the Darwin Initiative for the Survival of Species (http://www.nbu.ac.uk/darwin/), the Euro+Med PlantBase project (http://www.euromed.org.uk/) and the Global Biodiversity Information Facility (Wilson, 2000a). There are also taxon-specific schemes such as the Global Plant Conservation Strategy (http://www.biodiv.org/programmes/cross-cutting/plant/resolutions.asp), the Species Plantarum project (Brummitt et al., 2001) and the US-based Partnerships for Enhancing Expertise in Taxonomy (PEET) grants (http://web.nhm.ukans.edu/peet/). Despite such programmes there remains a lack of investment in the infrastructure and expertise required to gather information for taxonomic research (Disney, 1998), particularly in those regions where biological diversity is concentrated (Roos, 1997).

Ten years after the first House of Lords report (House of Lords, 1992) and shortly after their follow-up inquiry (House of Lords, 2002), several issues remain important to any assessment of the state of systematics. These include the number of trained taxonomists, the place of systematics in higher education, the citation impact factor of taxonomic publications, and the UK Research Councils' criteria for reliable and worthwhile scientific research. One way to consider these issues is to approach the whole of systematics as one 'grand project' (Donoghue, 2001: 755) which must expand and embrace new (i.e. electronic) means of presentation and publication (Godfray, 2002). But neither new technology nor increased overall funding can provide a complete solution to the plight of UK systematics if it continues to be treated as a single broad discipline. It is essential also to acknowledge the growing division between high-profile, high-technology research including evolutionary and phylogenetic studies, and low-profile species inventory and description projects that fail to reach high-impact journals (Valdecasas et al., 2000). Here we investigate the current situation in systematics, reassessing its scope in terms of a number of distinct research agendas, surveying the relative status of these agendas, and quantifying the past and present contributions of both morphological and molecular-based research.

THE SCOPE OF SYSTEMATICS: PHYLOGENY RECONSTRUCTION AND TAXONOMY

Stace (1989: 5) defines systematics as 'the study and description of the variation of organisms, the investigation of the causes and consequences of this variation, and the manipulation of the data obtained to produce a system of classification'. Taxonomy is sometimes viewed as synonymous with systematics, or as part of a systematics that also incorporates a breadth of studies in cytology and genetics (biosystematics), phylogeny reconstruction, anatomy, floristics, monography and biogeography (Stace, 1989). Here we use the restricted definition of taxonomy within this circumscription, incorporating species discovery, description, nomenclature and classification (Heywood, 2001). Taxonomy has been associated with a number of

different terms, such as classical, practical and traditional (Turrill, 1935, 1938). One such frequently cited expression is 'alpha taxonomy', introduced by Turrill (1935) to describe the use of morphological data in producing floras, monographs, keys and classifications that contribute to the inventory of species. Turrill's (1935, 1938, 1964) intention was to distinguish between practical, specimen-based, taxonomy and 'omega taxonomy' in which 'place is found for all observational and experimental data relating, even if indirectly, to the constitution, subdivision, origin and behavior of species and other taxonomic groups' (Turrill, 1935: 105). This was in response to the emerging and expanding impact of ecology and biosystematics upon taxonomic research, particularly below the species level.

The scope of systematics and its constituent disciplines has altered markedly since Turrill's time. In addition to the introduction of new sources of data (such as chemotaxonomy, pollen ultrastructure and molecular sequencing) and methods of analysis (such as cladistics and statistical techniques), the very questions being addressed have changed, as evidenced by a growing interest in phylogeny reconstruction. Modern definitions should take into account the way that this research agenda has developed. Today alpha taxonomy and revisionary work (sometimes separated as beta taxonomy) contribute to the documentation of the earth's species, which we call taxonomy; omega taxonomy has primarily become associated with reconstructing higher-level phylogeny (e.g. Kornas, 1997) rather than the lower-level population genetics of Turrill's definition. The research priorities for the systematics community have changed and it is now pertinent to reassess the methods most appropriate to address them.

Modern systematics research is often divided into sequential steps: alpha taxonomy preceding beta (revisionary) taxonomy, and omega taxonomy being viewed as the ultimate, intellectually challenging and worthwhile scientific goal (e.g. Review Group on Taxonomy, 1979). We believe this perpetuates the pejorative and negative connotations of such terms as alpha, classical and traditional taxonomy, seen as mere precursors to the more highly valued reconstruction of phylogeny. A more appropriate conceptual framework (e.g. Anon., 1994) advocates concurrent research programmes to discover and identify the earth's species, where they occur, what properties they have, and how they are related. In this framework, taxonomy (which examines all four issues) and phylogeny reconstruction (which focuses on relationships) become equal priorities for modern systematics. Phylogeny should not be considered the ultimate goal of systematics, nor the species-delimitation and inventory part of taxonomy its poor relation.

As Wilson (2000a: 1) discussed, 'phylogenetic reconstruction, currently the dominating focus of systematics, obviously is worth doing, but more scientifically important and far more urgent for human welfare is the description and mapping of the world biota'. This sentiment is not reflected in current research activity, perhaps because the UK funding bodies and higher education establishments continue, consciously or subconsciously, to draw upon the outdated, sequential description of systematics. Anecdotal concerns over the state of systematics, exemplified by the

Systematic Biology Initiative statement to the government (Claridge, 2001), thus focus on the plight of descriptive taxonomy (e.g. Kruckeberg, 1997; Lammers, 1999; Wilson, 2000a; Landrum, 2001). Below we investigate one method – a survey of published systematics research – to measure the relative condition of phylogeny reconstruction and taxonomy. This confirms the discrepancy identified by these authors and the problems it may create.

THE PLIGHT OF SYSTEMATICS: LITERATURE SURVEY

Biological Abstracts is a web- and CD-based index of worldwide life sciences research publications in c.9000 journals, including most of those that publish systematics (both taxonomic and phylogenetic) research. These include, for example, *Acta Botanica Yunnanica*, *Annals of the Missouri Botanical Garden*, *Botanical Journal of the Linnean Society*, *Brittonia*, *Bulletin of the American Museum of Natural History*, *Edinburgh Journal of Botany*, *Harvard Papers in Botany*, *Herpetological Monographs*, *Kew Bulletin*, *Memoirs of the New York Botanical Garden*, *Molecular Phylogenetics and Evolution*, *Mycotaxon*, *Novon*, *Phytologia*, *Smithsonian Contributions to Zoology*, *Systematic Biology*, *Systematic Botany*, *Taxon*, *Wrightia*, and many more (Biosciences Information Service, 1986). The annual index can be searched for articles that mention a specified term or combination of terms, employing standard Boolean operators.

To document the state of research published in systematics, taxonomy and phylogenetics, we searched the 'title' and 'abstract' fields of Biological Abstracts, by year, for the terms 'systemat*', 'taxonom*' and 'phylogen*'. The use of the wildcard symbol (*) instructs the search program to extract all records containing (for example in the case of 'phylogen*') phylogeny, phylogenetic, phylogeneticist, and so forth.

We are aware that our approach, based on a broad survey of life sciences publications, can achieve only a preliminary estimate of the situation; it is impossible to extract *all* relevant references through these searches. For instance, many taxonomic papers (e.g. Sun *et al.*, 2001) do not include the term 'taxonomy' in their title or abstract. Moreover, while the index includes the majority of biological journals including some that publish monographs and taxonomic revisions, it cannot cover taxonomic descriptions published only in floras, or phylogenies presented only on the World Wide Web. Even those publications that *are* extracted may not be strictly comparable: it has been suggested that a monographic work featuring several hundred species should be weighted more heavily than a small phylogeny paper in, for instance, *Molecular Phylogenetics and Evolution*. Equally, however, a large collaborative phylogenetic analysis such as reported by Chase *et al.* (1993) may represent a great deal more research effort than a single nomenclatural change reported in *Taxon*. We hope that at least some of the shortcomings of our analysis offset one another in this way, or apply to a similar degree for all search terms. It should also be noted that a quantitative survey of published research is liable to underestimate the current scale of the problem in systematics, since it will inevitably lag behind any actual

decline in numbers of researchers or coverage of systematics in undergraduate teaching.

Figure 1, the total number of papers recorded each year in Biological Abstracts, shows a steady growth in numbers of taxonomic and systematics papers since 1985, but at a much slower rate than the growth in phylogenetic research over the same period. However, this increase is an artefact of accelerating publication rates across the life sciences as a whole (the number of papers included in the index has risen each year, from 195,815 in 1985 to 356,834 in 2000). This increase, known as Price's law (Price, 1963; Lopez *et al.*, 1996), is ubiquitous in similar surveys (e.g. Start *et al.*, 1995). To offset Price's law we scaled the results against the total number of papers recorded in the index. Figure 2 shows that the scaled number of references to systematics has grown slightly since 1985 but, while the relative number of phylogenetic papers has increased at an escalating rate, the relative number of taxonomic papers has fallen over the same period.

Not every paper including the terms phylogen* or taxonom* is necessarily a piece of systematics research. There are, for instance, more papers citing phylogen* than systemat* in many years (see Fig. 1). To focus more closely upon the components of systematics we therefore carried out a second search in which we retrieved articles with a title or abstract containing the term systemat* *and* phylogen* or taxonom*; there were no records containing all three terms. The results of this search are summarized in Fig. 3 and indicate a growing imbalance in publication rates *within*
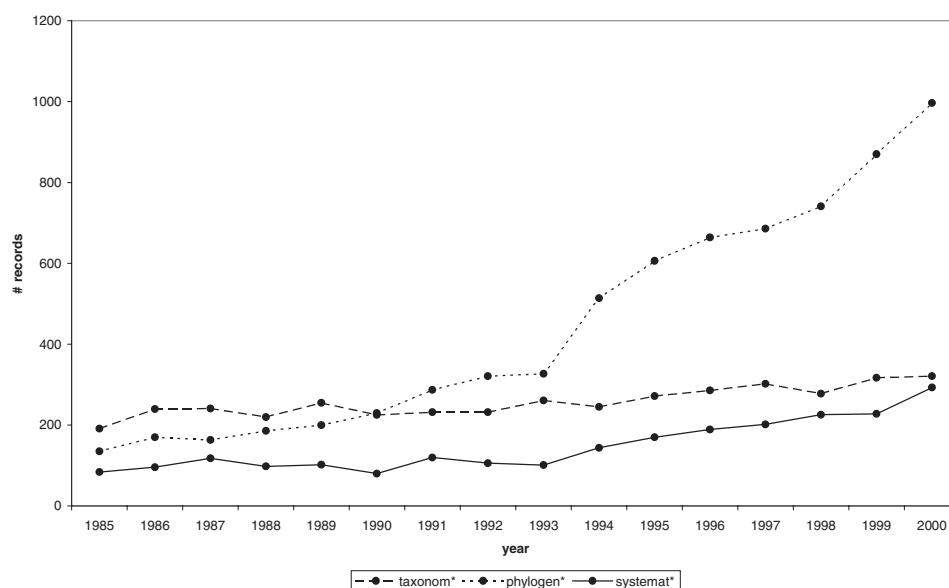

FIG. 1. Total number of records in Biological Abstracts featuring taxonom*, phylogen* or systemat* in the title or abstract, by year (1985–2000).
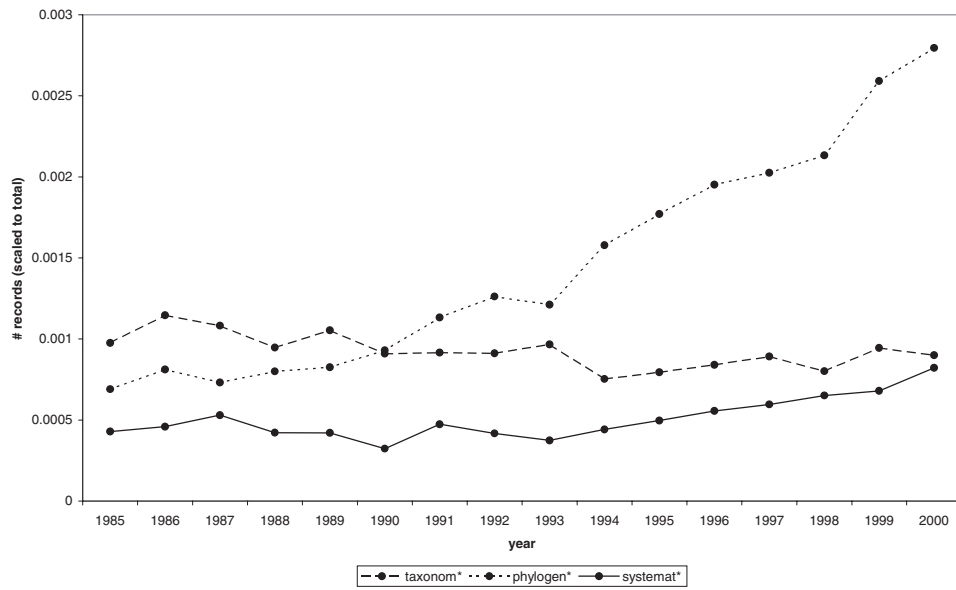
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FIG. 2. Number of records in Biological Abstracts featuring taxonom*, phylogen* or systemat* in the title or abstract, by year (1985–2000), scaled against the total number of records in the index.
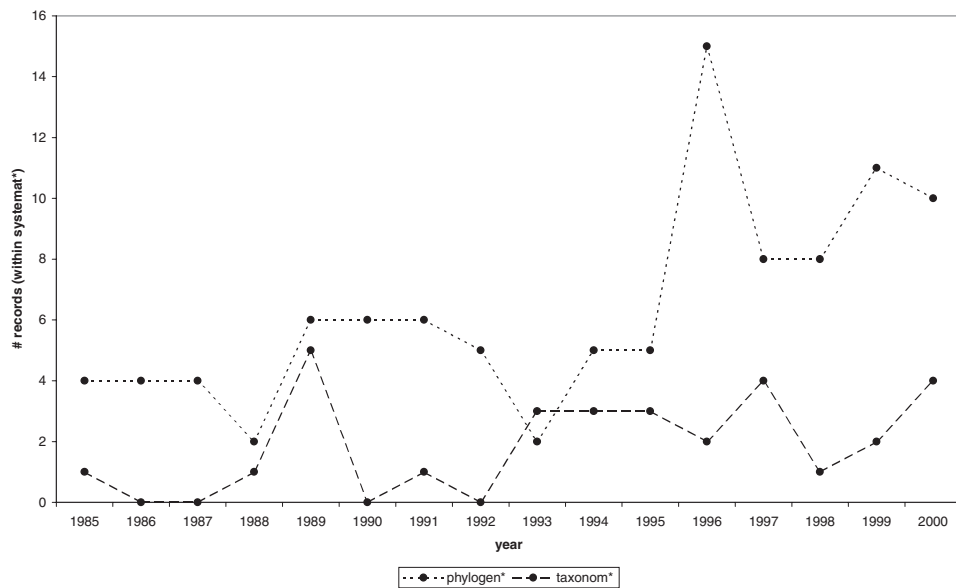

FIG. 3. Total number of records in Biological Abstracts featuring systemat* and taxonom* or phylogen* in the title or abstract, by year (1985–2000).

systematics. Since 1985 the proportion of systematics papers based upon taxonomic research has fallen while there has been rapid growth in phylogenetic research.

This imbalance is reflected in citation rates as well as publications. Rupert Barneby was 'one of the most outstanding plant taxonomists of the 20th century' (Welsh, 2001: 285) and one of the most productive. Twenty-two of his papers published in the decade 1988 to 1998, the last year in which he published, are recorded in the Web of Science citation index (http://wos.mimas.ac.uk/). These papers register a total of 12 citations in the index, an average of 0.5 citations per paper. By contrast, Douglas Soltis, the highest-placed molecular phylogeneticist among the most-cited plant and animal scientists of the last decade (R. Olmstead, pers. comm.), records 104 papers in the Web of Science index over the same period. These received a total of 4410 citations, or 42 citations per paper. Although these are again very imprecise estimates, they serve to indicate further the disparity in profile between the taxonomic and phylogenetic research agendas within systematics.

As Figs 1–3 show, total systematics research worldwide is relatively healthy, although the situation in specific countries may differ (Buyck, 1999). Indeed, the field of phylogeny reconstruction is growing rapidly relative to other biological research. However, taxonomy is declining compared with other biological sciences, and particularly relative to phylogeny reconstruction. It is this fact, that the growth and profile of the two areas of systematics is not balanced, that gives cause for concern. Systematists are increasingly following the agenda of phylogeny reconstruction, and hastening the decrease in interest and funding in taxonomy. We conclude that the widely discussed (e.g. Wilson, 2000a; Landrum, 2001) crisis in systematics, to the extent that it exists, is concentrated in taxonomy.

The Importance of Morphology and Molecules in Systematics

The two research agendas on which we focus here differ in several key respects including philosophy, personnel, systematic practice and methods, and relative suitability of data sources. For many systematists (e.g. Nixon & Wheeler, 1990) delimiting species and discovering their phylogenetic relationships are conceptually separate issues. In practice, although there are of course many exceptions, researchers with skills and interests in taxonomy are often perceived as distinct from those whose primary concern is reconstructing phylogeny. The methods of the two disciplines clearly differ. The practice of taxonomy includes a wide range of activities such as field collection and observation, morphological study and assessment of variation and collation of distribution data, but is often regarded as outdated, obsolete and amounting to little more than 'shuffling specimens' or 'stamp collecting'. By contrast, phylogeny reconstruction has benefited from progress in a number of areas (Donoghue & Sanderson, 1992): the explicit criterion of monophyly (Hennig, 1966), an increase in availability of molecular data, and the development of computer technology capable of manipulating large data sets (Nandi *et al.*, 1998).

A key difference between taxonomy and phylogeny reconstruction lies in the data

used. DNA sequences and gross morphology currently predominate in phylogeny reconstruction and taxonomy respectively. The relative value of these sources of characters, particularly in phylogeny reconstruction, has been the subject of continuing debate (e.g. Hillis, 1987; Sytsma, 1990; Donoghue & Sanderson, 1992; Doyle, 1998; Scotland et al., 2002).

Despite the current high profile of molecular systematics, most of what we know about the diversity of plants at all taxonomic levels stems from classifications (Platnick, 1979) based on morphological study (Scotland et al., 2002). At species level, all angiosperms so far discovered have been described almost exclusively on the basis of morphological characters. Moreover, a significant proportion of groups recognized on morphological characters is now agreed to be 'correct', through comparison with molecular-based phylogenies. For instance, in an analysis based on rbcL sequences, Källersjö et al. (1998) found 73% of previously circumscribed angiosperm families to be monophyletic. The significant role morphology has played in phylogeny reconstruction and in species-level taxonomy is often underestimated due to the absence of an explicit scientific methodology. One attempt to measure its importance to systematics is outlined below.

The total information (sensu Nelson & Platnick, 1981) that can potentially be determined through systematics study may be measured in terms of nodes (uncovered through phylogenetic reconstruction) and terminal taxa (in this case species). Considering first the nodes, and taking flowering plants as an example, estimates of the total number of species in existence range from 225,000 (Kubitzki, 1993) to 422,127 (Govaerts, 2001), with most (e.g. May, 1990; Heywood, 2001; Prance, 2001) agreeing on approximately 300,000. The number of informative nodes in a fully resolved rooted tree with 300,000 species is equal to two less than 300,000 (Mickevich & Platnick, 1989), or approximately 300,000. The number of nodes so far estimated on the basis of morphological data may be roughly estimated as the number of higher taxa found in flowering plant classifications. Given that intermediate ranks are often controversial, ephemeral and always sufficiently fewer than the total number of genera to make little difference to our crude calculation, we concentrate only on familial and generic classifications. The number of angiosperm families ranges from 250 (Kubitzki, 1993) through 419 (Mabberley, 1997) to 490 (Thorne, 2000), and the number of genera from 12,000 (Kubitzki, 1993) through 13,479 (Brummitt, 1992) to 13,678 (Thorne, 2000). Although many of these groups have been confirmed through molecular analysis, they were erected before the widespread use of molecular data and are diagnosed by morphological characters (Chase et al., 2000). Thus the total number of nodes generally agreed to be resolved in the angiosperm phylogeny on the basis of morphological characters ranges from 12,250 to a little more than 14,168. Taking an average 'ballpark' figure of 14,000, we can therefore estimate the small but significant proportion of flowering plant nodes that have been elucidated using morphological data as 14,000/300,000, or approximately 5%. While this figure might be larger if we included infrageneric taxa, it would be smaller if we accounted for the lack of information contained in monotypic groups and excluded non-monophyletic taxa.

Turning to the other half of the information in a systematic classification, the 300,000 species, we know at least something diagnostic about the morphology of the approximately 250,000 flowering plants so far described (Anon., 1994). Thus 250,000/300,000 (83%) of the possible information about flowering plant species has been generated by taxonomy based on morphological data.

It would be premature to conduct a similar quantitative analysis in such a fast-growing field as molecular systematics. It is claimed that, potentially, 100% of nodes could be resolved using molecular data once suitable markers have been identified (Mishler, 2000) and correct alignment achieved. Whether such markers can be obtained for all phylogenetic problems remains to be seen. Currently, plant molecular systematics has been most successful at familial (e.g. Kim *et al.*, 2001; Soltis *et al.*, 2001) and ordinal (e.g. Bayer *et al.*, 1999; Ito *et al.*, 1999) levels and for resolving several high-profile nodes of land plant phylogeny (e.g. Hoot *et al.*, 1999; Pryer *et al.*, 2001). Although its contribution is still to be fully realized, there is a degree of optimism in the botanical community that a completed, accurate phylogeny based on sequence data is achievable (e.g. Donoghue, 1994; Soltis & Soltis, 1995). Researchers in other fields of biology are equally hopeful, claiming that through molecular sequencing technology we are now looking forward to a 'global classification' (Wheelis *et al.*, 1992: 2930) or 'universal phylogenetic tree' (Doolittle, 1999: 2124).

It is also too soon to assess quantitatively the contribution of molecular data to species-level taxonomy, but indications are that it is smaller than in phylogeny reconstruction. At least in the flowering plants, molecular sequence data have so far had little or no impact here (Wiens & Servedio, 2000), although they may play a more substantial role in the future. In other taxonomic groups molecular data have been more readily applied: for instance, many fungal and bacterial strains and species are already identified on molecular sequence characters alone (e.g. Dumler *et al.*, 2001; Menendez *et al.*, 2001).

Conclusions

New species of plants continue to be discovered at a constant rate of approximately 2500 per year (Prance, 2001), but they can only be fully described, diagnosed and understood on the basis of morphological data. As Friedman (2001: 14) noted, 'for all of the recent progress in analysing the phylogenetic relationships of plants ... much of the organismic diversity of extant plants has yet to be studied, even at the most rudimentary level'. Correct description of new species, revision of poorly circumscribed groups and uncovering of synonymy remain crucial, yet most vascular plant genera have not been monographed for over a century (Minelli, 1994), and the vast majority of species descriptions include only the most basic facts of morphology and provenance (Heywood, 2001). This falls far short of a satisfactory species description including synonymy, diagnosis, description, taxonomic discussion and details of ecology and distribution (Winston, 1999). It is therefore vital that

morphological taxonomy keeps pace with research in phylogeny reconstruction, and it is worrying that it appears to be losing both eminence and investment to systematics' more high-profile second agenda (Disney, 1998).

We have focused here upon the flowering plants since these are our area of expertise, and because more is known about them than about most other taxa. A greater proportion of species has been described and there are more UK systematists working on flowering plants than on any other group of organisms (Blackmore, 1996). The flowering plants therefore provide a baseline for measuring the plight of systematics. The problems and needs identified and portrayed in this group are undoubtedly prevalent, probably to a much greater extent, in non-angiosperm taxa. If we extend our concerns to all groups of organisms, the total complement of species on earth has been estimated at anything from three to 30 million (Wilson, 2000a). Only 1.4 to 1.7 million species (4.7 to 57%) have been described (Wheeler, 1995). Of this small percentage, many are not even adequately differentiated from one another (Gauld, 2001). Worryingly, the case is worst in the 'hyperdiverse' taxa (such as arachnids, nematodes, fungi, microbes, and most groups of insects; Colwell & Coddington, 1995) that make up most of life on earth. For example, only 7.5% of the estimated one million species of spiders and mites and 3% of the 500,000 or so nematodes have so far been described (Anon., 1994). Worse still, it is estimated that less than 1% of even this small minority has been subjected to any examination beyond the minimum anatomical and habitat details needed for diagnosis (Wilson, 2000a).

The state of our knowledge is not geographically uniform and is currently worst in the tropics (Prance, 2001), where the smallest proportion of species has been described and those that have been, to a much lesser degree of detail (Prance *et al.*, 2000; Heywood, 2001). However, this situation is undergoing a reversal. In the developing world the situation is beginning to improve through intensive collecting in well-defined regions, for example in Colombia, Mexico and Costa Rica (Prance, 2001). For instance, the non-profit-making Instituto Nacional de Biodiversidad (INBio; http://www.inbio.ac.cr/en/inbio/Inbio.html) in Costa Rica, set up to generate knowledge about biodiversity, cites biodiversity inventory as its first activity. It is perhaps now in developed countries such as the UK, where the availability and apparent power of molecular data in phylogeny reconstruction have masked the continued need for morphological description and inventory of species, that the plight of systematics is most critical.

By comparison with phylogeny reconstruction, morphology-based taxonomy is sometimes viewed as unfocused, imprecise (Godfray, 2002), and therefore unfundable. Yet other, analogous data-gathering exercises such as the Human Genome Project (http://www.ornl.gov/hgmis/) are both high profile and well funded (Wilson, 2000b), perhaps because the medical applications of the project have caught the imagination of the public and funding bodies alike. Taxonomy too underpins other areas of the life sciences and conservation, and provides the identity of the initial units of comparison for phylogenetic investigation (Wilson, 2000a; Daly *et al.*, 2001).

It is important to make more widespread use of contemporary (World Wide Web-based) channels to communicate taxonomic results (Godfray, 2002), but this will not solve the underlying problems of methodology and data-application in systematics. Nor does the solution lie solely in allocating increased resources to systematics as a whole, although this may be appropriate in the USA (Donoghue, 2001). In the UK resources are more limited, and without careful targeting we may simply reinforce the supremacy of molecular phylogenetic research, perpetuating the under-valuation of morphological taxonomy.

The problems in UK systematics research involve issues more profound than presentation and funding. The plight of systematics is localized in taxonomy and reflected in an inequality in investment across the two disciplines of systematics. This may be due in part to the poor perception of morphology-based taxonomy and to a feeling that it is only the first step to phylogeny reconstruction and thus is largely completed and rightly declining (Janzen, 1993). In fact, and in stark contrast to the rapid completion of that other data-gathering enterprise, the Human Genome Project (Venter *et al.*, 2001), it is unlikely that the taxonomic inventory of species will ever be completed to a satisfactory degree of detail. However, these are not reasons to concentrate our efforts on phylogeny reconstruction, nor to overlook the potential of morphological data. Instead it is crucial to highlight the importance of morphological taxonomy to systematics, biology and biodiversity conservation. While DNA sequence data supply the broad coverage necessary for phylogeny reconstruction and may in future prove useful in species delimitation, only morphological characters provide the starting point for sampling, describing and delimiting biodiversity for a comprehensive understanding of life on earth.

'Mistakes are costly, not only in misallocation of limited resources, but also in lost time and opportunity to study many soon to be extinct species' (Wheeler, 1995: 477). Systematics is heading for just such a mistake through an undue focus on molecular sequence-based phylogenetic research. A decline in morphological taxonomy will affect all areas of biology. It is therefore essential to recognize the importance of all component agendas within systematics and take steps to ensure that they grow in parallel.

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