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Reinventing taxonomy: a curmudgeon's view of 250 years of fungal taxonomy, the crisis in biodiversity, and the pitfalls of the phylogenetic age¹

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Abstract — Biological taxonomy is bleeding. The fungi are but one example. There is an almost ignored crisis of impending loss in biodiversity, while the funding—necessary to provide basic inventories and monographic studies—is simultaneously siphoned away by the misuse of the great potentials of molecular biology. One disturbing result has been frequent support of needless, repetitive phylogenetic studies. A seminal paper, “Taxonomic triage and the poverty of phylogeny,” by entomologist Quentin D. Wheeler, is cited as required reading for all biologists. His theses are that “Taxonomy, already weakened by decades of neglect, now suffers the loss of positions and funding,” and that “Considering what is at stake for human and environmental welfare in the biodiversity crisis, it is time to triage and move descriptive taxonomy to the forefront of science funding priorities.” Reinventing taxonomy may provide answers.

Key words — collecting, monographs, inventories, PhyloCode, DNA

Introduction

The title of this paper refers to this as “a curmudgeon’s view.” I have intentionally used the phrase that was also part of the title of an address I gave at the Seventh International Mycological Congress (Korf, 2002), in which I noted: “The noun *curmudgeon* is defined and used here in two, not necessarily exclusive, ways: *n.* 1. *archaic*: a crusty, ill-tempered, churlish old man. 2. *modern*: (i) anyone who hates hypocrisy and pretense and has the temerity to say so; (ii) anyone with the habit of pointing out unpleasant facts in an engaging and humorous manner.” Let us hope that I succeed here to fit one or both of those modern options.

I intend to look here at taxonomy as practiced for the past 250 years in the field of mycology, to trace its roots and highpoints, and to point to the inescapable truth that

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all taxonomy must now reinvent itself and regain its *primary function* in biology. To these ends I shall briefly review the mycological terrain from the days of Linnaeus to the golden explosion at the time of Persoon and Fries in the early 19th century, through the comparative morphological studies of the next century, through the dark days of the New Systematics, and the fortunate birth of Hennig's *Phylogenetic Systematics*. In the last 30 years the decline in taxonomic work has been catastrophic, to the point that taxonomy is today potentially bleeding to death.

Much of what I have to say has recently been covered in great depth by a former colleague of mine at Cornell University, Quentin D. Wheeler, a brilliant taxonomist and entomologist and now Keeper of the insect collection at the British Museum, in a seminal paper entitled *Taxonomic triage and the poverty of phylogeny* (Wheeler, 2004), a paper I consider required reading for all biologists. Throughout my remarks I shall cite this paper frequently, and if all anyone remembers of my analysis is his paper, I shall be satisfied.

Following the introductory historical view, I shall discuss critical areas of what we must now reemphasize: the crisis in biodiversity and the need for collecting, the production and the importance of monographs and of inventories; as well as of what we need to deemphasize: DNA Taxonomy and the PhyloCode, plus much of the unproductive phylogenetic biology now so bandwagon popular; of how funding must be redirected for the good not only of taxonomy but of phylogenetic systematics; and of how taxonomic renaissance must be mounted.

A brief history of 250 years of mycological taxonomy and its technologies

Though Linnaeus' work (1753) is now the official starting point for all mycological taxonomy, he was by no means the earliest to record fungi, nor indeed is he considered to have been well-versed in fungi. His major contribution was the development of the system of binomial nomenclature that has stood the test of time as adaptive to advancing knowledge and allowing the proposal of hypotheses of relationships at all levels. The preeminence of two mycologists, Christiaan Hendrick Persoon [1761–1836] and Elias Magnus Fries [1794–1878], aptly called the “fathers of mycology,” overshadows many others of the early 19th century. They and the others of this exciting time of discovery based their species, genera, and higher ranks on comparative morphology, often aided by developments in microscopy. The intent was almost always to provide a classification that reflected relationships, deduced from comparative morphology. A few systems were proposed that attempted to replace such phylogenetic hypotheses by numerical arrangements, and a major compiler of descriptions, Pier Andrea Saccardo [1845–1920], was wedded to the idea that spore septation, shape, and coloration were dominant features by which fungi should be catalogued. His thinking adversely affected generations of mycologists, and one can justly refer to “the dead hand of Saccardo on the advancement of fungal taxonomy.”

The use of chemotaxonomy began early, with a few chemicals, and expanded primarily with lichenized fungi to a degree astounding to most non-lichenologists. The

reliance on the presence or absence of specialized lichen-substances as diagnostic tools for species (and generic) identification still remains an anachronism for many of us. Genetics as a tool in taxonomy began in the early 1930's, and mating systems rightfully remain one of the tools some taxonomists still use for species distinction. Reproductive isolation does not always, however, precede speciation, especially in allopatry (Coyne & Orr, 2004). Mycological taxonomists anxious to develop systems of classification that reflect phylogeny have exploited each and every tool that seemed to promise *predictive value*.

The largest blow to taxonomy came with *The New Systematics*, in which, in Wheeler's (2004) words, "Mayr (1942, p. 7) belittled traditional taxonomy.... Since that time, the goals of taxonomy have been confounded with those of related areas of science whether population biology, tropical biology or molecular biology and few individual or institutional voices have made unapologetic assertions of the importance and credibility of taxonomy for its own sake.... Although Hennig (1966) returned respectability to studies at and above the species level, taxonomy has never fully recovered from being thus tainted as non-scientific (even non-biological!)." We have seen many new tools, have their brief day in the sun, each in turn touted as "cutting edge." These include technologies, *e.g.*, electron microscopy (first TEM, then SEM), isozymes, RFLPs—then RAPDs and cognate approaches such as AFLPs, and now DNA sequence polymorphisms particularly in the nuclear ribosomal DNA repeat. These tools include schools of analysis, such as phenetics, cladistics, and recently Bayesian statistics. DNA sequence data have facilitated the inference of phylogenetic trees resulting in proposals for realignment of many taxa, (sometimes generating nomenclatural consequences that have yet to be proven correct). New combinations and new arrangements have been proposed on the basis of a study of far too few genes and consideration of far too few taxa.

There is a balance to be found between the quantity and the quality of informative characters and the number and distribution of taxa sampled. Higher standards are required. One of the reviewers of this paper believes that we will look back on the recent era of the molecular-phylogeny bandwagon as quaint and not very enduring. He points to some serious and excellent phylogenetic studies, including the exceptional one by Rokas et al. (2003) on a 100+ gene phylogeny of *Saccharomyces* species, which advocates 20-or-more simultaneous gene analyses.

Single-gene phylogenies have often been confused with species phylogenies. This is the sorry state in which we find mycological taxonomy today, forty years since Hennig and the promises his work provided. Molecular biologists have criticized taxonomists for conducting descriptive work, yet much of molecular biology is descriptive and *not* hypothesis-driven. Good science is, unequivocally, hypothesis-driven.²

²One may wonder what a hypothesis is in a taxonomic study. Implicit in a phylogenetic study is the hypothesis of monophyly - for any taxon in the hierarchy. Other hypotheses would be associations with morphology or ultrastructure (the dolipore septum was acquired once in Phylum X), or nutritional mode (the lichen symbiosis has evolved once in Family Y), or physiology (members of Genus Z all degrade cellulose by one common enzymatic pathway) or pathogenicity (species of Genus Q have co-specified with their hosts).

Taxonomists today are almost afraid to label themselves as that. Once more I quote from Wheeler (2004): “Mayr’s (1942) “population thinking” led thinkers in systematics to coin the term “biosystematists” to distinguish themselves from traditional taxonomists. Today, “tree thinking” has led to a segregated study of phylogeny that may, according to O’Hara (1997), be the beginning of another new splinter science. Once again a new name, phylogenetic biologist, distances these tree thinkers from taxonomy.”

The crisis in biodiversity

Surely all taxonomists are aware of the crisis that we face in biodiversity. An oft-quoted estimate for fungi is that we have described only 4 to 5% of the world’s species, leaving 95% or more yet to be recorded. The loss of habitats is proceeding so swiftly that the problem is critical. Unless these habitats are sampled now we will have lost forever our chance to document the world’s living biodiversity, to save that in museum specimens and, in the case of fungi, often in culture collections. To do that documentation requires an immense increase in the number of taxonomists and parataxonomists able to collect and identify the taxa. With the number of taxonomists dwindling each year, and with many of these now engaged only in *studies of known taxa* and who display no interest in the undescribed ones, we have little chance to survive the crisis with honor. Those who follow us will bemoan our lack of foresight in documenting the very diversity that could yield the answers to life on earth, past and future.

The answer is so simple it is easy to overlook. We *must* collect, collect, and collect. We need to spend our monies collecting, and to train our students to leave the air-conditioned laboratory and to go out into the field, from the frozen arctic to the humid tropics. Without documented specimens no assay of biodiversity has meaning. In Wheeler’s (2004) words, “Although the most visible products of alpha taxonomy are specimens, their associated data will be increasingly valuable as the biodiversity crisis progresses.” Specimens typically carry with them immense amounts of data on ecology, geography, and the environment that are critical for any modern biological investigation.

The biodiversity crisis pervades most of the issues I am discussing in this paper.

On monographs and inventories

I single out the importance of monographs and inventories because without them no real progress in taxonomy (nor also in phylogenetic biology) can ever occur. Monographs are the summation of scattered reports of species and subordinate taxa, carefully reconsidered and revisited. Given the paucity of taxonomists, few fungal groups ever get a substantial revisionary study even once or twice in a century. Monographs are the essential tools for progress in understanding biodiversity. Similarly, checklist inventories that do more than merely listing species determined and do include ecological and critical morphological data, contribute importantly to the summation of knowledge. It has long been my belief that monographic study on a not-too-large group remains the best subject for a doctorate thesis in taxonomy, providing the student with

the intellectual tools to investigate the past, and to learn the processes of discrimination, synonymy, and the intricacies of nomenclature.

Some pitfalls of the phylogenetic age: avoiding DNA taxonomy and the folly of the PhyloCode

Wheeler (2004) hit it on the head. “Well-intentioned proposals for a DNA-based taxonomy present a new and growing threat to the advance of taxonomy. Although DNA barcoding is an exciting new identification tool for taxonomy, it lacks the theoretical base for taxonomy and, unless handled rationally, could undermine the intellectual content of taxonomy making it a service industry providing an inferior service (Lipscomb. *et al.* 2003). DNA is simply data.” To me, it is clearly impossible to equate DNA sequences with taxonomic insights.

An even worse pitfall is the PhyloCode and its absurd rankless classifications. It seems incredible that a whole school of well-intentioned biologists has wasted countless time and effort on such a proposal, antithetic to the whole concept of hierarchal taxonomy that has served us so well for so long. I shall make no attempt here to do more than ask you to read Wheeler’s (2004) comments, summed up as “what the PhyloCode seeks to do does not need to be done and what it claims to do it does not. Taxonomy faces important and exciting intellectual and scientific challenges and should waste no more effort on what Carpenter (2003) aptly describes as ‘pure folly.’”

On funding

The individual taxonomist faces an almost impossible task these days to fund collecting trips for her/himself and for graduate students and postdoctoral students. When I was supported by the National Science Foundation (NSF) for many years from the 1960’s till the 1980’s, obtaining funding for collecting in Asia, the Caribbean, and Macaronesia was very easy, perhaps because it cost so little to do. I took one student for a year to Asia, and up to six at a time for two-week trips to the Caribbean and the Bahamas, and finally 4 scientists at a time for three month-long trips to Macaronesia. We skimmed by on very modest hotel rooms where we would study, document, and sometimes photograph specimens, often culturing them, and setting them to dry, from after dinner till midnight or later. We would arise by 6 am to go out in the field to collect all day, often lunching on slabs of bread, cheese, sausage, and a bottle of wine. The cost per specimen collected was minimal, and to this day the specimens we collected are being cited regularly in papers worldwide since many of the places we went were and still are only poorly-collected. The only grants that NSF supported in later years (when my applications were no longer funded) were *required* to have a molecular and phylogenetic component. Those that were funded, primarily phylogenetic studies, had budgets ten to fifty times the funding I had requested. Few of the successful grants in the 80’s and 90’s ever generated many new specimens, but did support comparatively expensive molecular analyses and equipment.

On the “bean-counting” mentality

Probably the most distressing aspect of the current scene in biology is the “bean-counting mentality” rampant in research institutes and universities worldwide. Under that mind-set many of us are now evaluated, compensated, employed, and given or not given tenure on the strength of ill-founded formulas in which ridiculous journal impact factors, numbers of papers, and grant monies are the variables. Given that an excellent monograph can be equivalent in research hours to 5–10 papers documenting single species descriptions or non-taxonomic research, and is likely to be published in a journal with a modest “impact factor” yet accrue citations over a time scale of many decades, not years, taxonomists will not be favored by the bean counters.

Towards a taxonomic renaissance

The sad truth is, in Wheeler’s (2004) words, “The diversion of funds from taxonomy to phylogenetic biology is an international phenomenon.” I know this to be a fact for the UK, Canada, the United States, and China. Nonetheless, I am deeply heartened as I see alpha taxonomic mycological work still being supported in most of Europe. Resources there are still being used for impressive monographic book-length studies like those of the *Flora Agaricina Neerlandica*, for the many superb volumes produced by the Centraalbureau voor Schimmelcultures, with others from France, Scandinavia, Switzerland, and especially Italy’s Associazione Micologica Bresadola. Alpha taxonomy is alive and well in the professional mycological journals of Britain, the Czech Republic, Estonia, France, Germany, the Netherlands, Scandinavia, and Switzerland, as well as in Asia (China, Japan, Korea). Much more evident is the quality alpha taxonomy that is being published throughout Europe by societies that are essentially manned by amateurs ably assisted by professionals: journals like Belgium’s *Miscellanea Micologica*, Denmark’s *Svampe*, France’s *Bulletin Mycologique et Botanique Dauphiné-Savoie*, Germany’s *Mycologia Bavarica*, Italy’s *Rivista di Micologia*, and Spain’s *Boletín de la Sociedad Micológica de Castellana*, to name but a few, whose pages abound with excellent photographs and frequently artistically produced line drawings. Couple that with some of the web-based bulletin boards (ASCOFrance comes immediately to mind) where amateurs and professionals can chat at length about their exciting finds and you can see why I have such faith in these alternatives to grant-financed phylogenetic papers and to symposia that add *so little* to the taxonomic imperative.

As an American I can only hang my head in shame at the lack of such publications by our amateur societies.³ Europe, on the other hand, clearly continues to nurture the naturalist’s involvement in taxonomy, as it has successfully done for the last century.

³ Some alpha taxonomic works are accepted both in *Mycologia* (which has suffered from a lack of taxonomically-trained and nomenclaturally-savvy editors in recent years), and in the *Canadian Journal of Botany*. My Belgian colleague, Grégoire L. Hennebert, and I founded what may be the only strictly taxonomic/nomenclatural mycological journal, *Mycotaxon*, in 1974. It has recently revisited its focus (taxonomy and nomenclature) and now excludes purely phylogenetic papers. Instead of hard-copy checklists, it encourages *web-based* checklists that can be frequently updated.

In my deep concern for the need to redirect funding towards collecting, comparative morphology, and monographic studies, my unstated but equal concern for effective support of phylogenetic biology and genomics may appear to be lost. The contributions of these new technologies have been not only exciting but also illuminating, and intellectually stimulating. Nevertheless, phylogenetic studies mean nothing if the data on which they are based is flawed. As Wheeler (2004) points out, “Continuing emphasis on the mere computerization of label data from museums and herbaria is misguided, when eight out of ten records may be mistaken. There is little benefit in rapid electronic access to unreliable data.” Amen.

When taxonomists examine herbarium specimens, confirmation of identifications should be part of the deal. If molecular phylogeneticists capture a misidentification, what is the process? For that matter, are we vigilant on re-annotation of GenBank sequences when misidentifications are discovered? (My information is that only the original depositor can correct the identification of a GenBank entry.)

The huge sums supplied by the National Science Foundation (NSF) to support ATOL (Assembling the Tree of Life) (\$8 million in 2002, \$12 million in 2003), or in the case of fungi, the Deep Hypha program—with many good aspects—may be deeply compromised by the few taxa involved. As one of my reviewers of this paper noted, “alpha taxonomy can both *enhance* Deep Hypha and remediate its shortcomings.” The problems of missing taxa are well summed up in Wheeler’s (2004) words, “Although the precise impact of species excluded from an analysis varies from case to case, there is general agreement that such missing taxa are a serious concern to the recovery of phylogenetic patterns (e.g. Novacek 1992; Wheeler 1992; Graybeal 1998; Hillis 1998; Hillis *et al.* 2003). For all but a few relatively well-known small clades, this ignorance of species diversity will pose an impediment to resolving phylogenetic relationships.... and phylogenies will be subject to frequent and major reorganizations.”

A recent turn-about in NSF’s priorities must be fully applauded: The PEET (Partnerships to Enhance Expertise in Taxonomy) program for training young taxonomists, and NSF’s funding of Revisionary Syntheses in Systematics as well as their Planetary Biodiversity Inventory are important steps in the right direction. That some of these were implemented during Quentin Wheeler’s three-year stint at NSF is not mentioned in his 2004 paper. Credit belongs to him and to his colleagues at NSF, Diana Lipscomb and Norm Platnick.

That in this day an alpha taxonomist can scarcely find a position in our universities is distressing. Positions in museums where there is time to generate monographs are equally hard to find. Where will universities and public museums find the money to support descriptive taxonomy? Wheeler (2004) has some cogent comments: “To meet the biodiversity crisis, taxonomy must rapidly transform to become big science. Its guiding agenda, after all, is to fully discover and describe the species of an entire planet. If it is worth billions to determine whether there is or ever was life on Mars, it is surely worth more to document the results of tens of millions of years of evolution on Earth.... Taxonomy not only deserves support, it deserves massive support to meet this last ditch effort to document species.”

Are the people at NSF or the National Institutes of Health in the US, or the granting agencies in the U.K. listening? Or, for that matter, is even your university or mine listening? Will budding fungal taxonomists recognize that alpha taxonomy is indeed more “cutting edge science” and definitely more crucial in this era of biodiversity crisis than any seductive phylogenetic studies in an air-conditioned laboratory? I’m keeping my fingers crossed.

I close with this advice to young fungal taxonomists: (a) forget the lure of instant fame in following the latest technological fad, but instead (b) go out into the field and collect, take ample notes, culture if possible, study—if you can take along a field microscope—while your specimens are alive (Baral, 1992) and while you simultaneously swat mosquitoes in a tropical rain forest, (c) learn to love sleuthing in the stacks of a good library as well as on the internet, (d) scour the world’s herbaria, (e) publish even if you feel you are only 95% correct, much preferable to being a perfectionist that never publishes—one whose data dies with himself or herself, (f) never be the graduate student who emails a scientist asking for cultures if you are incapable of doing your own fieldwork, of identifying specimens, and of using the taxonomic literature, and, (g) *above all*, leave a luxurious legacy of data for future taxonomists to build upon.

Whether you are working in a museum or in an academic position, maintain your central goals of producing the finest and most useful monographs, species descriptions, and floristic studies. Develop collaborations with your ecologist colleagues and build on the role that many fungi play in ecosystem function to make the strongest case for research funding. Forge collaborations between taxonomists and phylogeneticists that will get money to the taxonomists so that there is some product for posterity from their phylogenetic approximations. Collaterally, publish in the widest assortment of journals. Talk back to the bullies and to the “bean counters” and make the case for excellent, hypothesis-driven research in all areas of science — and make your own work an example.

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