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Invertebrate systematics or spineless taxonomy?*

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> Certain measurements are crucial to our ordinary understanding of the universe. What, for example, is the mean diameter of the Earth? It is 12,742 kilometers. How many starts are there in the Milky Way? Approximately 10^{11}. How many genes are there in a small virus particle? There are 10 (in φX174 phage). What is the mass of an electron? It is 9.1×10^{-28} grams. And how many species of organisms are there on Earth? We do not know, not even to the nearest order of magnitude.— E. O. Wilson, 1985, p. 21.

What progress has been made since these words were written by Wilson more than twenty years ago? The answer is a mixed one. We have so far to go in our inventory of Earth's species that it is easy to be discouraged by advances measured in hundreds of thousands of new species rather than millions. Yet there has been progress and the potential exists for rapid advances. Excellent work continues to be done as evidenced by this special issue of *ZooTaxa* and the burgeoning popularity of this e-journal. Innovative new funding has appeared at the U. S. National Science Foundation including the Partnerships to Enhance Expertise in Taxonomy (PEET), Assembling the Tree of Life (AToL), and particularly encouraging, the Revisionary Syntheses in Systematics (RevSys) and Planetary Biodiversity Inventory (PBI) projects that focus specifically on descriptive taxonomy. Most promising is an emerging new field, cybertaxonomy, that represents the convergence of traditional taxonomic goals with new, equally ambitious ones, fueled by the full potential of cyberinfrastructure, digital technology, information science, and computer engineering (Atkins et al. 2003, Page et al. 2005, Wheeler 2004, Wheeler et al. 2004).

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It is important to state clearly the missions of cybertaxonomy. They embrace the traditional missions of taxonomy to *discover and describe Earth's species; classify species according to their phylogenetic relationships; and make what is known about them accessible through Linnaean classifications and names.* They include also the added missions to *network specimens, experts, instruments, data, literature, and other research resources into a virtual "species observatory"; and organize experts into coordinated international taxon "knowledge communities" that expand, enhance, and share our knowledge of species and higher taxa.*

Four disturbing trends must be reversed if taxonomy is to realize its potential. First, the trend toward constructing branching diagrams divorced from formal Linnaean names and classifications (Franz 2005). Second, the trend toward constructing branching diagrams divorced from serious thought and analysis of complex characters, most notably morphology (Wheeler 2008d). Third, the trend of demurring to some other discipline or applied benefit to justify the importance of taxonomy. And fourth, allowing inferior approaches to be considered as possible alternatives to credible taxonomy, most recently DNA barcoding (Little & Stevenson 2007, Prendini 2005, Wheeler 2005) and the PhyloCode (Carpenter 2003, Nixon et al. 2003, Dominguez & Wheeler 1997, Keller et al. 2003).

The term 'systematics' is sometimes used as a code word for 'molecular phylogeny' or 'phylogenetic biology', an intentional emphasis of so-called phylogeny reconstruction (more accurately, a cladogram at best and, more often, a phenogram: Nelson & Platnick 1981) and de-emphasis of 'descriptive' taxonomy. Previously, 'systematics' was used as code word for a focus on population level phenomena and microevolution, again at the expense of attention to 'descriptive' tasks of taxonomy (e.g., Mayr 1969, Simpson 1961). In each case there is an intention to distance 'systematics' from taxonomy, the latter thereby relegated to the formal practices of naming and classifying. In the context of taxonomy, the ultimate goals are classifications and names; phylogenetic analysis is done by taxonomists specifically and primarily for the purpose of informing a classification (Hennig 1966) so that it may be informative (Farris 1979) and predictive (Nelson & Platnick 1981). The so-called 'descriptive' aspects of taxonomy are in fact the most important tasks of taxonomy. The widespread impact of phylogenies, classifications and names on biology suggest that all are necessary and deserving of support.

Unapologetic Character Analysis

The focus on characters and character analysis is as central to taxonomy as are formal names, species, or phylogeny (Hennig 1966). The species-as-individuals thesis (Ghieslin 1969, Hull 1969) has unfortunately shifted the emphasis away from what is at once most interesting, most observable, and most testable about taxonomy: characters. This has led to a focus on ontology of species and monophyletic groups separated from the epistemology necessary to discover or test them (de Queiroz 1988). One result is the Phylo Code that, at least in some of its several ill-defined versions, ignores the only evidence that exists to explore species: characters.

In order for taxonomy to be respected as an independent science it must return a focus to the exploration of characters. The imbalanced reliance on molecular characters only came about as a result of seeing taxonomy as a service to other branches of biology and a means to re-analyze existing knowledge of morphology. Because other biologists focus on interesting phenomena and properties of organisms, they logically need a phylogenetic context in which to understand and interpret their findings. When taxonomy was done for its own sake, it too focused on characters that were sufficiently complex to store historical information and be of inherent interest. For centuries, taxonomists have sought to unravel, document, and order the patterns of similarities and differences seen among species (Nelson & Platnick 1981). This research program has only recently been set aside. It is time to restore focus to comparative biology in the form of taxonomy. Among by-products of taxonomy done for its own sake are, of course, phylogenetic and species hypotheses as well as classifications and names. Doing taxonomy as an independent science advances simultaneously both the aims of taxonomy and its users.

Take No Hostage Taxonomy

Considering the urgent need to explore species before many succumb to the biodiversity crisis, it is time to promote taxonomy as an independent science with unique needs. Support will be found among constituencies that depend upon taxonomy… but only if taxonomists articulate why their science is different. The only alternative to promoting taxonomy for its own sake is to promote it directly as a service. This approach, however, rarely works. End users simply want to identify species, enjoy a reference system, and access useful scientific names. Many users do not appreciate the depth of science behind identification schemes, classifications and names. Thus some users are easily persuaded by the superficial arguments of alternatives such as DNA barcoding. Described as 'new' (which is, in our culture, an implied synonym of better), faster, and cheaper, such approaches sound good to those who do not understand the philosophy, history, mission, and constraints of good taxonomy.

Taxonomy is so important and so fundamental to credible biology that I have complete confidence that it will be restored to its proper central place in our research priorities. This can come about by one of two means. Taxonomists can courageously assert the importance of their work and demonstrate by an overwhelming show of excellence what taxonomy is capable of doing (Wheeler 2008b). Or, we can continue to ignore taxonomy and wait for an inevitable taxonomic tragedy. By ignoring the traditional jobs of taxonomy (describing and corroborating species and characters, making species identifiable, providing informative names and predictive classifications, and continually exploring biological diversity at and above the species level) it is only a matter of time until untested species, outdated names, or unimproved classifications lead to mistakes of enormous cost. A misidentified disease vector or pest species at a port of entry; conflated species with similar barcode genes but significantly different attributes; use of a name that no longer reflects an accurate understanding of natural patterns; or misidentification of a study organism can contribute to decisions with disastrous consequences in applied or experimental biology. Must we witness such disasters before restoring support and resources to taxonomy?

A New Solution to the Old Species Problem

Species remain unnecessarily problematic. We need to examine several aspects of species as they pertain to taxonomy and the perception of taxonomy: the belief that species are arbitrary; the perception that describing species is a one-time activity; and the need for a unit species concept in biology.

Are Species "Real"? Ernst Mayr (1963, 2000) was correct about the reality of species. That is, species exist in Nature independent of human thought. This view is independent of how we go about discovering species and independent of whether or not we get them right in practice.

Many who were educated in the context of the New Synthesis believe that genetic variation is essentially continuous in Nature. This emerged in part from the focus on population genetics and the emphasis of studying the origin and distribution of mutations within and among populations. The confusion was deepened by Mayr (1942, 1963) and others who, whether by accident or design, conflated tokogenetic patterns and phylogenetic patterns. This failure to distinguish between "traits" and "characters" (in the strict sense of Nixon & Wheeler 1992) reinforces the belief that species boundaries are artificial ones of convenience. Were species merely arbitrary, then approaches like DNA barcoding would be more serious alternatives to good taxonomy; but they are not. Species emerge when traits and characters are differentiated and patterns of distribution of the latter are critically analyzed. It is disingenuous to point to traits that are polymorphic within species as evidence that species boundaries are subjective when there are unique combinations of constantly distributed characters distinguishing species, at least those formulated by pattern criteria, such as the Phylogenetic Species Concept (e.g., Wheeler & Platnick 2000).

If we base species hypotheses on observable, testable distributions of characters it avoids the narrowness associated with species delimited by particular processes. We know that many processes contribute to speciation, so why cling to species concepts that are consistent with only one or a few of them? Is a species that arises by sympatry and intense selection fundamentally different from a species that arises by allopatry and random drift, or is it the processes that differ? Species ought to be seen as the results of an evolutionary process or processes. They are indicated by patterns of characters that suggest that they are irreversible “kinds” reflecting the results of a history of divergence. In seeing species in the first instance as patterns, we set the stage for interesting evolutionary biology studies to explain their origins (see below).

Species as Hypotheses. We can treat species as hypotheses about historical patterns of character distributions based on theories of character transformation (Platnick 1979). Species descriptions include characters as conjectures of evolutionary sameness, not simply as phenotypic descriptions of the animals studied (Nelson & Platnick 1981). Character transformations and speciation are two sides of a coin. They come about simultaneously through the removal of ancestral polymorphism by processes of extinction (Nixon & Wheeler 1992). To recognize species we need not know which process or processes were involved.

The beauty of the phylogenetic species concept (Eldredge & Cracraft 1980, Nelson & Platnick 1981, Cracraft 1983, Wheeler & Nixon 1990, Nixon & Wheeler 1992, Wheeler & Platnick 2000) is that it can be applied prior to cladistic analyses, is consistent with ancestral and daughter species, and is consistent with known processes contributing to speciation. And because it makes predictions about character distributions that are Popperian all-or-nothing statements (Gaffney 1979), phylogenetic species are imminently testable. This version of the PSC is not to be confused with the autapmorphic concept advocated by Mishler and Theriot (2000) among others.

Acknowledging that taxonomists’ treatments of species serve as testable hypotheses emphasizes that descriptions of species are not one-time activities. Descriptions are expanded, modified and improved over time as additional specimens and characters are observed. Suggestions to the contrary are false (e.g., Janzen 1993) notwithstanding that the shelf life of good descriptions may be a century or more.

Unit Species Concept. Many have given up the search for a unit species concept (Mishler & Donoghue 1982), concluding that the diversity of speciation processes among taxa dictate a need for multiple species concepts. When species concepts are based upon processes (e.g., isolation, recognition, etc.) this is a legitimate argument. However, the alternative (above) is to focus instead on character patterns. This is not unlike the logic of constructing cladograms first and worrying about their correspondence to phylogenetic trees later (Nelson & Platnick 1981). It is similarly a very general statement of unique combinations of characters as a precursor to contemplating possible causal scenarios. Such descriptions make explicit predictions about character distributions that may be tested as new populations are sampled and new characters discovered.

Why should we care whether we have a unit species concept? It is human nature to make comparisons. Unless we have a comparable, unit species concept it becomes meaningless to compare the numbers of species in two ecosystems or two higher taxa. It is similarly meaningless to ask whether two evolutionary processes over similar periods of time result in different numbers of descendant species. The phylogenetic species concept, based on patterns rather than processes, can even make comparable asexual and sexual species.

The “species problem” is not really a problem at all. It is the result of the same old confusion of pattern and process that led to so many difficulties before Hennig (Eldredge & Cracraft 1980).

Leadership

Taxonomy must reassert its unique position among the biological sciences and develop three levels of leadership to assure that its missions, goals and needs are met. Individual taxonomists should stress the complementarity of taxonomy to experimental branches of biology such as population biology, ecology, and molecular genetics. Descriptive aspects of taxonomy would be fully justifiable were they simply descriptive as in the case of mapping stars or plotting ocean floors (Grimaldi 2007). However, it happens that taxonomy is driven by hypothesis testing top to bottom. Homology statements; apomorphy assertions; species hypotheses; and cladistic relationships each make explicit predictions about patterns in Nature testable by further observations of specimens and characters. The fact that many experimental biologists seem to confuse experimental methods with a philosophical demarcation principle should not deter taxonomists from continuing to do good non-experimental science.

Groups of taxonomists, and taxonomists working in concert with other experts (cyberinfrastructure specialists, computer engineers, etc.), need to lead by example. Let's demonstrate what the PBI model is capable of when museums and taxon experts join forces in large-scale taxonomic projects (Knapp 2008, Page 2008). Let's demonstrate what such "knowledge communities" armed with a taxonomy-specific cyberinfrastructure are capable of accomplishing. It is not an exaggeration to predict an acceleration of 'descriptive' taxonomy by orders of magnitude within the next five years. The point is best made by simply doing.

Last, but not least, there is a great need for institutional leaders and leaders of institutions. Museums and botanical gardens have a very special and important role to play as symbolic leaders of taxonomy for taxonomy's sake. At the very heart of taxonomy are collections and the keepers of the largest, most comprehensive collections are museums and gardens. When the greatest taxonomic institutions support molecular genetics, conservation, and ecological studies at the expense of leadership in taxonomy, what are others to think of the importance of the latter? If taxonomy is not important enough for us to make our own top priority, why should any agency or individual seriously entertain supporting it financially?

This lack of institutional leadership is intertwined with the question of leaders of institutions. Over the past thirty years there has been a rapidly growing necessity for increased external funding of both collections and research programs within natural history museums. Two factors have pushed such institutions farther away from the taxonomy mission. One is the temptation to reach for the low-hanging fruit: grants to do molecular genetics or ecology or conservation can be significantly easier to get than grants to do taxonomy. And the lack of leadership in doing taxonomy and demonstrating its importance only reinforces the situation. The other is the hiring of museum directors whose primary job is fund raising. Such leaders often have little or no background in collections-based taxonomic research, adding yet another tendency to go for non-taxonomy funds. Some have little or no biological background, often coming instead from successful fund-raising in other non-profit sectors of society and having degrees in law or other non-related fields. Is it any wonder, then, that museums have drifted far away from their unique leadership role in taxonomy and species exploration? The irony in this situation, of course, is that museums are not doing what they can do uniquely well: taxonomy and species exploration. Were there to be museum directors who understood the unique role of taxonomy and museums who had courage to lead by example, they would certainly create their own opportunities.

I am stating the situation in harsh terms because we are in dire shape and standing at a crossroads. We can either reassert our importance to the growth of knowledge of biodiversity or we can continue to operate in the shadow of other disciplines under the tacit assumption that we are handmaidens to them. Handmaidens may do their jobs exceedingly well, but they seldom achieve their independent dreams or accumulate sufficient wealth to even pursue them.

I want to emphasize that taxonomists should be proud of their support of such important disciplines as ecology and conservation biology. However, it is my observation that the best taxonomy is done for its own sake. It follows that the best taxonomic services are spin offs of taxonomy done for its own sake. We need to be good partners to experimental biology, as we always have. This, however, does not justify abdicating leadership for our own field.

In the absence of leadership it is inevitable that someone in need of results will step in to fill the void. This explains proposals like DNA barcoding that could only compete with the rigorous hypotheses and species concepts of taxonomy when the latter are in short supply. The die is not yet cast for the future of species exploration or taxonomy. The time remaining for taxonomists to exert leadership, self organize, and lead by example is limited. Unless we respond to the urgent need to explore biological diversity someone else will. There is no more time for delay. Failure to lead could result in a decade or more of lost time, funding and opportunities.

Back to Basics

A taxonomic study of a single genus may require the study of thousands of specimens from scores of museums in dozens of countries. With so many regional collections, restrictions on collecting, and limitations of time and money to visit distant cities, few such studies are as comprehensive as they could be.

The time to testing for most species is much longer than it might be. In diverse taxa, including most invertebrates, the ratio of species to taxon experts is so skewed that a species described today may not be tested for decades to come. This is because of the revisionary cycle of taxonomy. Comprehensive revisions or monographs review every species, including synonyms, described in the past and examine as many specimens as possible that have accumulated in museum collections since the last revision. In this way species are tested by new specimens. Knowledge of morphological variation, geographic distributions, and character distributions is tested and refined. New species are distinguished and described. Then the cycle is repeated. This whole cycle of species testing can be compressed in cybertaxonomy. Instead of species being tested one or two times per century in a large group it is possible to test them frequently, in principle as fast as new specimens are collected or new characters discovered.

Cybertaxonomy promises a “species observatory” with which a taxonomist can compare specimens regardless of what collection they reside in, where they were collected, or when. Accelerated species testing will make classifications and names more reliable. A taxonomic study is logically limited only by monophyly and monophyly by observed distributions of synapomorphies (Hennig 1966). With such a distributed, virtual “species observatory” (Wheeler 2008b, 2008c), taxonomists will for the first time in a 250 year history be able to “see” species across all scales of time and space. The significance of this advance will soon become apparent as taxonomists make a flood of discoveries about species, characters and clades.

Armed with such powerful new tools and an ability to efficiently collaborate with experts around the globe, taxonomy can profitably return to seeking answers to its grand challenge questions: what are Earth’s species? How are they related? What is the history of character origins and transformations? Where are species distributed in geographic and ecological space? How have those distributions changed through time? And related questions (see Cracraft 2002, Page et al. 2007).

Univocal Urgings

Science done well is adversarial. The clash of ideas is often loud and seldom pretty to witness. These confrontations take place in publications, at meetings, and in classrooms and hallways. As ideas permeate a discipline they are ultimately accepted or rejected by a majority and thereby become the norm that peer reviewers use to measure grant proposals. Beware of anyone who seeks to quiet dissent. The secret is not to suppress opposing ideas but rather to conduct such fights within the community while presenting a single voice to the outside world. Taxonomy has many opportunities to rally around shared or prioritized needs. In the immediate future, the community should demand construction of a taxonomy-specific cyberinfrastructure and support for natural history collections. And undertake the challenging process of selecting some high profile, large scale inventory and revisionary projects (Wheeler & Valdecasas 2005).

Conclusions

Linnaeus captured the imagination of his generation with clever and provocative classifications and a sense of discovery. He opened the world of biological diversity to an ever widening audience and sparked an age of species exploration. As society's need for reliable information about species expands and threats of extinction accumulate, the time has arrived to revive taxonomy. Theoretical (Hennig 1966; Nelson & Platnick 1981) and technological (Atkins et al. 2003) advances also indicate that now is the time. Armed with a new generation of tools, sprit of cooperation, and sense of purpose, taxonomists can overwhelm the opposition with a positive demonstration of what taxonomy is capable of achieving (Wheeler 2008b).

It is time that taxonomists find their backbones. A series of compromises and accommodations in the 20th century only served to further marginalize taxonomy. Taxonomy must logically and epistemologically be pursued on its own terms. And it similarly must meet its own unique needs for infrastructure from collections of specimens and tissues to a finely tuned cyberitaxonomy infrastructure (Wheeler 2008c). No apologies are necessary to reinvest in educating and supporting comparative morphologists; anyone looking closely at the diversity of morphology and its rich historical information content will agree. The noble work of discovering and describing species begun by Linnaeus is well worth revival. Nothing else we can achieve, aside from assembling collections, can match such a legacy for the future. Speaking with a single voice, it is possible to have all these things.

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