The Seven Great Questions of Systematic Biology: An Essential Foundation for
Conservation and the Sustainable Use of Biodiversity
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THE SEVEN GREAT QUESTIONS OF SYSTEMATIC BIOLOGY: AN ESSENTIAL FOUNDATION FOR CONSERVATION AND THE SUSTAINABLE USE OF BIODIVERSITY[1]

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ABSTRACT

The three missions of Systematics Agenda 2000 (SA2000)—to inventory Earth's species, to understand their relationships, and to use the latter to create predictive information systems—define an agenda of research for systematic biology. The recognition that systematic knowledge underpins biological knowledge in general, and applied biology in particular, has resulted in an amazing growth in systematics over the past decade. Increasingly, systematics is being used to solve societal problems. This paper describes seven great questions within systematics and discusses their relevance for, and contribution to, conserving and sustainably using biodiversity. These questions fall into four broad categories: *Questions about diversity*: What is a species? and How many species are there? *Questions about phylogeny*: What is the Tree of Life? and What has been the history of character transformation? *Questions about biogeography*: Where are Earth's species distributed? and How have species' distributions changed over time? and *Questions about phyloinformatics*: How is phylogenetic history predictive?

Key words: biogeography, diversity, inventory, phylogenetics, phyloinformatics, systematics, Systematics Agenda 2000.

Systematic biology occupies the central core of biodiversity science. The four great themes of systematics—diversity, phylogeny, biogeography, and classification (to be subsumed here into a broader context termed phyloinformatics)—form a critical foundation for all other disciplines of biology. The discovery and naming of life's diversity, its evolutionary history, its distribution across Earth to form habitats and ecosystems, as well as how comparative information about organisms can be organized in a predictive manner, underpin, to one degree or another, all biological knowledge.

Beginning in the early 1990s systematists became increasingly engaged in conservation and the role played by systematics in solving societal problems (Systematics Agenda 2000, 1994a, 1994b). Since then, systematists have published numerous papers that address the contributions of systematics to conservation biology, focusing especially on such topics as diversity patterns, species concepts, geographic distribution, and endemism. The recogni-

tion of the importance of systematics has never been stronger.

There is a sense, however, in which some of these discussions linking systematics and conservation can be said to be too narrow, both from the perspective of systematics and from conservation. Thus, "conservation," at least in the expansive sense it will be used here, is more than just efforts to save endangered species and ecosystems, or to create protected areas. While certainly embracing these objectives, conservation in the real world covers much more ground philosophically, as well as in practice. In a world losing its biodiversity at an accelerating rate, systematics needs to be seen as a crucially relevant and important science in meeting the challenges of global environmental change (sensu lato), at the same time contributing strongly to traditional conservation practice.

It will therefore be a theme of this paper that systematics and systematists should be approaching conservation as a subset of solutions that must be

implemented to mitigate the adverse effects of environmental impacts in general, all the time realizing that the contributions undertaken to sustain and improve human well-being can themselves be seen as a conservation initiative. Stemming the loss of biodiversity is essential, but the factors leading to that loss are imbedded in a complex causal nexus that encompasses all aspects of society. People across the globe use tens of thousands of species to sustain their lives in one way or the other, and the causal complexity of that use is what makes saving biodiversity so difficult—it cannot be separated from how societies function. This reality is encapsulated in the activities of the Convention on Biological Diversity (CBD) and many nongovernmental organizations. Effective conservation efforts cannot be separated from the elimination of poverty, which cannot be separated from the improvement of women's health, education, and economic enfranchisement, which cannot be disentangled from governmental policies of many kinds, and on and on. New knowledge about the world (science) is necessary to meet the many environmental challenges created by human activities, and thus systematics can help in all sorts of ways not generally realized by most practicing systematists or other biodiversity scientists. This is what I mean by the need for systematists to have a more expansive vision for their discipline and for its importance.

This paper explores the contributions of systematics to science and society, firstly, by summarizing some of the literature published since the mid-1990s, when participants in Systematics Agenda 2000 (SA2000) released many of their assessments, and secondly, by pointing to new developments that will become increasingly important in the future. This will be done within the framework of what might be called the seven great questions of systematic biology, which to me at least, encapsulate most of the research agenda, and importance, of systematics to society. Not all of these questions will be treated equally here, inasmuch as some have been the subject of a substantial recent literature (see citations below).

SYSTEMATICS AGENDA 2000: BRINGING
SYSTEMATICS TO SOCIETY

In the early 1990s the Society of Systematic Biologists, the American Society of Plant Taxonomists, and the Willi Hennig Society, in cooperation with the Association of Systematics Collections, launched an effort to document the importance of systematics to society (Anonymous, 1991). Through its many publications, Systematics Agenda 2000

transformed the way systematists view their own discipline, and it helped create an atmosphere in many countries throughout the world in which systematics gained in stature and importance as an integral component of biodiversity science.

Because many systematists, both young and old, might be unfamiliar with the rich panoply of published results of this effort, these are summarized in Table 1. These papers cover a broad range of subjects that articulate the importance of systematics. Collectively, they have reached out to systematists and biodiversity science policymakers around the world and have been responsible, in varying degrees, to promoting and building systematics. Thus, to take one example, following SA2000 symposia at the Royal Society in London (Claridge, 1995) and the French Academy of Sciences in Paris, new initiatives were formed to promote the objectives of systematics across Europe (Blackmore & Cutler, 1996).

Systematics Agenda 2000, although begun in North America, was developed as a global effort. Thus, the core documents of SA2000 were intentionally not copyrighted so that they could be taken, and used, by systematists to promote systematics research and capacity building anywhere. Translations were encouraged, and that strategy worked as numerous individuals and groups adopted the language and content of SA2000 in their efforts (Table 1). Today, SA2000 is truly international. Systematics Agenda 2000 International (SA2000I) is a program of the International Union of Biological Sciences (IUBS) and functions as the systematics core element of the international biodiversity science program DIVERSITAS [DIVERSITAS]. Through DIVERSITAS, SA2000I has been active in providing advice on systematics science and capacity building to the Convention on Biological Diversity (CBD) and its Global Taxonomy Initiative [GTI]. Some of the SA2000I/DIVERSITAS documents in support of the GTI are available on the CBD website; these documents contain recommendations that have been adopted by the CBD Conference of the Parties (the 181 countries that have ratified the Convention). (For the record, as of 12 September 2001, only six signatory countries to the CBD have failed to ratify: Afghanistan, Yugoslavia, Thailand, Tuvalu, Kuwait, and the United States of America.)

THE SEVEN GREAT QUESTIONS OF SYSTEMATICS

The scientific agenda of systematics and its relevance for society occupy four great themes: diversity, phylogenetic history, biogeography, and clas-

Table 1. An overview of the papers produced by participants in Systematics Agenda 2000 over the last decade. These publications treat the role and importance of systematics to society, discuss aspects of building systematics science capacity, or address policy issues involving systematics and biodiversity.

Publication	Theme
General SA2000 Documents	
Anonymous (1991)	Announced formation of SA2000
Systematics Agenda 2000 (1994a)	Color brochure discussing importance of systematics and describing SA2000's three missions
Systematics Agenda 2000 (1994b)	Technical report providing detail for 1994a
BioScience 1995 (vol. 45, no. 10)	
Simpson & Cracraft (1995)	Overview of systematics and papers in *BioScience*
Savage (1995)	Role of systematics in biodiversity science
Miller & Rossman (1995)	Role of systematics in agriculture
Brooks et al. (1995)	Role of systematics in ecology and behavior
Lauder et al. (1995)	Role of systematics in comparative morphology and physiology
Davis (1995)	Systematics and public health
Biodiversity and Conservation 1995 (vol. 4, no. 5)	
Claridge (1995)	Introduction to SA2000 symposium held at the Royal Society, 12 April 1994
Eshbaugh (1995)	Overview and history of SA2000
Cracraft (1995)	Building systematics and biodiversity science capacity
Wheeler (1995a)	Biodiversity and systematics inventories
Prance (1995)	Systematics, conservation, and sustainable development
Jones (1995)	BioNet-International and capacity building
McNeely (1995)	Systematics and conservation
Annals of the Missouri Botanical Garden 1996 (vol. 83, no. 1)	
Richardson (1996)	Introduction to SA2000 Symposium, 41st Annual Systematics Symposium, MOBOT
Monson (1996)	Phylogenetics and comparative plant physiology and development
Rossman & Miller (1996)	Role of systematics in agriculture and forestry
Vecchione & Collette (1996)	Role of systematics in fisheries and marine biodiversity
Oliver (1996)	Importance of systematics for public health
Vane-Wright (1996)	Role of systematics in conservation
Balick (1996)	Systematics and ethnobotany
Other publications	
Systématique Agenda 2000 (1994)	French translation of SA2000 (1994a)
Wheeler (1995b)	Systematics and biodiversity policy
Agenda Systematik 2000 (1996)	German translation and expansion of SA2000 (1994b)
Blackmore & Cutler (1996)	Building SA2000 in Europe
Wheeler & Cracraft (1996)	Building systematics capacity
American Museum of Natural History (1999)	Workshop report, cosponsored by SA2000 International, on Convention of Biological Diversity Global Taxonomy Initiative
Baas (1999)	SA2000I, DIVERSITAS, and the CBD
Cracraft (2000)	Building systematics capacity

sification. Each of these four themes leads to a series of fundamental questions—the seven great questions of systematics. These questions broadly cover what systematists do, and are why, in my opinion, systematics is the central, undeniable core of biodiversity science.

THE FIRST GREAT QUESTION: WHAT IS A SPECIES?

No question, probably, has generated more controversy, been so opaque to solution, and yet remains as crucial and important today as it ever has, than "What is a species?" In systematics, which is

a taxon-based science, it is unquestionably the most fundamental question that can be asked. Astonishingly, many biologists profess to be tired of the controversies over this question, yet instantly remain willing to engage in the debate, whether or not they themselves are professionally concerned with individuating species limits, i.e., whether they are systematists or not. Everyone, it seems, knows what a species is, or more likely, what is not!

The reason for the dispute is fairly obvious: at some level, notions of species are at the very heart of biological understanding and so there is a lot at stake. Species concepts intersect with a whole series of conceptual and disciplinary agendas, from those of systematists who discover and describe Earth's diversity, to those reconstructing phylogeny and biogeography, to those attempting to understand the origins of species from a genetic or ecological viewpoint, to those interested in conservation, ecology, and applied biology. Species are the basic units of systematics, evolutionary biology, and diversity. Thus, species concepts touch upon elemental philosophical arguments about the reality of the units of nature as perceived by biologists of varying disciplines as well as scientific opinion about how life evolves.

Given this crucial importance, it is ironic that there is so much divisiveness over "What is a species?" You would think biologists could have solved this issue by now. Yet each year brings forth numerous papers on the subject, and books keep flowing (most recently, for example, Ereshefsky, 1992; Kimbel & Martin, 1993; Claridge et al., 1997; Howard & Berlocher, 1998; Wilson, 1999; Wheeler & Meier, 2000), all with no diminution of differences of opinion.

Nevertheless, it can be argued that over the last decade, practicing systematists—those biodiversity scientists whose research most directly bears on this issue—are gradually converging upon a common solution to this question, either as a result of practical or theoretical considerations, or both. These systematists see species as basal (smallest) clusters of diagnosably distinct populations (groups of individual organisms). Most of these systematists do not endorse a particular concept of species; they go about their work inventorying, describing, and monographing without a heavy burden of theorizing. But if one had to put a name on their concept, it would appear to be most similar to that advocated by supporters of a phylogenetic species concept (Nelson & Platnick, 1981; Cracraft, 1983, 1989a; Nixon & Wheeler, 1990; Wheeler & Platnick, 2000).

The reason why this is the most common approach to species is very practical, as well as simply a matter of numbers: the majority of systematists working on invertebrates, especially insects, many plant groups, and various vertebrate taxa view species as basal diagnosable units because this best fits the way they partition the taxonomic variation they have observed. How could this not be the case when the large majority of described species are known from a handful of specimens, often single individuals? Or when nothing is known about their biology or patterns of genetic variation?

Thus, the debate over species, in a practical sense, comes down to a choice between a phylogenetic species concept (PSC) and a biological species concept (BSC). The latter, surprisingly, is applied by very few practicing systematists who inventory and describe species, but has strong support from advocates of the evolutionary systematics of Mayr (1942, 1963, 1982, 2000) and by those whose interests lie with population genetics (Coyne et al., 1988; Avise & Ball, 1990) or evolutionary biology in general (e.g., Bock, 1987; Futuyma, 1998). The interchanges among advocates of the PSC and BSC have been incessant. It is not my purpose to review these debates as the central arguments and positions can be found in Wheeler and Meier (2000). Instead, pursuant to the theme of this paper, I comment briefly on the relevance of species concepts to conservation and applied biology.

Species concepts are important because they allow us to propose hypotheses about the ontology of nature: different species concepts generally imply a different ontology (Cracraft, 1987, 1989b). This is not just philosophical mumbo-jumbo. One needs a clear idea of the entities of nature so that one can count and describe patterns of diversity, as well as understand how entities behave (i.e., how they participate in processes). Thus, there are very practical consequences stemming from the adoption of a particular species concept, especially in the description and enumeration of diversity.

Conservation biology, although inherently cross-disciplinary, emerged primarily from an ecological tradition, and ecologists and other non-systematist biodiversity scientists have come to their understanding of species and speciation through their formal university training in ecology, genetics, and evolution. Most of that training has accepted the BSC because it has been the canonical view of species since the early influential work of Ernst Mayr (1942, 1963) and because it has been followed in most contemporary textbooks (e.g., Futuyma, 1998). However, many conservation biologists began to see a problem with applying the BSC because of its

ambiguous treatment of discrete taxonomic varia-
tion. Thus, under the BSC, diagnosable populations
might be ranked either as a species or subspecies,
or subspecific rank itself might be applied to diag-
nosably distinct forms as well as to arbitrary sub-
divisions of clinal variation.

In an influential paper, Ryder (1986: 9–10) sum-
marized the opinions of conservation biologists
working within the zoo community: "Out of a sense
of frustration with the limitations of current mam-
malian taxonomy [broadly using the BSC] in deter-
mining which named subspecies actually represent
significant adaptive variation, those assembled at
the Philadelphia conference [of zoo biologists] will-
ingly discarded the concept that all subspecies are
equal. Rather, it emerged that zoos ought properly
to address the conservation of evolutionary signifi-
cant units (ESUs within species)." They went fur-
ther to suggest that identification of ESUs be made
on the basis of concordance across multiple kinds
of data and that "when geographic distribution data
indicate the existence of *discrete* [italics added]
populations within the range of a species, an esti-
mate of genetic distance, for example, should be
made to determine whether the populations have
ESU status." It is fairly clear what these conser-
vationists were getting at: the traditional BSC ap-
proach to individuating units of nature was not
working for their purposes. While the determination
of whether a population could be judged to have
"significant adaptive variation" verges on nonoper-
ationalism, the key recommendation of their pro-
posal—identifying discrete populations—does not.
They grasped the reasonable idea of trying to con-
serve and manage (in situ and ex situ) diagnosable
and distinct populations, or ESUs as they were
called.

A very large literature has since developed with-
in conservation biology on the concepts of species,
ESUs, and other recently introduced terms such as
"management units." Systematists have pointed out
that ESUs have broad equivalence to the species
units identified by the phylogenetic species concept
and that use of the PSC meets the needs of the
conservation community not currently satisfied by
the BSC (Cracraft, 1991, 1997; Vogler & DeSalle,
1994; Barrowclough & Flesness, 1996). Other con-
servation biologists, notably those having a popu-
lation genetic approach to the problem, have con-
tinued to support the BSC and seek ways to refine
theoretical and practical approaches to the ESU
concept (e.g., Moritz, 1994a, b, 1995).

There is, however, a powerful and crucial argu-
ment often left out of these debates: if conservation
biology is to be a science that relies on a rigorous

description of diversity, then it should adopt the
language and conventions of systematic biology and
taxonomic practice (Cracraft, 1997; Wheeler,
1997). Although systematists may argue vehement-
ly over which species concept is best, they agree
on many issues of formal taxonomy—that species-
level taxa have formal Latin names, that those
names are tied to type specimens, that there are
standard rules of nomenclature (the international
codes) so that scientific names can be organized
and managed over time, and that there must be
voucher specimens to document taxonomic deci-
sions and descriptions. None of this is found in
concepts such as ESUs or management units.

Conservation biology should therefore abandon
such concepts as evolutionarily significant units.
ESUs are not a substitute for formal taxonomy. Un-
like formally described taxa with their types and
historical continuity in rules of nomenclature, ESUs
cannot have "legal standing." ESUs cannot, and
should not, be the units we regulate in trade, pro-
tect with legal instruments, or expect to be used by
applied biology for biotechnology, biodiversity in-
formation systems, and many other uses. This is not
the case with *taxonomic units* (Geist, 1992). Thus,
the power of systematics and taxonomy: despite ar-
guments over the most fundamental units of na-
ture—species—protagonists share disciplinary
standards that prevent names, and thus the iden-
tified taxa themselves, from devolving into chaos
over long periods of time.

THE SECOND GREAT QUESTION: HOW MANY SPECIES
ARE THERE?

Discovering and describing Earth's taxonomic di-
versity is the starting point for all biological knowl-
edge. Because of its scope and complexity, however,
knowing how many species inhabit Earth's ecosys-
tems is one of the megascience questions of biology.
While it is generally accepted that around 1.5–1.7
million species have been discovered and de-
scribed, estimates of unknown diversity range any-
where from 10 to 100 million species, with 13–20
million being the most frequently seen number
(e.g., Stork, 1999). So the answer to this megasci-
ence question is: We don't know!

But we must find out. When one realizes that the
use of biodiversity drives the world economy and
this has come from knowledge of about 1.5–1.7 mil-
lion species—probably less than 10% of all species
on planet Earth—it is clear that abundant new ben-
efits will flow from newly documented diversity.
Among these benefits of inventories identified by
SA2000, one could include:

- they document patterns of diversity across habitats and ecosystems
- they provide baseline data for monitoring activities
- they identify areas of endemism and regions in need of conservation and protection
- they discover new species having economic and social value to societies (pharmacological, agricultural, fisheries, biotechnological)
- they provide the baseline data for implementing an ecosystem approach to conservation and sustainable development
- they support and promote tourism.

We are disastrously ignorant of the natural world. That this is so was highlighted in the 45th Annual Systematics Symposium of the Missouri Botanical Garden (Richardson, 2000), which summarized the need for, and challenges to, systematic inventory (e.g., Prance et al., 2000; Lundberg et al., 2000) and also highlighted that we are in a new age of discovery (Donoghue & Alverson, 2000). We know so little that even in the most well-known groups such as birds and mammals, new species are being discovered each year (e.g., Giao et al., 1998; Beresford & Cracraft, 1999; MacKinnon, 2000). The most outrageous and spectacular example of this is probably the description of six new species of lemurs (in three separate genera) from Madagascar, all published in the year 2000 (250 years post-Linnaeus) in a single issue of the *International Journal of Primatology* (Thalmann & Geissmann, 2000; Groves, 2000; Rasoloarison et al., 2000).

THE THIRD GREAT QUESTION: WHAT IS THE TREE OF LIFE?

Reconstructing the Tree of Life (TOL) is the third great question of systematic biology. This is also a megascience question for systematics for several well-known reasons. First, given N taxa, there are N − 1 nodes that need to be resolved. The consequence is that as the solution to the second great question of systematics—How many species are there?—plays out, the domain of this third question gets larger and larger. A second major reason relates to the first: as the number of taxa in the tree increases, it gets more and more difficult to obtain sufficient data on these taxa, and the computational complexity of finding an objective answer also becomes astronomical. Compared to deciphering the TOL, the determination of the sequence of the human genome, which for all intents and purposes was solved by a single, relatively small corporation, turned out to be a rather simple problem (it just required a little money and coordination among sci-

entists). In contrast, as a scientific problem, resolving the TOL is much more comparable in complexity, say, to knowing all the genes in the human genome, how they function, and how their gene products interact to form a blueprint for development.

So the answer to the third question is, of course: we don't know. As an index to the vastness of the problem, we can estimate that there are right now about 1.7 million nodes on the TOL, reflecting the number of species that have been discovered and described. Yet, where do we stand presently? No one knows for sure, but roughly—very roughly—perhaps 50,000 to 60,000 species are represented on one kind of tree or another. That is a pure guess inasmuch as there is no comprehensive database of trees. The only repository approaching what is needed is TreeBASE [TreeBASE], which has approximately 12,000 taxa, but the sample is highly biased in being mostly botanical.

Assuming 50,000 taxa already placed on one or more trees, it is fair to say the position of most of those is poorly supported by character evidence. While it is perfectly accurate to say our knowledge of the TOL is growing very rapidly, as measured by the numbers of phylogenetic papers being published, it is equally accurate to say a large percentage of the nodes on those trees have relatively little support. There are many reasons for this, among the most important being poor taxon and character sampling, poor choice of character system, and ambiguities in the methods used to analyze the data. Moreover, because taxon sampling is generally poor in most published phylogenetic studies, it is not at all clear how the different results can be linked with one another to form a general view of the TOL, a "supertree of life" if you will.

The most remarkable observation is that our understanding of the TOL—at least in terms of the 50,000 taxa just mentioned—is a product mostly of the last decade. Modern phylogenetics is only about 30–40 years old, and serious "tree thinking" not much older. The rise of "evolutionary systematics" in the 1930s and 1940s, with its emphasis on a population biology/genetic approach toward the history of life, slowed the discovery of the TOL because it was largely assumed that if ancestors could not be found in the fossil record, there was little hope of understanding phylogeny.

If that seems a misrepresentation of history, one only has to examine the content of the major systematics journals (for example, *Systematic Zoology*) prior to 1960 to see that depicting relationships as trees was not of major importance. There was remarkably little "tree thinking" prior to the intro-

duction of numerical taxonomy, a discipline that created trees, but was ambivalent in its interpretation of them. Many proponents of this approach saw their trees as purely representational of phenetic similarity, not history; others hoped these diagrams might reflect some trace of history. The important point here is that, compared to evolutionary systematics, numerical taxonomy developed repeatable methods that produced trees.

Both evolutionary systematics and numerical taxonomy were eclipsed by Willi Hennig's conceptual and methodological development of phylogenetic systematics, or cladistics. The broad adoption of cladistics formalized tree-thinking in terms of phylogenetic relationships and history. Also, the numerical methods that were rapidly introduced brought a much needed objectivity, both philosophical and analytical, to the study of phylogeny. The explosion of phylogenetic knowledge over the last decade has resulted just as much from the conceptual and analytical revolution of the 1960s to 1980s as it has by the introduction of efficient methods to gather new kinds of data, especially those from molecular sequences.

Why phylogenetics matters

These advances in phylogenetic theory and methodology have revolutionized systematic and comparative biology, and the transformation of systematics into a truly historical science could not have come at a better time. Society is desperate for knowledge about phylogeny. While many systematists still see an understanding of phylogeny as a goal in itself, numerous segments of society are looking to phylogenetics to solve entirely new kinds of problems. Consider the following examples:

1. Tracing disease transmission

The first application of phylogenetic analysis to examine disease transmission employed parsimony analysis to investigate whether a Florida dentist, discovered to be HIV-positive and who had contracted AIDS, had transmitted the infection to any of his patients (Ou et al., 1992). These investigators chose the HIV envelope (env) gene because of its high variability and compared sequences from the dentist to those of HIV-positive patients and HIV-positive nonpatients as controls. Phylogenetic analysis showed clear patterns of genetic relationships between the dentist and at least five of his patients who had no identifiable behavioral risks to contract HIV infection (Fig. 1; for discussion of other uses of phylogenetic methods in analyzing HIV evolution, see Holmes et al., 1996, and Crandall, 1999).
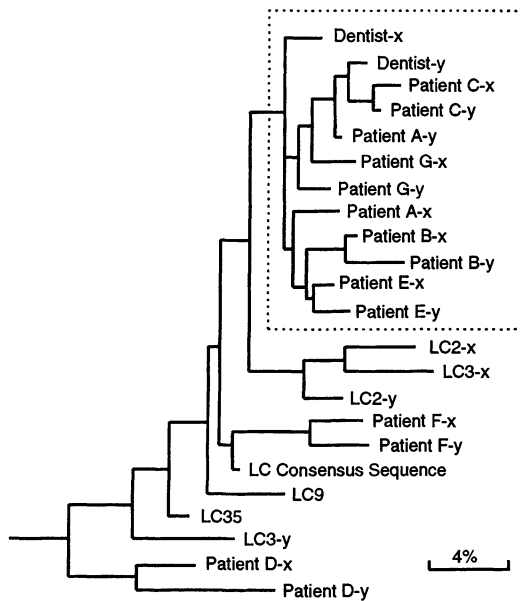

Figure 1. Phylogenetic tree of HIV-1 env V3 sequences from a HIV positive Florida dentist and his patients A–G (x and y notations refer to divergent clones, LC refers to local controls; see Ou et al., 1992, for details). These results were consistent with the hypothesis that the dentist was the source of the patients' HIV infection. This was the first use of phylogenetic analysis to examine disease transmission. Reprinted with permission from Ou et al. (1992), *Science* 256: 1165, figure 1. Copyright 1992 American Association for the Advancement of Science; http://www.sciencemag.org.

2. Tracking the spread of "emergent" diseases

Phylogenetics is playing an increasing role in the medical sciences, especially in identifying disease agents that spread from one region of the globe to another. DNA sequences from disease entities can be rapidly obtained and compared to sequences housed in databases such as [GenBank]. The summer of 1999 in the New York City area brought a strange confluence of events. A number of people were stricken with an encephalitis that had the etiology of a flavivirus. At the same time large birds, including American crows (*Corvus brachyrhynchos*), were turning up dead in unusual numbers in the wild and in local zoos. Viral particles were eventually isolated and their polyprotein nucleotide sequence determined. Phylogenetic comparison with other sequences identified the newly emergent disease as being related to West Nile Virus (Fig. 2; Lanciotti et al., 1999), which circulates between birds and mosquitos and from the latter into humans. Similar strains in the Mediterranean region and Middle East were also associated with increased avian mortality. The virus has now spread
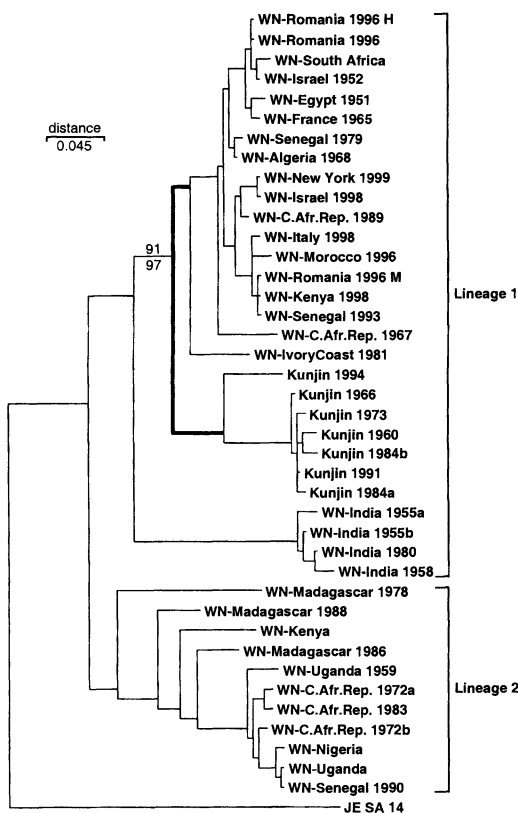
Figure 2. Phylogenetic analysis was used to trace the origin of the West Nile-like virus that broke out in the New York City region in 1999 (Lanciotti et al., 1999). These results indicate the New York strain is closely related to strains from central and northern Africa, the Middle East, and eastern Europe and was derived from that region. Reprinted with permission from Lanciotti et al. (1999), *Science* 286: 2333, figure 2. Copyright 1999 American Association for the Advancement of Science; http://www.sciencemag.org.

well beyond the New York region and also into non-human mammalian hosts.

3. Discovery of "new" emergent diseases

In addition to tracking diseases from one region to another, phylogenetic analysis is being used to discover new disease entities. In late 1998 and early 1999 a new mosquito-borne virus, called Nipah, emerged in Malaysia (Chua et al., 2000). Using pigs as a vertebrate host the virus jumped to humans, causing symptoms that first suggested Japanese encephalitis. Eventually 265 cases were reported and 105 people died from severe nervous system pathology. To control the epidemic, over a million pigs had to be slaughtered.

Phylogenetic analysis played a major role in helping to characterize Nipah virus (Chua et al.,

2000). Comparative sequences were obtained from the nucleoprotein (N) gene and compared to other members of the subfamily Paramyxovirinae. The resulting tree demonstrated the relationship of Nipah to another recently discovered virus, Hendra virus, and the sequence differences indicated they were distinct (Fig. 3).

4. Monitoring and predicting viral host switching

Karposi's sarcoma virus is endemic to central Africa and has associated with it a rhadinovirus, Karposi's-sarcoma-associated herpesvirus (KSHV). Until recently rhadinoviruses (γ_2-herpesviruses) were found in various Old and New World monkeys but not human's closest relatives, the great apes. After determining sequences of herpesvirus DNA polymerase taken from wild *Pan troglodytes* and *Gorilla gorilla* from Cameroon and Gabon, Lacoste et al. (2000) reported the discovery of new strains of these viruses. When those sequences were compared to others already known using a phylogenetic analysis, Lacoste et al. (2000) showed that these new viruses are closely related to KSHV (Fig. 4). The phylogenetic closeness of these new herpesviruses and KSHV raises the potential for host switching into humans as they hunt and consume great apes for food. Phylogenetic analysis contributes importantly to identifying and monitoring this new health threat.

5. Genomics, development, gene expression, and disease

Phylogenetic thinking and methodologies are taking hold in the fields of genomics and molecular medicine (e.g., Eisen, 1998; Pollock et al., 2000) and promise not only to increase our knowledge of the relationships of organisms but also surely will lead to insights into understanding and predicting gene structure and function. Developmental biologists have long acknowledged the predictive and explanatory power of phylogenetic relationships in reconstructing the historical pathways of development (reviewed in Raff, 1996), and the rapidly expanding field of evolutionary development ("evo-devo") will, reciprocally, result in major new advances in understanding developmental mechanisms and will inject new character systems into systematics that will inform phylogenetic relationships of major organismal groups.

6. Identification of invasive species

The transport of alien species is a major global environmental problem. The United States alone
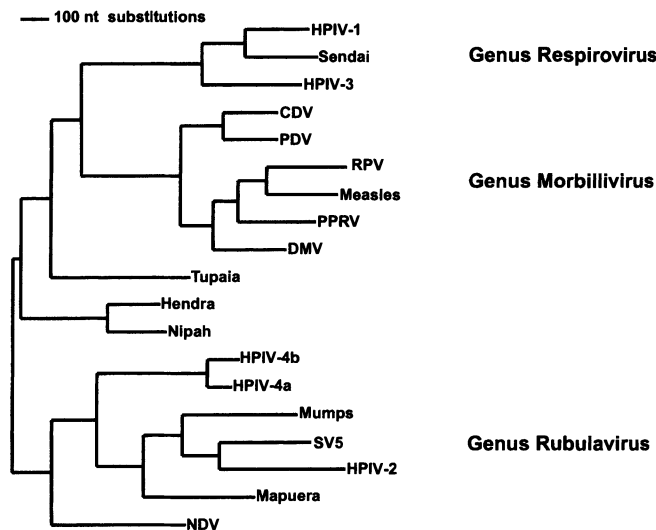
Figure 3.   Phylogenetic analysis of the nucleoprotein (N) gene of the so-called Nipah virus that broke out in Malaysia in 1998 and 1999 (Chua et al., 2000) showed this new emergent virus was closely related to another recently discovered paramyxovirus, Hendra virus. Reprinted with permission from Chua et al. (2000), *Science* 288: 1432, figure 4. Copyright 2000 American Association for the Advancement of Science; http://www.sciencemag.org.

harbors about 50,000 invasive species at a loss of nearly $137 billion annually to control and mitigate their effects (Pimentel et al., 2000; Wolfenbarger & Phifer, 2000). Identifying potential exotic species is a major priority and a first-line of defense against them. In 1984 a tropical marine green alga (*Caulerpa taxifolia*) escaped from an aquarium and invaded the Mediterranean Sea. This particular strain proved remarkably hardy and competitive, and spread rapidly to devastate populations of native species (Jousson et al., 2000). The species was recently discovered at several locations along the California coast. Jousson et al. (2000) posed the question whether the California populations of *Caulerpa* could be identified as an invasion of the Mediterranean strain, representing a potentially serious threat to coastal ecosystems. Comparing DNA sequences from the internal transcribed spacer of ribosomal DNA from multiple populations, phylogenetic analysis united 11 of 12 sequences from samples in California with those from the Mediterranean; one sequence clustered with a Red Sea/IndoPacific clade (Fig. 5). It was concluded that an immediate eradication program was warranted.

7. Discovery of microbial diversity

Phylogenetic analysis of DNA sequences has become a major tool in the discovery of new microorganisms, especially bacteria. Because most of these organisms cannot be cultured, microbiologists have turned to molecular probes for inventory and identification (Pace, 1997). Typically using probes for rRNA genes, the sequences are compared to those in databases by various phylogenetic techniques. Phylogenetic methods have thus opened up entirely new approaches to understanding the microbial diversity of extreme environments (Horikoshi & Tsujii, 1999) and have led to a greater understanding of the distribution of microbial life forms. It is now appreciated, for example, that archaebacteria are not only found in extreme environments such as hydrothermal vents and hot springs but are much more widespread than previously thought, including a variety of coastal and open ocean habitats (DeLong, 1992).

THE FOURTH GREAT QUESTION: WHAT HAS BEEN THE HISTORY OF CHARACTER TRANSFORMATION?

The proposition that the history of character transformation might be considered a great question of systematics may strike some as a bit strange, but reflection will confirm that all we know about the evolution of form and function derives from how character change is interpreted relative to a given tree. There have been two main ways in which character transformations are studied. First, in generating phylogenetic hypotheses under maximum parsimony, characters used to build the tree are optimized on it thus allowing inferences about their transformation across the tree. A second method has been to take some tree as given and then optimize, or plot, characters on it. There is a growing
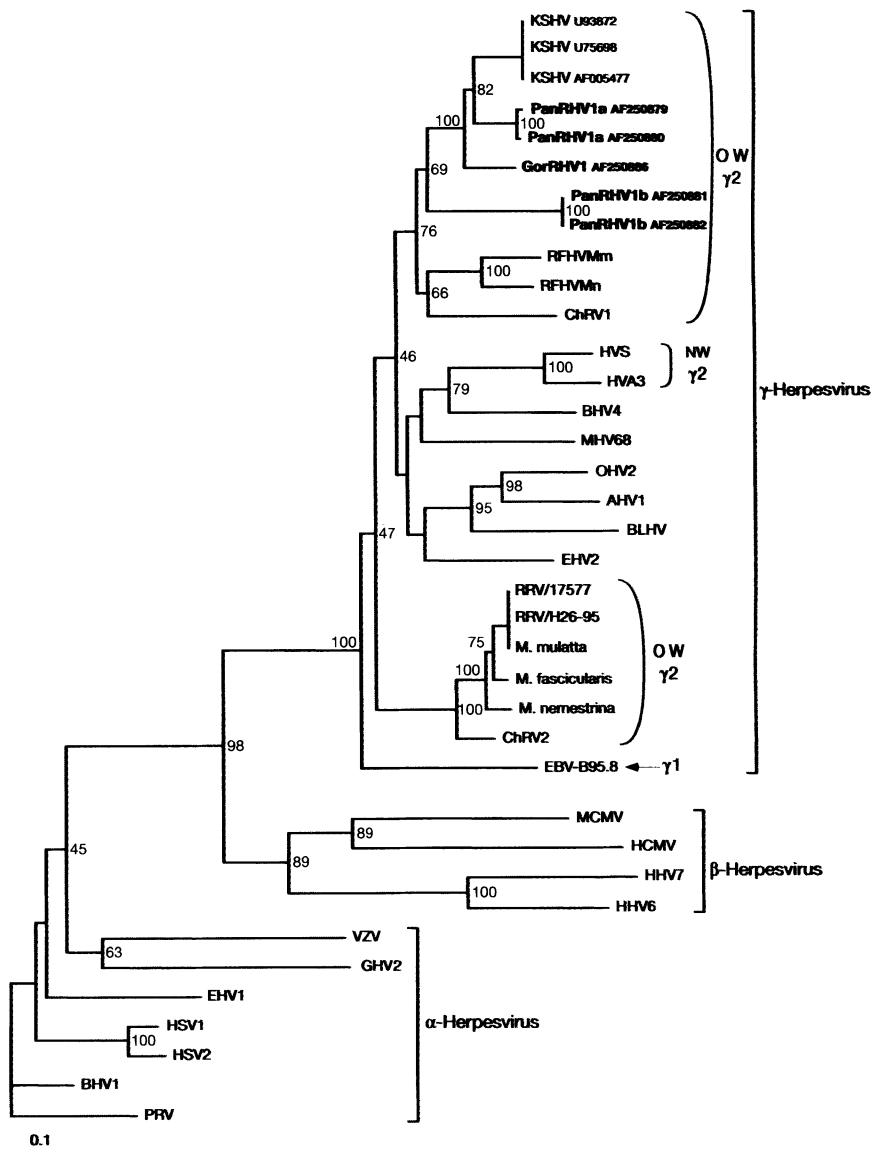
Figure 4.   A phylogenetic tree based on sequences of the DNA polymerase gene for several herpesviruses newly discovered in the chimpanzee (*Pan troglodytes*) and lowland gorilla (*Gorilla gorilla*) in Cameroon and Gabon (Lacoste et al., 2000). These results indicated these new viruses were closely related to the Karposi's-sarcoma-associated herpesvirus (KSHV) found in humans. This suggests the possibility that the new herpesviruses might be transmitted to humans since chimps and gorillas are frequently used for food; thus, phylogenetic analysis can be used to predict possible outbreaks as well as help establish a monitoring program for new infection. Tree modified and reprinted with permission from Lacoste et al. (2000), *Nature* 407: 151–152, figure 1. Copyright 2000 Nature; http://www.nature. com/.

literature arguing and demonstrating empirically that the first approach is to be preferred, primarily because the characters of interest are often determinative with respect to choice of most parsimonious tree. The second approach tacitly presumes that the characters being examined have little or

no phylogenetically relevant information, which is seldom true.

Nevertheless, the second approach of plotting organismal attributes on a phylogenetic tree will remain popular and exceedingly important. Indeed, the main benefit that nonsystematists gain from a
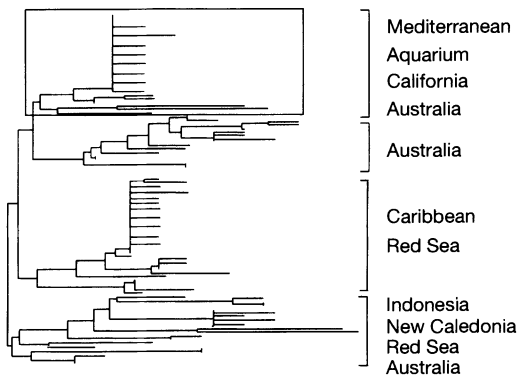
Figure 5. Phylogenetic analysis was used to ascertain the place of origin of a recently discovered invasive alga (*Caulerpa taxifolia*) along the California coast (Jousson et al., 2000). Comparing sequences from the internal transcribed spacer of ribosomal DNA among different algal strains, it was found that the California strain clustered with those from the highly invasive strain that has caused considerable damage in the Mediterranean. This suggested the need for an immediate eradication program. Reprinted with permission from Jousson et al. (2000), *Nature* 408: 157–158, figure 1b. Copyright 2000 Nature; http://www.nature.com/.

fuller understanding of the Tree of Life is that it helps them understand the history of characters and make predictions about taxa for which those characters are yet unknown. Significantly, many of the users of phylogenetic information are themselves contributing data about character systems that will potentially inform our understanding of relationships.

Literally hundreds of papers have used phylogenies to interpret nonsystematic data, and there is no question that this has led to numerous insights into the history of many character systems in behavior, ecology, physiology, and other sciences (e.g., Harvey et al., 1996). More important, perhaps, will be the power of character transformation analysis in applied biology. It has been used, for example, to guide the search for new pharmaceuticals or biochemical products (see Monson, 1996, for review), understand the history of gene regulation (Peterson & Davidson, 2000) and body complexity (Graham et al., 2000; Cameron et al., 2000), among others. Answers to the fourth great question will take on more importance as phylogenetic knowledge and comparative databases expand and become more available.

THE FIFTH GREAT QUESTION: WHERE ARE EARTH'S SPECIES DISTRIBUTED?

This is the most fundamental question of biogeography and any answer will only be as good as the

inventories on which it is based. Thus, knowledge of distributions relies on the presence of georeferenced specimens housed in the world's natural history collections. Ultimately, the characterization of Earth's habitats and ecosystems depends on these data, as does the ability to manage and conserve biodiversity.

The practical importance of having knowledge of species' distributions is acknowledged by the desire of nations, intergovernmental organizations, and nongovernmental conservation organizations to have specimens in natural history collections databased and made freely available on the internet. The development and availability of geographical information systems (GIS) and other software programs for mapping diversity are also increasing the value of digitally captured specimen data (e.g., Funk, 1997). Although such data are increasingly coming online, most of the world's collections are not databased. This has led some governments, most notably Mexico, to accelerate data acquisition on their own. The value of their efforts has been well documented (e.g., Bojorquez-Tapia et al., 1994; Soberón et al., 2000) and recognized the world over, as evidenced by the formation of the Global Biodiversity Information Facility [GBIF].

Distributional information for individual species leads to the search for patterns of diversity at different scales. Most importantly, this builds knowledge about areas of endemism, and discovering areas with high numbers of endemic taxa (sometimes referred to as "hotspots") is widely considered critical for setting conservation priorities (Forey et al., 1994; Nielsen & West, 1994; Nielsen, 1999). But distributional data have a much larger significance for society than simply that associated with conservation. Distributional information tied to specimens underlies drug discovery, ecotourism, trade in natural resources, pest control, control of invasive species, crop improvement using the genetic diversity of wild relatives, and analysis of global change, among many other applications.

THE SIXTH GREAT QUESTION: HOW HAVE SPECIES DISTRIBUTIONS CHANGED OVER TIME?

This great question of systematics, and the second pertaining to biogeography, can be looked at in two ways. First, in the here and now: The vast majority of research and activity in "biogeography" is in ecological biogeography, in which ecologists attempt to understand and explain why organisms are distributed where they are, how those distributions are tied to autecologies, and so forth. Yet, without accurate taxonomic descriptions and georeferenced

data vouchered by specimens, the quality of the ecology itself will suffer. A component of this research also looks to the future. Human activities are transforming the biosphere and there is interest in predicting how this impact will affect the distributions of organisms and, downstream, societal well-being, especially for critical activities such as agriculture.

The second way of thinking about changes in distributions is through the eyes of the historical biogeographer. Following the introduction and application of cladistic methods to distributional problems (Rosen, 1978; Nelson & Platnick, 1981), interest in the biogeographic history of taxa and areas of endemism expanded significantly. As was realized early on, the key to understanding the history of biotas is through an analysis of the history of areas of endemism (e.g., Cracraft, 1986). Areas of endemism are evidence that components of biotas (species) have become isolated and differentiated, and nested areas of endemism are evidence that biotas have expanded through dispersion to become more or less cosmopolitan, only to divide again. Yet, reconstructing this history has not been easy. It has become clear that most of these historical patterns of distribution are so complex that no single method of analysis—at least not one that is currently known—is capable of giving a completely satisfying resolution. Each method of biogeographic analysis, it appears, has various shortcomings in how it handles widespread taxa, redundant distributions, and missing taxa and areas, in addition to the fact that the history of areas itself may not always reflect a hierarchical (branching) pattern.

THE SEVENTH GREAT QUESTION: HOW IS PHYLOGENETIC HISTORY PREDICTIVE?

The third mission of systematics, as identified by SA2000, was to create an efficient, and predictive, systematic information system. This included databasing specimens and making the information widely available, linking to other biodiversity and biological databases, and building informatics capacity to utilize biological—and systematics—knowledge globally. The predictive element was envisioned as coming from using phylogenetic classifications to guide searches for information, and thus reflect the hierarchical relationships of life.

The expectation that closely related taxa share similarities not shared with more distant taxa is the foundation for comparative biology. An information system that is queried using the hierarchical relationships of life can be termed *phyloinformatics* (the

power of "phyloinformatics" was noted in an NSF-sponsored workshop [Tree of Life] and as well as by Edwards et al. (2000). Thus, the ability to search multiple databases using the nodes of a phylogenetic tree may be the single most important contribution of systematics to conservation and sustainable use of biodiversity. Searches that query across databases of various kinds from the perspective of phylogenetic groupings would therefore have immense predictive power because the resulting data can be expected to reflect attributes shared by, or potentially shared by, those groups.

DISCUSSION: THE FUTURE OF SYSTEMATICS AND ITS RELEVANCE

DIVERSITY

A safe prediction is that debates over the species question will continue. However, I think there is far more actual agreement among practicing systematists than could be concluded by recent papers supporting the BSC. This comment is not to disparage these viewpoints. Rather, it is to reaffirm the opinion of others (Nixon & Wheeler, 1990; Wheeler, 1997) that taxa, and taxic limits, as well as the rules governing names, are the primary domain of practicing systematists. And adjudicating taxic limits, moreover, is very much a practical process: as taxa are analyzed with the purpose of understanding patterns of character variation, geographic distributions and endemism, relationships, and biogeographic history, we will more and more need a species concept that looks at basal taxonomic units. That is the trajectory of research by young systematists doing these kinds of studies, and that trend will certainly continue.

But fighting over species limits is not the frontier of the theme of diversity—rather it is discovering and describing the other 95+% of life. Society needs to know what species share the planet with us, and the urgency has never been greater. Inventorying life's diversity is a megascience question because of its enormous intellectual and technical challenges. Even understanding how to inventory a single taxonomic group in a circumscribed region is a difficult problem (e.g., Coddington et al., 1991), let alone thinking about what approaches and designs of inventories might be appropriate for investigations that are global in scope (Wheeler, 1995a; Wheeler & Cracraft, 1996). A global inventory of life will therefore require meticulous long-term planning and capacity building in infrastructure and human resources, and it will be expensive. But it should be a shared expense of governments, intergovernmental institutions, and the private sector.

Indeed, the private sector is getting involved, and with a larger imagination than currently witnessed within most governmental and intergovernmental circles. Thus, a consortium of technology leaders with a track record in futurist thinking have recognized the need for a global inventory of species and are beginning to organize a long-term effort to see the job accomplished [All Species Inventory]. Because of this brilliant and far-sighted effort, inventory should take on new life!

PHYLOGENETIC HISTORY

In the previous section so much space was devoted to phylogenetics and the Tree of Life because it is often not widely realized, even in the systematic community, how crucially important that branch of systematics is becoming. Phylogenetic knowledge is exploding and the rate at which this is happening will not diminish for quite some time. Problems that undermine the quality of phylogenetic research are commonplace and unfortunately will probably continue to persist. Many non-systematically trained biologists, almost all using molecular data, have paid scant attention to taxonomic documentation, nomenclatural issues, or to proper vouchering of sequences by reference to specimen data. Failure to heed these problems will lead to errors and even to potentially dangerous conclusions in fields like human health (Ruedas et al., 2000). Systematists need to work with editors and editorial boards of journals, and with data depositories like GenBank, to improve this situation.

There is a tacit assumption on the part of many researchers building trees from molecular data that their results are inherently superior to those relying on morphological data. Results are presented, with little or no discussion, and often outright dismissal or total ignorance, of prior morphological studies. This attitude developed soon after molecular studies were introduced (the "molecules versus morphology" debate; e.g., Patterson, 1987), and as I said, it continues.

This conflict is likely to increase as high through-put methods of genomics find their way into laboratories doing comparative phylogenetics. The vast majority of current studies utilize small taxon samples and molecular data samples, leading to a significant accumulation of questionable results because of sampling artifacts. But this situation is changing. As methods improve and more resources are allocated to molecular work, more studies are significantly expanding the sizes of matrices in terms of both taxa and characters. Thus, I predict there will be an increasing tendency to think that

molecules alone are yielding the "true" tree of life. But this would be a big mistake. All major groups of living taxa have many long-branched lineages that are monotypic or have relatively few closely related species, and these will in all likelihood continue to confound analysis of deep-branch relationships. To resolve those relationships satisfactorily, it will almost certainly take the addition of morphological characters, especially those from fossil taxa. The relationships of many higher taxa, such as mammals and birds and many others, have been exceedingly difficult to resolve because of the problems just mentioned, and our future hope of understanding the history of life will lie in using all available data.

Applied phylogenetics, as it might be termed, is an easily identifiable wave of the future. One of the most remarkable signs of the vitality of phylogenetics is the expansion of its use into human health, developmental biology, forensics, natural resource management, and other areas. A large number of phylogenetically oriented young systematists are seeking careers in the biotechnology and genomics industries where understanding of phylogenetic methods, and a comparative approach to problem-solving, are needed. This trend will continue for a long time to come.

BIOGEOGRAPHY

Given the current state of knowledge of global biodiversity (5–10% known), and given that most of the species (insects) already described are known from only a handful of localities, it is fair to conclude that we have very imprecise knowledge of the distributions of Earth's species (although single localities could be interpreted as being fairly precise). The task ahead is daunting because virtually all of Earth's habitats and ecosystems have been incompletely inventoried, even for well-known groups such as birds (e.g., Peterson et al., 1998) and mammals (Patterson, 2000). Although an increase in our knowledge about distributions will ultimately be linked to the intensity of inventory efforts, electronically capturing and correlating what we have already collected will surely increase our understanding of distributions and patterns of endemism.

Biodiversity cannot be managed or conserved without distributional information, thus the undeniable importance of databasing the world's natural history collections. Moreover, as global climate change accelerates, and as the anthropogenic conversion of habitats continues, predictions about the

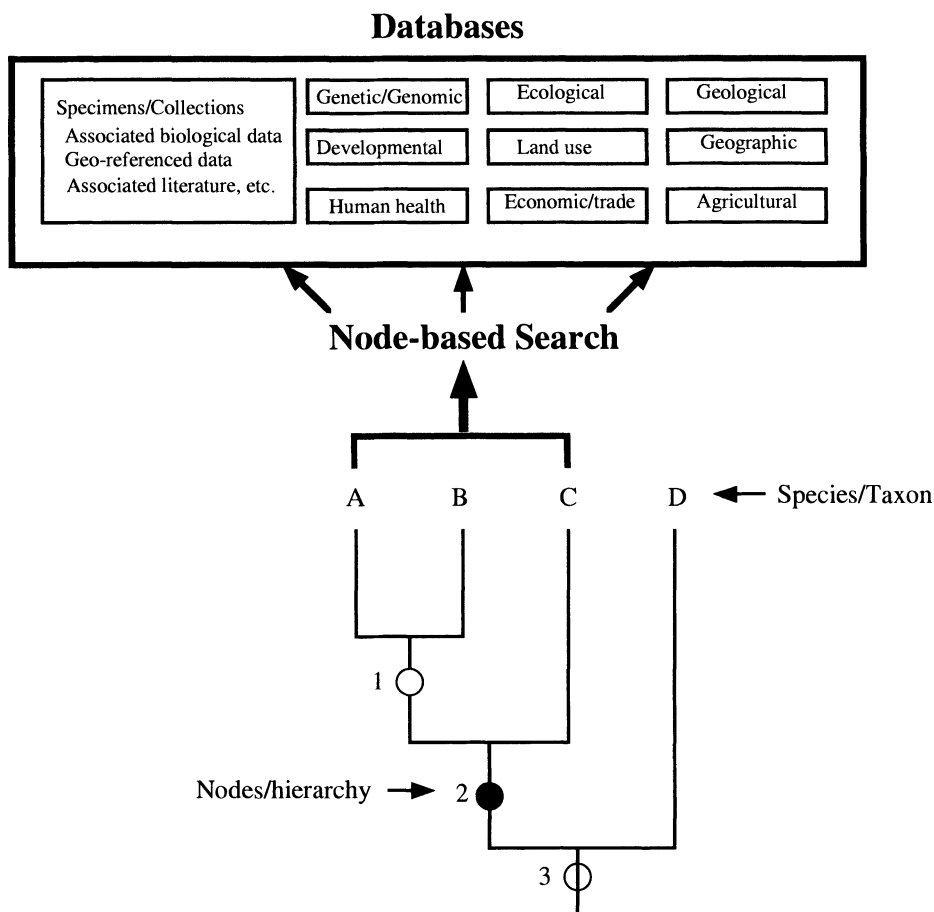# Phyloinformatics: A Conceptual Framework

Databases

Figure 6.   The concept of a phyloinformatic search strategy uses the hierarchy implied by knowledge of phylogenetic relationships to drive queries among multiple databases. Instead of undertaking searches one species at a time, nodes of a tree could be used to power searches for information shared by related species. Here, searches on node (or lineage) 2 would query for information for all species/taxa (A–C) above that node. This figure was first used in a NSF workshop on the [Tree of Life] held at Yale University in July 2000.

consequences of these changes become more and more important. Many of those predictions will flow from the use of historical distributional information linked to specimens.

Biogeography is one of the great frontiers of systematic research. Factors such as widespread, redundant, and missing distributional data hinder understanding of biotic history, but these problems themselves suggest that the field is still wide open to theoretical, methodological, and empirical research. Knowledge of biogeographic history is so central to understanding patterns and processes of biological diversification, including speciation, as well as to how biotas evolve over time, that it will continue to be a core

area of research for many years to come. There have been very few studies of biotic history that integrate patterns of relationships among areas of endemism with information from paleontology, paleoclimatology, and paleogeography. There is an unfortunate disjunct, on the one hand, between paleontologists who study diversification over time and rarely concern themselves with present-day patterns and processes such as speciation, and those neontologists who look at patterns of historical biogeography using distributions of the Recent biota but who rarely incorporate paleontological data on changing diversity. A bridge will have to be built before we have a satisfactory picture of biotic history.

PHYLOINFORMATICS

I predict that phylogenetics will have its greatest societal impact by empowering and enriching the search for information and data associations across many different kinds of biological and systematic databases. Information flow will make peoples' lives better. That is what phyloinformatics can, and will, do.

While queries of biodiversity databases will always make use of species' names as pointers to information (Bisby, 2000), the use of node-based queries can expand and integrate searches and information to another order of magnitude (Fig. 6). Phylogenetic classifications will facilitate a new way of gathering biological information and linking it to other nonbiological databases. The establishment of the Global Biodiversity Information Facility ([GBIF]; see Edwards et al., 2000) on 1 March 2001 holds the key to making biodiversity information readily accessible to all. Phyloinformatic queries will expand the potential of GBIF in ways not previously imagined.

The predictive power of phyloinformatics, based as it is on an understanding of the relationships among Earth's species, argues persuasively for discovering all branches of the Tree of Life as rapidly as possible.

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[All Species Inventory]: http://www.all-species.org/
[DIVERSITAS]: http://www.icsu.org/diversitas/

[GBIF]: http://www.gbif.org/
[GenBank]: http://www.ncbi.nlm.nih.gov/
[GTI] Global Taxonomy Initiative: http://www.biodiv.org/spec-tax/gti/index.html
[TreeBASE]: http://phylogeny.harvard.edu/treebase
[Tree of Life] NSF Workshop Reports: http://research.amnh.org/biodiversity/features/tol.html