

SHORT ESSAYS ON MACROEVOLUTION IN CLASSIFICATION

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Summary - As a message placed on Academia.edu (as of October 30, 2009) — Phylogenetic systematics seeks to eliminate macroevolution from classification, while creationism tries to eliminate macroevolution from the classroom; the difference is that creationism has failed.

Phylogenetics deals only with clades in systematics, namely groups of terminal taxa (as exemplars). Lineages, as concatenated series of nodes in a cladogram, are not named because to do so would violate the phylogenetic principle of classification by holophyly (strict phylogenetic monophyly). This is a principle or axiom, maxim or slogan, designed to simplify classification, not a scientific fact or theory. Phylogeneticists thus reject paraphyly, a group from which other taxa—at the same taxonomic rank or higher—are derived as seen in molecular cladograms. Modern evolutionary systematists celebrate paraphyly, however, as signaling “good” or natural taxa demonstrably the ancestors of other taxa. A paraphyletic taxon plus its derived taxon is an example of evolutionary monophyly, but is not phylogenetic monophyly. When a phylogeneticist encourages one to follow “monophyly,” this does not mean evolutionary monophyly, which is a real scientific theory not an a priori “principle.”

The practice of following the principle of holophyly (strict phylogenetic monophyly) with molecular cladograms is now resulting in taxonomic outrages, such as the sinking or threatened sinking of Aves into Reptilia, the Cactaceae into Portulacaceae, and polar bears into brown bears, because the second of each pair would be paraphyletic if recognized separately.

A cladogram may be totally represented by placing the terminal taxa into a nested set of parentheses. Thus, the clades are given as sister groups and commonly named, but lineages are not represented or named, even though they could be by recognition of paraphyletic taxa. A phylogenetic Tree of Life is much the same as a Nested Parentheses of Life.

This researcher and others of reasonable thought ask other scientists to seriously consider the ramifications. Words are needed for real things in nature. If words are eliminated for the products of macroevolution, how can one discuss them or use them in scientific research? If evolutionists, ecologists, biogeographers, and others use recent phylogenetic classifications, a serious distortion in the results of their research will be inevitable. In my opinion, phylogenetic systematics involving molecularly based cladograms is proving a disaster for western science.

Molecular cladograms commonly tout highly supported branches. But, though such branches are well supported, what about the effect of the possibility of extinct lineages, particularly those involved in paraphyly, on the accuracy of retrodiction of the sequence of macroevolutionary branching?

(1) Clades are taxa that exist at a point in time, while lineages are taxa in stasis or changing through time. (2) Paraphyly (and extended paraphyly) infers a natural taxon through some stretch of time (using a kind of evolutionary uniformitarianism), and the taxon may be in two (or more)

lineages. (3) Natural taxa inferred as one or more nodes on a cladogram make for better evolutionary classification. (4) At any point in time, paraphyletic groups may differ due to extinction of old lineages and “budding” of new daughter lineages from an ancestral group. (5) The proportion of extant paraphyletic taxa in any one group may prove a guide to the proportion of past, different paraphyletic groups. (6) Thus, any extant sister-group molecular lineage has a certain chance of having an extinct lineage of its natural taxon below or beyond that molecular split on the cladogram. Although in groups with little paraphyly of natural groups that chance may be small, every sister group on a molecular cladogram has that same chance of actually being a paraphyletic group with an extinct branch, and therefore the ancestor of its opposite sister group on the molecular tree, or even the ancestor of two or more different lineages. This is an additional and quite significant contribution to lowering of accuracy in molecular systematic analysis. Ignoring it, as is presently common, leads to aleatory classification but apparently that is preferable to acknowledging that natural taxa can occur in two or more lineages and this makes molecular cladograms inaccurate.

The actual limit of resolution depends on the judgment of the scientist on the reasonable patristic distance (e.g. number of nodes) as a measure of phylogenetic constraint among which two or more lineages of a natural taxon might be separated by splits leading to other taxa. It is on this criterion that one should evaluate the actual advances contributed to systematics by molecular parsimony, maximum likelihood, or Bayesian analyses. For instance, a taxon found to be greatly misplaced, perhaps because of extreme reduction in morphology, and in fact belongs to another large group may be reasonably moved to that group. Wholesale renaming of lineages just to preserve strict phylogenetic monophyly is, however, largely an exercise in empty precision.

INTRODUCTION

These messages were sent by me, between February and October, 2009, to the listservers Taxacom and Bryonet, and occasionally elsewhere online as referenced. These were part of various public discussions on phylogenetics, largely concerning macroevolution in classification (or rather the lack thereof), and confidence (or lack thereof) in reconstruction of evolutionary splits in lineages.

The messages are largely restricted to my responses to the public comments of others, and are listed in approximate order of date. The nearly complete give-and-take of messages is archived by Taxacom at:

<http://mailman.nhm.ku.edu/pipermail/taxacom/>

and by Bryonet on the IAB Blog at:

<http://internationalassociationofbryologists.blogspot.com/>

If full context and complete attribution of fragments of comments or implied comments of others are of interest to the reader, there is thus recourse (above) to the original messages.

My collected postings are offered as a source of interesting ideas and, in my opinion, healthy attitudes, and possibly may afford some amusement. Listservers, as well as blogs, e-forums, and mail exploders, are becoming active marketplaces of scientific ideas. Though, as battlegrounds of informed opinion (at their best), listservers will not replace peer-reviewed scientific papers, they offer much in the development and self-policing of science through their immediacy and potential for vigorous give and take. The messages below are my own, but may be intellectually derivative (through an extensive literature) to a significant degree, so be warned. Few of the thoughts presented below have not already been published by others, and I cannot even claim originality in organizing a coherent rejection of phylogenetic insistence on suppression of macroevolution in classification. See the [Modern Evolutionary Systematics Web site](#) for additional discussion on macroevolution in classification, and some relevant bibliographic references and reprints.

These listserver postings are repetitious in some respects, yet it is only by hammering at a wall of quasi-theories and

half-facts mortared by misdirection and redefinition that even the possibility of informed re-decision is effectuated. Brainwashing and subsequent deprogramming are quite similar. It is, however, only on the cusp of abreaction that we can choose freely, after 30 years of formal and informal education in phylogenetics, exactly which methodological vision—phylogenetics or evolutionary systematics—is more firmly rooted in reality, is more utilitarian, and is more true to proven principles of science.

All comments in this presentation, I repeat, are my own, except for occasional short quotations that are marked as such. To smooth things for the reader, nearly all personal names are elided, and obvious misspellings are corrected.

THREE MISCELLANEOUS BACKGROUND STATEMENTS

1. ONE WOULD DO WELL TO REJECT as arbitrary and presumptive the following ideological maxims or precepts of modern phylogenetic systematics, which should not apply to evolutionary taxon trees:

- (1) that extant species must almost always be derived from an ancestral species different from the sister lineages, i.e. there are expected to be no or few surviving ancestors of present-day species;
- (2) that species are not phylogenetically complex;
- (3) that splits in molecular trees necessarily signal a speciation event;
- (4) that genetically isolated populations must speciate, i.e., that the biological species concept is universally and instantly applicable, or even if merely inexorable, must be applied now and not later (when there may be actual evidence of speciation);
- (5) and, that reconstruction of the past evolutionary history is through mapping morphological and molecular trait changes on a dichotomous tree.

ONE'S SCIENCE WOULD PROFIT BY ACCEPTING, however:

- (1) that both taxa and traits, not solely traits, are the topics of interest in descent with modification, and lineages should to the extent possible be expressed in terms of genealogies of taxa;
- (2) that expressed traits that are either neutral or involved in selection are the focus of evolution, not DNA markers of lineage continuity, which only track evolution;
- (3) that it is possible that ancestral taxa have diagnoses or morphological descriptions and can be placed on a taxon tree;
- (4) that two phylogenetically disjunct (patristically distant) exemplars on a reliable molecular tree imply that they are surviving populations of a shared ancestor with the consensus traits of whatever taxon the exemplars represent, and any dependant lineages of different taxa are descendants;
- (5) that although convergence is a possible explanation, in those cases when other explanations are possible or even more likely, enforcing phylogenetic monophyly in systematics by treating heterophyletic taxa (species, genera, families, etc., somewhat distant on a molecular tree) as fully cryptic separate taxa reduces evolutionary information in classification;
- (6) and, that molecular trees to the extent they reliably detail genetic continuity help arrange an evolutionary tree of taxa.

2. If evolution is to be part of a classification, then judgment is necessary and to the degree that judgment evaluates the evolutionary significance of data, any classification is subjective. Deciding on the weight of traits in parsimony study or the value of Dirichlet priors in Bayesian analysis is subjective. Merely agreeing to equal weights is agreeing on identical bias, and this is not a way to say the study is more scientific because it is now replicable.

Classification by holophyly increases distance between systematics and users (evolution, law, biodiversity, ecology, biogeography) who expect both sister-group relationships and ancestor-descendant relationships reflected in classification.

Following cladistic thinking, ancestors are ignored unless they are invoked to establish phylogenetic monophyly. Take two taxa of the same rank as sister groups. The shared ancestor is unknown, and in my opinion this is the only reason the cladistic split is acceptable. If the shared ancestor were known to be the same as one of the sister group

taxa, then that taxon would be paraphyletic, and the other sister taxon would necessarily be synonymized with the first to preserve phylogeny. Monophyly ultimately is thus supported by ignorance. One could, I suppose, make a good guess at the taxonomic identity of the unknown shared ancestor by judging how similar it is between one of the sister groups and the next nearest neighbor lineage farther down the tree. If it seems intermediate between one of the sister groups and the next nearest neighbor, then synonymy can begin and the classification can collapse further. To invent an unknown taxon of the same rank as the shared ancestor begs the question and is not parsimonious.

3. *Instauration of Evolutionary Taxonomy:*

The difference between morphological and molecular analyses is based on taxa as associations of expressed traits being punctuational in evolution (first a stage of gradualistic change then stasis) but molecular traits are largely gradualistic (except for some heterogeneity in rates). This difference allows analysis of additional information on evolution.

Alpha taxonomy infers that which evolves as a present instance in time.

Molecular analysis infers continuity of lineages, as trajectories of evolving taxa in time.

Multiple instances of the same taxon (species, genus, family) on a molecular tree imply a shared ancestor of that taxon, whether the taxa are phylogenetically monophyletic or not.

Taxa may be mapped on a molecular tree just as traits are mapped.

Morphological cladistic analysis is a nonultrametric clustering technique that associates similar taxa along the logic of like begets like. It is based on a simple model of evolution (akin to physics' "least action") that is phenetic if all traits are weighted alike, and phyletic if weighted according to perceived importance or estimated evolutionary conservativeness.

A reconstruction of evolutionary taxonomy combining characterization of taxa as they are constituted in the present with their evolutionary trajectories in time is a better implementation of Darwin's natural system, combining both genealogy and differences.

John Dewey ("Reconstruction in Philosophy" Introduction) felt that the greatest discovery of modern thought is the notion of progress, that is, versus absolute values (Truth, Reason, first principles). Holophyleticists are atavistic when leaning towards absolute solutions (patterns of holophyly) versus judgment and reason based on all facts and relevant weighty theories.

THE ONLINE MESSAGES

Taxacom Feb. 3, 2009:

Well, I'm always leery of "facts" presented as direct apprehensions of Ultimate Reality by someone else. "Well-documented observations" as a definition of fact is about as far as I'll go in support of scientific realism. Probabilistic suspension of disbelief, governed by feedback from Out There, is a pretty good balance, I think, between the potential horrors of extreme realism ("do as I say because I see reality better") and antirealism ("you probably don't exist, either").

Your concern is well-grounded. Homology has been treated solely as a probability issue because "saturation" (a mutation is mutated and again mutated back) is a concern for phylogeneticists. Only when there are only a few mutations in a sequence is it assumed that there are no mutations that overwrite

another mutation because it is improbable that this would happen.

With morphological characters, I object to phylogeneticists saying that two traits must have been separately evolved if they are in two molecular lineages. The species of ancestor of the two molecular lineages may be the same as the extant exemplars. The species simply did not change even though there are two separate populations that have been isolated long enough to have different molecular mutations and to have separately generated new species of their own. It is not only possible that one taxon be in two different molecular lineages, it is demonstrated many times in the case of "cryptic" species, or genera or families that have been split by phylogeneticists ONLY because they comprise two different molecular lineages.

Because two or more morphological traits may be linked in that two or more are needed for selection into a particular new habitat, parsimony analysis of morphology data sets is probably only good for genus relationships or family. Sister-group relationships of species are probably only poorly analyzed by parsimony of morphological traits.

For more discussion of the last paragraph, see my papers

<http://tinyurl.com/27fq62>

and

<http://tinyurl.com/6frd9l>

Taxacom Feb. 20, 2009:

One respondent indicates that he himself has good judgment and cares about what classification represents, and doubtless has much sympathy for evolutionary taxonomy (as opposed to phylogenetic monophyleticism), and attributes what I agree is a moderate, excellent viewpoint to all his relatives, friends, and colleagues. Well, what about that crowd of devils that increasingly happily names fully (phenotypically) cryptic species, genera, and families - splitting perfectly good taxa into evolutionary abstractions characterized by random traits, and which melds perfectly good evolutionary species into portmanteau lumpen-taxa of little use to biodiversity analysis, or anything else?

The other respondent places trust in the principles of nomenclature to, I think, at least allow taxonomists to resurrect an evolutionary taxonomy. In the first place, changing back from a phylogenetic classification requires distinguishing GOOD changes from the ones solely based on preserving holophyly. This is not a trivial endeavor and I suspect much labor in future years will be wasted on this. Secondly, nomenclature is hidden, merely implied, in phylogenetic classification and it takes work to use it effectively. A published classification that, for instance, does not recognize polar bears (just recognizes brown bears) or the cactus family (just recognizes the portulacca family), cannot be fixed by invoking nomenclature.

Nature Network blog Feb. 17, 2009:

Actually, paraphyly of *Drosophila* is not a problem but a wonderful opportunity to examine descent with modification of taxa. Clearly the paraphyletic group is the ancestor of the autophyletic taxa.

It is only an importunate homage on the part of phylogeneticists to their sister-group analytic method that requires enforcement of strict phylogenetic monophyly (holophyly) in modern classifications, splitting, excising, or reducing in rank taxa that should have unique evolutionary traits flagged at an appropriate level in classification. Because ancestor-descendant relationships are not recognized in phylogenetic classification, a major source of evolutionary information is gradually being deleted from the classifications that inform biodiversity and evolutionary study. This isolates systematics, which presently cannot or will not provide a general-purpose classification.

Nature Network blog February 17, 2009:

The analysis of sister-group relationships involving parsimony and other tools has given systematics much evolutionary information for classification purposes. Unfortunately, phylogeneticists commonly insist on classifications that reflect strict phylogenetic monophyly, in my opinion, solely as homage to the method. Ancestor-descendant relationships involving unique evolutionary directions (major autapomorphies) are not flagged at taxonomic levels the same as those of sister groups exhibiting the same degree of evolutionary change. All of us have seen perfectly good evolutionary taxa that have been split apart or synonymized as sacrifices to the sister-group relationship analytic method. Yet enforcing strict phylogenetic monophyly (holophyly) divorces systematics from other fields informed by classification (biodiversity, evolution, law) by eliminating information on descent with modification of taxa (as opposed to traits). Phylogenetics is in the process of destroying more information on evolution than creationism or intelligent design has or will ever do.

Forum E-biosphere Feb. 2009:

Evolution can be described and exemplified through ancestor-descendant relationships, e.g. fossils evidence, and also through sister-group relationships, e.g. cladistic analysis. Although sister-group analysis, particularly with molecular data, is valuable in systematics, phylogeneticists are presently constructing classifications that are solely based on sister-group relationships. Taxa must be holophyletic (phylogenetic monophyly), and any taxon previously recognized at a rank that makes another taxon paraphyletic (not including all descendants of one ancestor) must be lumped into that paraphyletic taxon

to make it holophyletic. Thus, the famous example that the class Aves (birds) should not be recognized at the same level as Reptilia. Also, the polar bear should not be recognized because it is molecularly midway between two brown bear lineages. Cactaceae should not be recognized because this is a lineage buried in the Portulacaceae. In a family I study in mosses, Pottiaceae, a new, influential phylogenetic classification lumps three families, Ephemeraceae, Splachnobryaceae and Cinclidotaceae, into that family without discussion, apparently based on previous studies that show them to be embedded in the Pottiaceae, yet all of these families have distinctive habitats and/or morphological novelties that justify recognition as evolutionarily significant groups (if ancestor-descendant relationships were recognized) at the level of Pottiaceae. If both ancestor-descendant relationships and sister-group relationships are NOT included in classifications, both evolutionary and biodiversity information is suppressed.

The problem then is that new classifications developed by phylogeneticists include both good reasons for lumping and splitting, and bad reasons for suppression of evolutionary and biodiversity information (including splitting of evolutionarily coherent taxa because they may be composed of two or more molecular lineages). Because of this, future correction of present phylogenetic classifications to retrieve evolutionary and biodiversity information will be difficult and tedious because only an expert can distinguish what changes were made solely to enforce phylogenetic monophyly, and what to reflect new discoveries beyond this artificial classification method.

For more reading on this subject, see: Dayrat, B. 2005. Ancestor-descendant relationships and the reconstruction of the Tree of Life. *Paleobiology* 31: 347--353. Also my Zander, R. H. 2008. Evolutionary inferences from non-monophyly on molecular trees. *Taxon* 57: 1182--1188, and particularly the chapter on evolutionary taxonomy of E. Mayr in Elliott Sober's *Conceptual Issues in Evolutionary Biology*.

Thus, how will phylogenetic classifications that suppress evolutionary novelties that are not sister groups be dealt with in the future, given that taxonomy is the foundation of biodiversity analysis?

Nature Forum Feb. 25: 2009:

Alpha taxonomy, I think, is getting a raw deal. "Omnispection" is surely not "subjective" but

involves considerable measuring, sorting and theory. Higher taxa generated by alpha taxonomists certainly combine metrics of similarity tempered by concern for convergence, often using cluster analysis and parsimony with morphological traits. Phylogenetics starts with exemplars representing alpha taxonomic concepts, then re-sorts them into groups using just a few, albeit important traits, while alpha taxonomists examine a host of specimens and thus evaluate those multifarious traits (as organized by the important traits), and have a grasp of the taxon beyond the phylogenetic data set. (This assumes phylogeneticists are not also alpha taxonomists or are successfully schizoid about their different roles.) Phylogenetics is supposed to be more objective and replicable, but this is only because phylogeneticists have agreed to the same biases and assumptions: weight all traits at one, use the same Dirichlet priors, gamma distributions, etc. This is not to say that phylogeneticists are not aware of the problems, but alpha taxonomy is our fundamental systematic interface with nature and is in dire need of support.

Note that there are two rules of thumb in evolutionary taxonomy: (1) taxa distant on a cladogram or UPGMA are evolutionarily distant, and (2) taxa distant on a taxon tree (distant in time) are evolutionarily distant. Exactly how does modern analysis of morphology add new information beyond being simply more accurate with the same poor information? Molecular analysis is the only decent new source of information, in my opinion, and even that should be restricted to demonstrating genetic continuity and lineage isolation in gene trees (given reliable analysis), because surely taxa that are evolutionarily static can exist in two different molecular lineages.

Taxacom on why paraphyletic taxa are the ancestors of autophyletic taxa, Mar. 2, 2009:

My logic is: if you have (((((XA)B)C)D)E).... with XA at the tip of a branch, and X is a unique taxon that if named at the same rank as ABCDE then X makes (ABCDE) paraphyletic, and SO if we invoke probability then the chance that X was the ancestor of EACH of the entirely different taxa in the larger taxon (ABCDE) is a lot smaller than if one of the taxa in (ABCDE) was the ancestor of X (or if some unknown extinct taxon in (ABCDE) was the ancestor of X).

I use the word clearly to strongly go up against the idea of holophyly as generative of classifications,

which ignores ancestor-descendant relationships entirely.

The idea is yes, your suggestion that one of the taxa making up the paraphyletic taxon might be the ancestor is correct, and possible, but unless there is evidence that this is so, the ancestor of X is “clearly” taxon (ABCDE). Phylogeneticists, when pressed, will agree.

Taxacom Mar. 2009:

I meant that when there are a number of alternatives, scientists generally feel they can act on one if the alternatives are improbable, and if the alternatives to the best are not so improbable, then they entertain the best, but do not necessarily act on it.

Also, regarding “stories,” humankind is a storyteller. This is our strength. Relying on methods guaranteed by those who sell them to produce great results is an old, sad story. Stories are hypotheses and scientific stories are scenarios usually based on interesting preliminary data. Then we test the stories. Scientific laws are stories generally accepted as histories teaching lessons applicable to today's problems.

“Stories” is a canard invented by postmodernists who shrug off all science as snippets of many stories stitched together into a new story.

Taxacom Mar. 16, 2009:

I think there is a rational (sort of) justification for using holophyly in classification. It goes this way:

Science is to religion as phylogenetic analysis is to ancestor-descendant relationships.

Science cannot deal with religion because religion is not amenable to the methods of science. Religion is commonly accused of being “intuitive” or a bunch of attractive “stories.”

Phylogenetics cannot deal with ancestor-descendant relationships because phylogenetic methods are solely analytic of sister-group relationships. Ancestor-descendant relationships are commonly found as products of alpha taxonomy, and are commonly accused of being “intuitive” or a bunch of attractive “stories.”

Intuition in science is of great pragmatic value when combined with data and a research program, while

humankind is correctly glorified for its story-telling abilities, e.g. informed hypotheses about nature that may be pursued.

A goodly portion of evolutionary knowledge concerns ancestor-descendant relationships, and eliminating their reflection in classification cripples both systematics and any field dependant on classification, such as evolution, ecology, biodiversity, biogeography, paleontology, and so on.

Forcing classification to reflect only the sister-group conclusions of phylogenetic analysis is an ideology, and like all ideologies (see Wikipedia) is a comprehensive vision, being logically consistent within a narrow and limited range of data about nature, reflecting an excessive need for apparent certitude and infallibility, is a relativistic intellectual strategy for categorizing the world, and is “normative” of group interactions (everybody agrees on a new paradigm). It certainly simplifies classification, but at what expense?

Ideological extinction is the fate of autophyletic (descendant groups recognized at same taxonomic level as ancestor) taxa, and of paraphyletic taxa split into non-recognition. Although taxa of high visibility (Aves, polar bears) seem immune to ideological extinction, many groups simply disappear from classification because they were found to be embedded in a molecular tree within an ancestral group of the same or lower rank. In my own field, bryology, three families (Ephemeraeae, Cinclidotaceae, and Splachnobryaceae) have been sunk in a recent influential phylogenetic classification into one larger one (Pottiaceae) without discussion because they were autophyletic in previously published molecular trees; their names do not appear anywhere in the classification, which offers no synonymy.

If absent, then the descriptions of their evolutionary novelty will also be absent in future taxonomic studies (family name synonyms of families are not usually given special descriptions) and the families will not be studied and discussed in the future in other fields relying on the expertise of such taxonomic studies. In my opinion, this excision of a whole class of evolutionary knowledge (ancestor-descendant relationships) from classification is monstrous.

It may be true that

Science : religion :: phylogenetics : ancestor-descendant relationships

But then, this only reflects that phylogenetics is valuable for ascertaining sister-group relationships, but other methods may be used for determining ancestor-descendant relationships. Such methods do exist and their results should be part of classification.

Taxacom Mar. 17, 2009:

1. It is uncommon for sister-group relationships of species to be well supported in detail (general clustering of species is well supported) as an advance or new knowledge over what is obvious from omniscience, although gene trees may be quite detailed. Molecular trees demonstrate only genetic continuity, not necessarily speciation events unless one invokes uniform gradualist speciation and the biological species concept, in which case anagenetic change in both sister groups then generate different species. Second, molecular paraphyly of species is not extremely rare since many cladograms in the literature with lots of exemplars of the same species demonstrate ancestor-descendant relationships. This goes for higher taxa as well, of course, but knowledge is presently somewhat limited by the general lack of multiple exemplars of the same taxon in any one study.

2. One of the points I commonly make on Taxacom is that given the data we have, including that of DNA, we cannot resolve many sister-group relationships reliably and it is even more difficult to resolve ancestor-descendant relationships though many are obvious as paraphyletic-autophyletic pairs. We must be satisfied with partial cladograms and partial taxon trees. Resolution itself is not support, as is well known, since totally random data sets commonly produce well resolved parsimony trees. I think that eliminating ancestor-descendant relationships from classification when they are known or are well supported as paraphyly-autophyly relationships is no solution.

3. Of course fossils may represent extinct lines. One can say that dinosaurs are the ancestors of birds but cannot say that *Tyrannosaurus* is the ancestor of anything alive today. I think that it is okay to say that a paraphyletic species (e.g. brown bear) is the ancestor of its autophyletic descendant (polar bear) given what we know even though any given brown bear fossil may not be the ancestor of anything alive today.

4. “. . . an artifact of the way a taxonomist chooses to draw up the taxa” seems a criticism dependant on

cladists' use of holophyly to delimit taxa under the assumption that it is more scientific. Nonsense. Holophyly is dependant on the cladist's choice of character weighting, sampling, and other assumptions and biases, and particularly on attitude about phylogenetic monophyly versus evolutionary monophyly. It's circular. I'm afraid I don't understand the irreducible paraphyly bit, and how this might support ignoring ancestor-descendant relationships in classification. Please explain.

5. Cladists write the histories nowadays. There are many techniques for pinpointing ancestors, mostly involving that old field biosystematics, now fallen into shadow. Chromosome numbers, crossing experiments, and biogeography come immediately to mind: of two closely related species, the tetraploid may be hypothesized as derived from the diploid, particularly if it is local and the diploid is widespread, and particularly if one can generate an identical tetraploid from the diploid experimentally with colchicine or whatnot. This is pinpointing, since science, like Obama, does not let perfection drive out the good. In addition, in my opinion, any paraphyly or even polyphyly of traditional groups on a molecular tree is evidence of a shared ancestor (at some taxonomic level) deep in the tree. They are not “devilishly hard to pinpoint”, but are obvious as the “massive homoplasy” that cladists vigorously suppress by insisting on strict holophyly and backing it up by making new combinations and new names that change nomenclature such that only sister-group relationships are recognized. This is ideological extinction of a major class of evolutionary information in classification. The only way to corroborate splitting molecularly paraphyletic or polyphyletic lineages (which may be evolutionarily monophyletic because they share a deep ancestor) is to demonstrate that the products of the split (separate lineages) are significantly better circumscribed by new circumscriptions by expressed traits than they were previously. This is because splitting in any way of a large taxon into smaller taxa will commonly result in some kind of description for each of the smaller taxa, which is a problem in statistics called multiple comparisons). That new description must be better than any previous description for a larger (or smaller) grouping at that rank to be corroborative.

6. I stipulate and asseverate that phylogenetic analysis resulting in clarified sister-group relationships is a good thing, an advance, a revelation of exciting details (as hypotheses) about evolution (using a non-ultrametric clustering method based on a simple model of evolution called parsimony), and a good use of time. I also think that wrenching all

ancestor-descendant information from classifications as a blood sacrifice in honor of this advance, and relegating the study of ancestor-descendant relationships to the same intellectual level as voodoo and metaphysics (pace voodoo doctors and metaphysicians among us) is a kind of latter-day Lysenkoism. Mine is not an extreme position, since (as I repeat from elsewhere) classifications and taxonomic treatments following strict phylogenetic monophyly have damaged evolution more strongly than creationism or intelligent design will ever do.

To Taxacom 09316:

I think the object of modern classification is to maximize useful, predictive information, with the assumption that including evolutionary relationships provides such useful, predictive information.

We could have a sister-group cladogram, and an ancestor-descendant Besseyan cactus, and a classification, which could be alphabetical or anything. The trick is to introduce evolution into the classification without damaging its general usefulness across science. Many of us use alphabetic systems to store specimens, but this specialist usage is not helpful to other fields. Maximizing useful, predictive information is the specialty of systematists, and limiting it to sister-group relationships is not a service to science in general but, like alphabetic classifications, is useful only to phylogeneticists, who study sister-group relationships.

What is needed are classifications that are generally useful and maximize all evolutionary information. It is not up to phylogeneticists to provide this if they just won't do so. Evolutionary taxonomists need to write these classifications. Yes, we can.

Taxacom Mar. 17, 2009:

Rank counts. There are only two ways to signal information in classifications, and those are rank and groupings. Enforcing monophyly limits rank as an informational metric.

The nature of bifurcating trees means that an autophyletic lineage (e.g. polar bears) is more closely related to one part of the paraphyletic taxon (e.g. one molecular lineage of brown bear) than to another (the other molecular lineage). Thus, if the molecular lineages of brown bear were named, the polar bear would be a form of a subspecies. **Headline: A Form of Brown Bear Extinct Across Arctic!** This seems no

big deal. If this were an ecologically important species of another taxon it would signal nothing to the public, to evolutionists, to biogeographers, to diversity specialists unless they were specialists. What if chimps were paraphyletic? Would it be important if the extinct form were *forma sapiens* or not? Rank matters.

The autophyletic cactus family is more closely related to one portion of the paraphyletic portulaca family than to another. If the two parts of the portulaca family were named as subfamilies, then the cacti would be a tribe, but if the two parts of the portulaca family had no real distinction then the cacti would have no rank at all.

Your solution, ----, is I think a third alternative to naming autophyletic groups at an appropriate rank or strict monophyly, but it is contrary to both phylogenetic and evolutionary taxonomy practice from what I understand of it. Can you give an example?

Taxacom April 3, 2009:

Lots of conceptual leaps, -----, where you support phylogenetic for all the good it has done, yet doggedly duck the elephant in the room.

“it just so happens that in higher taxa what we observe is a bifurcating tree of life, and this is best described with a strictly cladistic system.” Really? The software gives a bifurcating tree of life. Parsimony comes out of cluster analysis which represents clustering most atomistically as “these two are more close to each other than either is to a third” which can be in a great leap of logic extended to evolution of lineages. But then, what about a pectinate tree with the ancestor surviving to the present? That seems to be a bifurcating tree, yet the pleisiomorphic ancestor of all but one exemplar is much the same (except for gradual accumulation of minor molecular changes used for tracking the gradual peripheral speciation of daughter species). This isn't exactly what one envisions by a bifurcating tree of life. It is more like a bush, isn't it, yet if we estimate the number of surviving ancestors in any published tree by the number of identical taxa (particularly species) separated by other taxa on a molecular tree (heterophyletic), then we should expect oh maybe 10 percent of the exemplars in most cladograms that actually include duplicate exemplars of widespread taxa to represent surviving ancestors and therefore make “bifurcation” not the correct interpretation but polytomy of taxa based on

expressed traits. Since all but one exemplar may be an ancestor of another exemplar, one does not even have to postulate a nodal ancestor different from all the exemplars for these apparently branching lineages, which is certainly more parsimonious than “parsimony.”

I think that your focusing on successes of sister-group analysis does not imply that only sister-group analysis is now the correct means of generating classifications. Monophyly means phylogenetic monophyly, or holophyly, not evolutionary monophyly. Success in testing means getting the same answers with different data and different methods. If you get the same sister-groups consistently, well that's great. Sister-group analysis is no problem. (Well, repeatability is a problem when the only assurance of repeatability is everyone agreeing to weight all traits alike.)

It is the creation of a special-purpose classification that restricts the evolutionary content of classification to only sister-groups that I object to. Phylogenetics does generate, are professed to approach, an “accurate model of nature” in respect to phylogeny, but much evidence of ancestor-descendant evolution is ignored and the whole truth is not represented.

The evidence for higher-level taxa are the autophyletic taxa that have been given high rank in the past to flag comparatively (at a particular taxonomic level) major innovations in evolution that are not phylogenetically informative.

Phylogeneticists may not be interested in such traits, but evolutionists, ecologists, biodiversity specialists, teachers, governmental agencies, and so on really are, since they expect a classification to reflect what we know about evolution not just what we know about phylogenetics.

Yeah, I understand Scrophulariaceae was a mish-mash, and splitting and moving taxa about was called for. Certainly molecular analysis reveals where one taxon should be re-associated with other taxa. It is the LOSS of evolutionary information about ancestor-descendant relationships in classification due to enforcement of holophyly as the only way to form a taxon that is now crippling classification.

Regarding “it is about building the model that best describes what goes on/happened in nature.” I agree.

Taxacom April 3, 2009:

I think there is no such thing at a particular level as well, let's all agree to disagree. If phylogeneticists produce a phylogenetic classification and present it as the best representation using the Linnaean system of sister-group relationships, and eliminating descendant-ancestor relationships, that's fine. It's a special purpose classification like alphabetical classification for ease in accessing specimens, artificial hierarchies in keys to speed identification, organizations in popular identification manuals for amateur naturalists, and so on. But this is not the case with phylogenetic classifications because there is now no alternative. Apparently studying evolution is now taught to students as restricted to sister-group analysis, but tell it to evolutionists. “Allowing some paraphyletic families” is nonsense. They exist as products of evolution.

I stipulate that this would not be a problem if evolutionary taxonomists would recognize what is happening and generate alternative classifications. I'm working up an alternative paraphyly-safe classification for my own group, with vigorous justifications for the autophyletic taxa, but it's a drop in the bucket.

Taxacom April 3, 2009:

Some have questioned whether there is a metric for measuring degree of difference, such as is often implied by the accursed paraphyleticists. Since Linnaean classifications don't have much in the way of a built-in metric (taxonomic distance at best as measured by distance on a page or difference in and between ranks) one must refer to a cladogram or to a diagnosis or discussion for either sister-group or ancestor-descendant relationships. Polar bear white-furred, eats seals, A metric may be an absolutely new feature.

Therefore, the question, I think, is a non-problem, since the details of any difference between taxa need to be looked for elsewhere. The metric in classification is in the wording and indenting that signals sister-group and ancestor-dependent relationships. Just because the same metric possible as built into Linnaean classification must be used for both phylogenetic and phyletic importance is a limitation of the Linnaean system; fixing it should not involve elimination of a whole area of evolutionary knowledge.

Taxacom April 3, 2009:

ALL classifications are NOT special-purpose ones. Maximizing evolutionary information should produce a maximized predictive classification. This is from phenetics (total similarity) and phylogenetic (sister-group) and phyletic (ancestor-descendant) information, and should be of great use for general purposes by other scientists. This is as non-special purpose as one can imagine.

Taxacom April 7, 2009:

Well, actually, now that this has come up, cladistics is just a way of approaching the “paraphyletic” Darwinian Tree of Life (p. 95 of Darwin’s paperback) which has one taxon giving rise to another.

Saying cladistically that “these two taxa are more related to each other than either is to a third” is just a way of clustering the results of descent with modification of taxa (as opposed to traits, but that is a different problem). Descent with modification is evolution, not the bifurcating results of a cluster analysis, although the results of cluster analysis can help us understand evolution. If we had lots of information on descent with modification, which would be better, a sister-group classification or some kind of grade-based classification? Must we choose?

The Linnaean classification is what we have and is closest to a general-purpose classification if we mix all our interpretations of descent with modification, both sister-group and ancestor-descendant relationships into it, explaining our reasons, methods and data elsewhere.

Taxacom April 8, 2009:

Manifesto: The difference between molecular and morphological cladistic analyses has been misinterpreted as convergence, though convergence is a rare possibility and must be examined.

Phylogenetic paraphyly and polyphyly (heterophyly) may well be due to a deep shared ancestor diagnosable at the lowest rank inclusive of the exemplars.

Elimination of information on heterophyly by reclassification by holophyly eliminates information on ancestor-descendant relationships.

Darwinian evolution is ancestor-descendant relationships, or paraphyly. Phylogenetic polyphyly is paraphyly with multiple instances of autophyly

unless demonstrated otherwise. A deep shared ancestor is a better explanation of heterophyly than dismissal as convergence.

Cladistics does not diagnose ancestors (nodes) although traits might be mapped. Mapping of traits is dubious if some lineages consist of a surviving ancestor and its multiple daughter (peripheral isolate) species, in which case the surviving ancestor provides the plesiomorphic traits. Cladistics cannot diagnose ancestors (either as unknown or as one or the other apparently descendant sister-group being the surviving ancestor), and thus cannot demonstrate evolution as descent with modification.

ANY demonstrable paraphyly is preferable to sister-group relationships as evidence of evolution, and therefore paraphyly is important in classification on an evolutionary basis.

Taxacom April 12, 2009:

The reason some of us insist on paraphyletic taxa is because evolution, if defined as descent with modification, is described only by paraphyletic-autophyletic series, where the paraphyletic taxon is the descender (ancestor), and the autophyletic taxon is the descender. [Editor note: correction in next message.]

Actually, there is neither “phylo” nor “genetic” in “phylogenetic.” In a phylogenetic cladogram with paraphyly eliminated, we know what the descender is, it is the exemplar, but we don’t know what the descender is, it is only a node, without diagnosis or any real biological attribute. The central stem of a phylogenetic lineage is a series of nothings. Mapping of expressed traits on a morphological tree fails because (1) if traits are selectively linked then a synapomorphy of three traits may not be more parsimonious than one of two or one traits, and (2) if one of the exemplars represents a surviving taxon, then the plesiomorphic traits of all “sister groups” in the lineage are those of that exemplar, not the outgroup. Thus, a genuinely most parsimonious cladogram would have only a minimal number of nodes (as hypothetical ancestors different from any of the exemplars) as is necessary to explain branching patterns if punctuated equilibrium (maximal surviving ancestors) is most abundant. Molecular cladograms infer only continuity of lineages and genetic isolation, not speciation events, and therefore also cannot demonstrate descent with modification.

Cladistics is important because it popularizes phenetic cluster analysis. Parsimony with morphological data is a nonultrametric clustering method that uses a simplistic method of evolution that fails as described above, but is acceptable in general because it produces something like the results of molecular analysis. It is popular in part because one does not have to choose between Gower's or Mahalanobis' methods of cluster analysis, and there is a generally warm feeling that if everyone uses the same method (parsimony with no weighting of traits) the science is then more replicable and therefore more scientific. Mapping traits on molecular trees also fails if punctuated equilibrium (involving surviving ancestors and peripheral speciation) is common, which, judging from the numbers of "cryptic" taxa on molecular trees, it doubtless is. Such cryptic taxa are in most cases probably surviving isolated evolutionarily (in expressed traits) static populations of taxa deeply buried in a molecular cladogram, a taxon now with multiple autophyletic daughter taxa.

ONLY demonstration of descent with modification of taxa will demonstrate evolution. This may be done in several ways, but demonstration of paraphyly should be the one way systematists should try to preserve by not enforcing holophyly in circumscribing taxa.

Taxacom April 13, 2009:

Well, I got descender and descendeo mixed up in my post. The descender addresses an action to the descendeo, as in payer and payee. Ignore that and probably also the comment about phylog + genetics, which was doubtless vainglory.

The ancestor of Aves is the closest paraphyletic taxon. A natural taxon, that is, not a holophyletic taxon. If there are no paraphyletic taxa presently evident, then perhaps we have not studied enough (long isolated) exemplars of the same taxon, on a large scale.

There are other ways of identifying ancestors, e.g. in the most clear case, a taxon with a wide and long term distribution in geologically stable habitats, versus a similar taxon in a narrow, recent habitat, with double the chromosome number of the other. The first is hypothetically the ancestor (descender) of the second (descendeo).

Taxacom April 13, 2009:

You cannot refute the points I am making by making true statements about other things.

Classification should be based on evolution, most of us agree. My central point is that alpha taxonomy has the best grip on evolution-generated groupings, and that molecular analysis can demonstrate direct evolutionary relationships (paraphyly-autophyly series) between such groups as ancestor-descendant relationships (that is, involving descent with modification of taxa).

Classification by holophyly eliminates this information. The "natural" taxa are already classified by alpha taxonomists, and are chock full of evolutionary information that molecular analysis can reveal. Molecular analysis can let one know when one taxon is in the wrong cluster and point out the right cluster but otherwise the classification is already there in the original evaluation by an alpha taxonomist.

Discovery of paraphyly, "massive homoplasy," and "cryptic" taxa has been misinterpreted. These features are evolutionary information and should not be hidden by burying them (in synonymy or splitting into new names) in phylogenetic classifications.

Taxacom April 14, 2009:

Okay, using the paraphyletic method (where paraphyly implies ancestry of the autophyletic taxon (or taxa), the basalmost paraphyletic taxon in Aves is the bird ancestral to all the rest, at the resolution of the lowest grade inclusive of all the exemplars in the paraphyletic taxon. The ancestor of Aves would be the closest paraphyletic taxon to Aves in a molecular cladogram, that is, closest being the best resolution given the data.

Thus, if mammals had two branches below Aves, then mammals would be the ancestor of Aves:

((Aves) mammal) mammal)...

If you could name the mammals more accurately, you would have higher resolution. E.g.:

((Aves) hairy shrew) hairy shrew)

then hairy shrew would be the ancestor of Aves (an example, just an example). The trouble is that if there are few molecular analyses of multiple exemplars of, say, hairy shrews, then there is no data on paraphyly at that taxonomic level.

The metric is absolute patristic distance, an instance of paraphyly supported by molecular data at 95 percent credibility or more.

Criticisms of parsimony? It's a good clustering method, and gives general groupings that are commonly supported consistently by molecular analysis. It is not terribly good in resolving power because (1) equal weighting is nonsense, (2) traits if selectively linked confound parsimony (3) synapomorphies if linked may be equivalent to only one, evolutionarily, (3) punctuated equilibrium may allow a taxon terminal on a lineage to be the surviving ancestor of all the lower branches, and thus pleisiomorphic, (4) the multifurcation in morphological cladograms expected in punctuated equilibrium may not obtain since daughter species peripherally derived from a surviving ancestor may have some convergent traits that falsely are evaluated as synapomorphies, and (5) there is morphological convergence (doubtfully total except in cases of extreme reduction) that is not dealt with by molecular analysis since the latter only infers genetic continuity and isolation, not speciation.

Taxacom April 14, 2009:

Thus, classification (names for things) and cladograms (sister-group relationships) and evolution (ancestor-descendant relationships) are intertwined, and there is information available in systematic analyses about all three. All such information should be preserved, since all contribute to science.

Taxacom April 14, 09:

Okay. Again, -----.

You ask: "How exactly does a phylogenetic classification lose that information (vs. one that allows paraphyly)?"

Reply: Sometimes you lose the information, sometimes you only make the information less important. 1. Lump an autophyletic family into another family without making provision as a subfamily or tribe and the genera are scattered, maybe listed alphabetically, among the genera of the other family, and the information is not flagged as important in the classification. 2. Do the same but leave the autophyletic family as a subfamily or tribe signals that the autophyletic taxa is about as important evolutionarily as the other subfamilies or

tribes, being simply a sister-group; but actually it is more important if you take its unique evolutionary traits into account by flagging the group as a separate family in the classification. Lump a family into a genus and it becomes a subgenus at best, doubtless a rare extreme.

No, you can't tell the difference in the classification between (1) taxa with higher level names because of evolutionarily important unique traits or (2) because they are sister taxa at a particular level. But if you have cladograms and taxon trees to accompany the classification, then you can. Otherwise much, perhaps most, evolutionary information is lost. Sister-group relationships, remember, are indirect indicators of evolution, but ancestor-descendant relationships are direct indicators of evolution. [Later comment: Also paraphyly may be destroyed by splitting into "cryptic" taxa (species, genera, families), which have either (1) no expressed traits, only molecular ones and these associated simply with long isolated populations of static morphology, or (2) assigned expressed traits generated randomly by simple division of a larger taxon, which is a statistical problem called multiple comparisons.]

Well, heck, sure, autapomorphic traits are future synapomorphic traits for future speciation. Just another reason to recognize autophyletic taxa in classification.

You say "... when you describe a new genus, you are no longer in the realm of alpha taxonomy (because you are advancing a hypothesis that the species in that genus are more closely related between themselves than to other organisms, either phylogenetically or by some other criterion)."

Reply: My realm is greater than your realm, -----. My hypothesis is that the species in a genus are not only more closely related to each other than to species in other genera via sister-group relationships, but that they also comprise a taxon tree of ancestor-descendant relationships (ignoring reticulation here).

Taxacom April 20, 2009:

A Web-based science encyclopedia:

<http://science.jrank.org/>

has an article by Peter A. Ensminger:

<http://science.jrank.org/pages/6711/Taxonomy.html>

which says in part:

“Evolutionary taxonomy can be considered a mixture of phenetics and cladistics. It classifies organisms partly according to their evolutionary branching pattern and partly according to the overall morphological similarity. Evolutionary taxonomy is basically the method used by the early evolutionary taxonomists and is also called classical taxonomy. The major limitation of evolutionary taxonomy is that it requires a highly arbitrary judgment about how much information to use for overall similarity and how much information about branching pattern to use. This judgment is always highly subjective, and makes evolutionary taxonomy a very poor method of classification, albeit one that survives in the hands of certain older taxonomists.”

Anent “older taxonomists” let's discuss tree-thinking. In “Mathematical Taxonomy” by N. Jardine & R. Sibson, 1971, John Wiley, New York, on page 150 it says: “Prima facie the case for using numerical methods of automatic classification to construct taxonomic hierarchies for all kinds of organisms can be made to appear quite strong. The case rests upon the following assumptions. First, the purely phenetic approach to taxonomy must be accepted. Secondly, it must be assumed that automatic classification based upon an adequate selection of populations and attributes can be guaranteed to produce optimal phenetic classification.”

This is from 1971. What are the results of phenetic cluster analysis? Trees. Parsimony analysis also generates trees through a nonultrametric method based on a simple model of evolution of traits), and I have it on good authority (Pierre Legendre, pers. comm.) that parsimony analysis really is cluster analysis. Cluster analysis, whether phenetic or phylogenetic or even MCMC Bayesian, produces trees and does not identify ancestors.

Evolution does not act by clustering. It acts by descent with modification of one biological entity (identifiable at some degree of resolution) into another. Paraphyly is one method of identifying an ancestor at some degree of resolution.

“Automatic classification” by clustering methods to create trees as hierarchical sister-groups has been around since the late 1960's and is now at least 40 years old. Clustering methods with morphology and molecular data are valuable in investigating evolution, but more information may be had about evolution than that obtained from clustering methods and presented to us in classification via holophyly.

I think it is time for students to confront their doddering geezer or geezette professors of phylogenetics with a paradigm change that calls for an eclectic approach to evolutionary content in classification, and reject holophyly (and other automatic or judgment-free aspects of phylogenetics) in favor of recognition of paraphyly and autophyletic products of descent with modification based on reasoned and seasoned judgment of all available information about evolution.

Taxacom April 23, 2009 (extensive remarks by Alexander Schmidt-Lebuhn as “---”):

There continue to be good responses to my inveighing against holophyly as a method of classification, so the flame seems eternal.

---: “It is very cunning to make the cut where you made it.”

My reply: Welcome to the Marketplace of Ideas.

---: “What I am saying is: the ancestors did not survive as a paraphyletic assemblage of lineages but instead they survived as both this paraphyletic “taxon” and the one that would have to be included to make it monophyletic.”

My reply: Ah, I see. In my opinion the extant taxa (by exemplars) did not arise out of a confusion of ancestral taxa, but, because a section of the phylogenetic lineage consists in part (basally) of a series of lines coming off and all of the same taxon, then the direct ancestor of THOSE lines was that taxon. AND the autophyletic taxon descended from THAT ancestral taxon.

---: “I still have to be shown how the history of evolution can be anything else but basically, largely, a tree.”

My reply: I'm not trying to do so. Darwin's Tree of Life was an ancestor-descendant tree, one taxon derived from another. Modern trees are usually sister-group trees, with taxa derived from nodes. They are both trees and address evolution. I think the Darwinian tree represents evolution more directly than the Hennigian tree.

---: “Mentha cannot be placed in a bifurcating tree because it has two extant ancestral species does not keep us from circumscribing the genus Mentha as monophyletic. Nobody says that bifurcation is the only thing that happens, but for higher taxa it is typically the only thing that we can possibly infer. We use morphological, chemical and molecular

markers for or inferences, and they all undergo lineage sorting over time.”

My reply: You must make a distinction in whether you are referring to phylogenetic monophyly (= holophyly) or evolutionary monophyly. Phylogenetic monophyly is an artificial classification, and you can classify anything artificially. Evolutionary monophyly simply refers to the dictum that every taxon is ultimately derived from another more ancestral taxon whether sequentially or bifurcating tree or bush.

---: “How the long-dead ancestral populations looked like can approximately be inferred by subtracting all apomorphies back to the node of interest. And what would you put in the place of this approach?”

My reply: You refer here to character mapping on a molecular tree, I think. Okay so far as it goes, but it assumes gradualist (not punctuational) evolution and the biological species concept (every split becomes a new taxon). In place of this I put taxon mapping. We can find ancestral TAXA by recognizing paraphyly for what it is, not just ancestral TRAITS, though the taxa are fully diagnosable by extant traits (as a kind of evolutionary uniformitarianism).

---: “As far as I understand, this: simply defining the ancestors as identical with only one fraction of their descendants, no matter how much they have changed in the intervening millions of years (just as long as they have not changed with regard to the apomorphies that the rest of the descendants have evolved).”

My reply: Yes yes! Paraphyly distinguishes the fraction of the descendants. Oh, and using TAXA instead of traits makes use of the single most important evolutionary feature of taxonomy, namely that species (and doubtless higher taxa) are morphologically static for thousands and millions of years, which is why we can do taxonomy at all.

---: “Of course genus is an arbitrary rank, as are all ranks except perhaps, in some ideal cases, that of species. The most important reason behind the decision where to apply that rank appears to be tradition.”

My reply: No it isn't. Genera are real (as distinguishable, describable clusters). Prove they are not. “Tradition” refers, I expect, to 250 years of taxonomic endeavor, sloughed off in favor of an artificial classification (holophyly). The only way I can think of to approach problems in standard taxonomy is to subject it to Quine's tests of simplicity:

<http://tinyurl.com/debto8>

---: “Otherwise, how could we explain that mammal genera usually contain 1-2 species, while genera are much more broadly described in all other taxonomic groups? That large genera such as *Justicia* s.l. (Acanthaceae) or *Satureja* s.l. (Lamiaceae) have been circumscribed in a very wide manner by some botanists but split into myriad segregate genera by others?”

My reply: This is called Science on the March. It involves dealing with data using every method that seems relevant to constructing a classification that reflects what we know about evolution in a group, struggling with the results, forming hypotheses and theories that may contradict each other, and so on. A quick fix, like automatic classification by holophyly, is no solution.

By the way, I'd like to state here that the endless wrestling over certain concepts to the point of burn-out or ennui is to a large extent what Taxacom is for. We all have made mistakes, gaffes, lapses, and foolishness, and have had moments of grace and discovery, but what I expect comes across to most members of Taxacom is how much all participants in these discussions love and respect science. I, for one, find it a privilege to live in a time when such colloquy is possible.

Taxacom May 4, 2009:

See if the following logic is appealing:

Phylogenetic classification methods (holophyly) try to reduce classifications to only those reflecting sister-group relationships, eliminating any taxa (by splitting or lumping) that are based solely on traits that are phylogenetically noninformative (that is, uninformative of sister-group relationships).

Phylogeneticists often map expressed traits (e.g. morphology) parsimoniously on a molecular cladogram.

What this comes down to is that, when mapping a single trait on a tree ((AB)C)...D, if one of the terminal branches has the same trait as the next lower in the clade (if A shares trait x with C), then that trait is mapped to the node shared by A and B (and x is a trait of the ancestor of A and B). This is a kind of paraphyly of traits, where A and C are a paraphyletic group, as far as morphological traits are concerned.

If morphological traits can be mapped on a molecular tree, then so can taxa. Mapping taxa immediately reveals ancestor-descendant relationships. A

paraphyletic group is a mapped taxon. So is the dependent autophyletic group.

If evolution is descent with modification, then ancestor-descendant relationships are a more direct indicator of evolution than sister-group relationships.

Therefore, if one has ancestor-descendant information from paraphyly available, one should use it in classification.

Classification should reflect evolution, whether ascertained by sister-group or ancestor-descendant relationships. After all, ancestor-descendant relationships are immediately inferred from the sister-group analysis. The same techniques are used as in mapping morphological traits but classification-by-holophyly gets in the way.

Contriving classifications from both ancestor-descendant and sister-group relationships demonstrated on a molecular tree does not mix two different kinds of information but maximizes evolutionary information about descent with modification, where modification means change, or differences between taxa.

In my paper
<http://tinyurl.com/6frd9l>

I extend the above logic to any kind of nonmonophyly.

If it occurs to Taxacomers that I'm repeating much the same things but in different ways, well

Taxacom June 1, 2009:

I think there are some specific problems that may be addressed that may alleviate the "dying out" of taxonomy.

It is the COMBINATION of molecular analysis (tracking genetic lineages and isolation events but not necessarily speciation events) and natural taxa (in Darwin's sense of genealogy plus differences, coupled with all aspects of biology including biogeography, chromosome counts, syn and autecology, chemistry, whatever, being a rational, consolidation of an evolutionary trajectory through time in space) that provides advances in systematics (molecular analysis providing evolutionary connections, and "traditional" taxonomy providing that which evolves along those connections).

Not genealogy alone. Strict phylogenetic monophyly is a ticking bomb in the heart of phylogenetics. It leads to:

1. The inability to identify organisms, particularly from expressed traits important in evolution.

2. Increasing reliance on an artificial classification (holophyly), which has got to alienate all rational biologists except phylogeneticists (whose methods only generate information on sister-group relationships as far as they are concerned).

If classification by holophyly is not soon identified as a shuck and abandoned, I give systematics five years before there are no students and the rest of us give up.

Taxacom June 2, 2009:

I did not attribute the decline and impending fall of systematics to cladistics. Nothing is wrong with cladistics, in its place. I merely revile and abominate (Taxacom is both informational and entertainment) the associated artificial classification system that splits and lumps taxa solely on the basis of sister-group relationships, ignoring ancestor-descendant relationships (autapomorphies, unique major changes in expressed traits). Sister-group analysis is fine, and even leads to ancestor-descendant relationships if holophyly is not followed.

Wonderful things occur when morphological and molecular results differ! If morphology evolves primarily by punctuation followed by stasis, and molecular (non-coding) traits evolve (change) by gradualism, then the difference can be informative. See my paper on the informational potential of nonmonophyly:

Zander, R. H. 2008. Evolutionary inferences from non-monophyly on molecular trees. *Taxon* 57: 1182--1188. or <http://tinyurl.com/6frd9l>

Taxacom June 4, 2009:

I agree with ----- about the need to update skills. I remember when, oh so long ago, taxonomists were downright proud to be jack-of-all-trades as far as techniques went, reveling in the ability to use chromosome squashes, cultivation in common gardens and reciprocal transplants, emerging blue from a walk-in freezer with a tiny tube of DNA,

struggling with phenetic analysis and MANOVA and whatnot.

Learning molecular analysis is not hard, and the techniques are more cut-and-dried than choosing a statistical method (Gower's? Mahalanobis?) and certainly more intuitive than the codes of nomenclature. I think if the associated baggage of classification by holophyly is eliminated, molecular analysis will be just another technique in evolutionary taxonomy that we use to reconstruct lineage linkages and isolation events.

Taxacom June 24, 2009:

However, the environment provides selection. The role of selection is commonly large, pace the inveterate neutralists, and stabilizing selection over thousands and millions of years is the basis for taxonomy, being that which keeps species together instead of just mutating into a stochastic blur of traits.

Lack of information on environmental effects on phylogenetics removes an important dimension in phylogenetic analysis. (The dog didn't bark that night. Can we make a deduction?)

Also, to what extent does some evo-devo gene complex as it exists in the present in different species help track phylogenetically changes in morphological trait complexes over geological time that correlate with selection pressures that change as environments change (whew, long sentence, isn't it)? If there is a mutation in the gene complex that matters in terms of selection on the basis of expressed traits (making the gene complex truly representative of a different expressed trait liable to environmental selection), then convergence must occur as different species adapt to the same environments, and this will screw up phylogenetic analysis, which assumes no or little convergence.

Taxacom June 27, 2009:

Much information about past selection of expressed traits or fixation of drifting traits will be there in the genome. Getting it out is the problem. Much history is overwritten in DNA. Slow-mutating sequences miss stuff. Extinct lineages have taken much with them into eraserhood.

If we could identify proteomically developmental genes generating different expressed traits associated with selection in nature then match them with history

accumulated by non-coding sequences, wouldn't that be nice? I think much is expected from QTL studies in this regard.

I think a feature of misunderstanding on Taxacom are the different ideas different people have about exactly what it is that is evolving. A species? A population? An organism? A trait? An enzyme? A codon? Is ANY change the same as evolution, or is evolution associated with change and the fixation of certain expressed traits in a species that is then stable over long periods of time through maybe stabilizing selection (which is my take on it)? Should we vote? Or is this even more embarrassing than our lack of agreement on something so basic? Look it up in the dictionary?

BTW, strong expressions are stimulating, instructive, and worthwhile on Taxacom. I would hate to see anyone blackballed from this listserver for occasionally being robustly annoying. Truth is not necessarily captured by tippytoeing up behind it.

Taxacom June 30, 2009:

There is also fellow traveler information that accompanies the genome. Think of the environment to which a particular organism is adapted as an extra chromosome floating outside the genome but affecting major aspects of the organism's existence. Stabilizing selection not only keeps a species in relative stasis morphologically for major periods of time, but also necessarily keeps the environment the same. A host, for instance, is a kind of environment for a parasite; a pond (through geological time) is much the same for a water bug.

Given this partnership of environment and genome, one should not look only to the genome for all possible information on evolution through time of a species.

Taxacom July 18, 2009:

Well, it's a little more complicated than that, -----
Read, for example, Vern Grant's 2008 paper: Incongruence between cladistic and taxonomic systems. *Amer. J. Botany* 90: 1263-1270. You may be able to get it as a pdf (try Google scholar).

There are two kind of monophyly, evolutionary and strict phylogenetic.
The former allows judgments of evolutionary process while the latter emphasizes patterns.

Phylogenetics groups taxa by branching order as a series of sister groups (following Hennig's Phylogenetic Method), while taxonomy groups by both similarity and differences (following Darwin's Natural System).

Phylogenetic classification allows (ideally) no ancestor-descendant relationships to be reflected in classification, while taxonomy allows both ancestor-descendant and sister-group relationships (to the extent discernible).

Phylogenetics eliminates all traits that are not informative of sister-group relationships, while taxonomy deals with all traits, even unique traits informative only of macroevolution (ancestor-descendant relationships involving evolutionary transitions between taxa).

Apparently dealing with ancestor-descendant relationships, that is, speciation and generation of higher taxa, is (1) not possible with sister-group analysis although inferences can be made, and (2) it is too hard because it involves judgment. Phylogenetics is thus a crippled form of taxonomy, focused on providing a quick fix and workaround for the usual give and take of scientific thought.

Creationism seeks to eliminate macroevolution from the classroom. Phylogenetics tries to eliminate it from classification. The difference in this respect between creationism and phylogenetics is that creationism has failed.

Taxacom July 20, 2009:

This discussion seems librarianish (pace librarians may they be blessed). Try substituting "good taxon" for "paraphyletic taxon" and see if what that group means to you changes.

A good taxon to a phylogeneticist is one that has a sister group at the same taxonomic level. Is that what we are talking about? Or have evolutionary concepts involving phylogenetically uninformative traits crept in to our thoughts, and there is a taint of common sense in some of our hesitation about accepting paraphyletic groups?

If you are a pattern cladist, then you should not waffle. You need to reject phylogenetically uninformative, unique traits entirely, and create a classification that ignores, rejects, and abominates the idea of one taxon giving rise to another.

Taxacom July 21, 2009:

Well, we all have premises, which we as typical humans defend might and main. On the other hand, I like Dewey's (the pragmatist) observation that the greatest advance for human thought is the notion of intellectual pursuit of process (as scientific theories), which ideally has taken the place of pursuing absolutes (Truth, Beauty, Goodness, whatever).

Thus, premises I suppose can be minimized by redefining absolutes as "what you do." My point is that classification by holophyly is a premise, a criterion, a maxim. It is a way to deal with patterns in nature. The problem is that naming a node as a taxon at the same taxonomic level as one of the sister lineages connected to it immediately makes the next lower lineage paraphyletic. Thus, nodes cannot be assigned a taxon at the same level as any one of their pair of lineages. If nodes cannot be named, then there is no real modeling or explanation of macroevolution in phylogenetic classification. Thus, speciation (and generation of higher taxa) is not demonstrated in phylogenetic classification, and, more importantly, is ignored in the "evolutionary analysis" on which the classification is based. That analysis is powerful but limited in interpretation by strict phylogenetic monophyly.

The premise of systematics should not be strict phylogenetic monophyly, but instead evolutionary monophyly, which allows paraphyly to represent a "good taxon" that generates evolutionarily another good taxon through macroevolution. This latter premise does not contain the fatal flaw of ignoring some evidence of evolution (ancestor-descendant relationships) and focusing only on other evidence (sister-group relationships).

Taxacom July 26, 2009:

One might even stretch -----' "religious dogma" aspect as follows:

Cladists must avoid any direct implication that one taxon gives rise to another because such is contrary to creationist doctrine. A paraphyletic group is an ancestor. Of course it is. Should anyone recognize a paraphyletic group then anathema sit! A purely cladistic tree is of only nested descendants, and is inferred from a cladogenetic model (not using ancestor-descendant inferences). One might even suggest that clades of the animal and plant kingdoms

match nicely the order in which organisms were created during the First Week.

(Okay, it's a silly conspiracy theory, but we all enjoy conspiracy theories, right?)

Although cladists do use the phrase "shared ancestor," never are such ancestors named, because if they are named then all taxa would be paraphyletic, and collapse via holophyly classification into one taxon. The alternative to this is to abandon the Haeckel-Hennig system and go back to Darwin/neoDarwinian evolutionary taxonomy. But Darwin fought the creationists, didn't he. What would he think of classification by holophyly?

Taxacom July 27, 2009:

Taxacom is where we can share curiosities and problems. Some of us lurk and learn, some lock and load, others get entertained, and we switch places depending on the topic. In honor of ----'s return to Taxacom, I submit an idea of what he might possibly mean when he says molecular data could be wrong and the true tree is ((man, orang) chimp, gorilla) or something on that order. Bear with me on this, since this has to do with self-taught statistics, which could be a good thing because it frees one from the competing schools, but is probably bad.

Different genes give different gene histories when their time of divergence is different from speciation events. Some genes seem to track species trees better than others, but given any three taxa terminal on a molecular cladogram, of say 40 DNA sequences analyzed, maybe half or 2/3 support one of the three possible resolved trees, and the other two trees are supported about half and half by the other DNA sequences. IF the null hypothesis is that different trees have an equal chance of appearing given equal chance of gene trees, then a superfluity of one gene tree would tend to support that gene tree as the species tree.

E.g. In the meta-analysis by Satta et al. (2000) of 39 hominoid loci, 23 supported the ((Homo Pan) Gorilla) gene tree, 8 supported ((Homo Gorilla) Pan), and 8 supported ((Gorilla Pan) Homo).

This works fine if one assumes all apes have a similar distribution of right (matches to species tree) and wrong gene trees. The mechanism of delayed gene history is understood, and one should be able to do a calculation that chi-square indicates the above distribution would occur by chance alone only 2

percent of the time (null proportion of 1/3). You can try this yourself:

<http://faculty.vassar.edu/lowry/csfit.html>

But the number of terminals on the tree are small, and the null may be wrong. Do other apes have this kind of distribution of more right gene trees than wrong? How do you tell? One way is to examine more than 30 gene sequences and see what kind of distribution we have? Is it much skewed?

E.g. the magic number 30 is apparently that minimum number of observations that allow calculations without prior assumptions of distribution. For instance, we test if a coin is loaded by flipping it. Given a binomial distribution (two equal columns of observations to match the normal curve) each should appear 50% of the time. But coins are not binomially distributed, since the head side is heavier, and the actual distribution (small as it is) requires not small number analysis (with assumptions of binomial distribution) but large number analysis (to see if there is a difference between expected number of heads from a coin naturally slightly loaded on the heads side and the number of heads from the particular coin you are flipping to see if it is additionally loaded and unlike other coins.

Thus, gene tree histories may be different from species tree histories by (1) chance alone, and (2) gene histories different from species histories in each taxon that may be due to linkage, selection, and whatnot that may confound analysis of shared ancestry.

As to (1), it could be that by chance alone the most common gene tree is not the species tree in the great ape complex. How might we tell this? A broad survey of lots of gene sequences might do it so we can maybe postulate a poisson distribution which would never demonstrate anything as wrong as that which we see in great apes, but we don't have this.

Another way is to see if the gene tree of many sequences but parsimoniously reflecting the most common approximates a tree from a different class of data. ----- suggests or implies or could imply, I think, that most of the ape/monkey molecular tree matches what is expected from morphology, but not with the great apes, and this difference is statistically to be expected (an occasional wrong inference because such occurs by chance alone, say 2% of the time). Is this right? Anybody who knows this kind of statistics better than me (doubtless anyone who has actually taken a course) have an opinion?

As to (2), there may be a mechanism that warps the null of all different gene tree histories being equally likely. This could be selection, linkage, mistaken orthology, or maybe cussedness. Then, the most unlikely gene tree might match the species tree in great apes. ----- has to at least demonstrate what these mechanisms might be and how they work to make his point better.

Taxacom July 27, 2009:

Now cladists perhaps know how an evolutionary taxonomist feels about the outrages committed on classification when holophyly (strict phylogenetic monophyly) is enforced. It's more than merely offensive because it is more than an imminent threat, like creationism is.

In the family of mosses I've worked on for 35 years, three other families have been dumped into it with no discussion apart from molecularly being derived from within the larger family instead of being sister to it. Brummit has reviewed in *Taxon* a list of flowering plant outrages. I've seen many published molecular cladograms with long-recognized higher taxa buried in other taxa of the same rank, and these are often not synonymized yet, but in a while, as courage builds, they will be.

Linnaean classification is in the process of being cleansed of any hint of macroevolution. Soon classifications will be totally sister-groups. Analysis of sister groups is important, but the "principle" of holophyly throws a spanner wrench into the analytic process, and eliminates even the possibility of naming ancestors.

It is easy to say, "well, anyone can discuss anything anytime," but that is not quite true. First, if classification eliminates words for ancestors, how can one talk about them, particularly in 20 years when the literature is considered ancient and out of touch? Cactaceae? What's that? Second, I've had reviewers ignore my papers for months. A major paper has been at *Plant Systematics and Evolution* since early January, and I was told 2 months ago that the assigned Associate Editor has simply ignored it, and it would be sent to someone else, no word yet. ----- told me that in the 1980's he had to publish out of the country because his statistical phylogenetics papers would not be published in the U.S.A. by the then ruling maximum parsimonyists. No, once the cladistic cleansing has wiped ancestor-descendant relationships from classification, there will be little discussion.

I abhor creationism, and am sorry that it is such a scary thing in California. On the other hand, classification is the basis for scientific study of nature, biodiversity, and natural processes. Classification by holophyly is a major disaster for Western science. And it is happening now.

Taxacom July 31, 2009:

This has come up once I think. Species paraphyly is generally considered something of a different thing than paraphyly of a genus. As far as I can figure it out, phylogeneticists expect a species that is paraphyletic (many exemplars with a different species coming out of the middle of the lineage of exemplars) to eventually become a sister group (reciprocally monophyletic is the phrase). Therefore, a paraphyletic species should be considered different from the autophyletic species because it will inexorably become a sister group to it as exemplars get their act together and homogenize their molecular data through recombination and gene conversion and whatnot.

For the time being, however, I see the paraphyletic species as ancestor to the autophyletic one; very clearly an ancestor. Seeing the future to imagine the former into a sister group relationship is typical of phylogenetic insistence on a classification based only on sister groups.

Evolutionary classification is messy because evolution is messy. Simplification of classification by eliminating macroevolution affects not just classification, but the perceived reality of natural entities. If they are not recognized using words, how does one talk about them?

Taxacom Aug. 4, 2009:

Regarding bar codes, one might remark that organisms may be thought of as probes that measure the environment, the habitat, into which they survive through selection (both neutral and selected traits must at least be tolerated if not contributing to fitness). The names of organisms may be thought of as observations or metrics on habitats. A barcode, in addition to the usual problems cited for such, is an additional step removed from the environmental, evolutionary dimension required for a decent understanding of nature using names as helpful descriptors. It again is a short cut, a kind of

Automatic Classification sensu Stuessy introduced by the pheneticists and continued by the cladists.

Taxacom Aug. 2, 2009:

Taxacom has a large number of users who simply read the sometimes entertaining messages and seldom participate actively in discussions, a much smaller group of fanatics with special agendas, and an even smaller number of blessedly centered people with clear ideas of how science works. What Taxacom needs is a lot more fanatics.

For example, gratis:

What's all this about "trees"? A phylogenetic tree can be completely replaced by a nested set of parentheses. Darwin's Tree of Life (page 95 of the paperback reprint I have) has actual taxa giving rise to derivative taxa along the central caulis and branches. The present Tree of Life project much in the news should actually be named the Nested Parentheses of Life.

One might admit that phenetics and cladistics both share a method that produces nested clusters that may be modeled as trees, with a node representing a pair of parentheses, but one might say cladistics uses a model of evolution in analysis. But it really isn't a model of descent with modification, is it? It is more a more limited model of cladogenesis. But wait a minute, is it really even that?

Parsimony only works if the data are statistically I.I.D. (independent and uniquely distributed), but fixation of traits during speciation is hardly random. Suppose we have ((AB)C)... and ((AC)B)... as possible terminal configurations with AB supported by three traits and AC by 2 different traits. IF these traits were independent, then there is more support for ((AB)C) ... BUT if the three traits were linked selectively, while the other two traits were, say, one neutral and the other selection-based, then ((AC)B) ... would be the correct configuration. This is always the problem, where details are NOT even commonly parsimonious although the cladogram at low resolution seems quite satisfactory.

Are molecular traits independent and uniquely distributed? Given that whole genes and associated non-coding regulator sites are commonly used in molecular taxonomy, linkage and therefore convergence is to be expected (in addition to simple codon bias). Check discussion on page 1267 of Grant's paper:

<http://www.mobot.org/plantscience/resbot/Repr/Add/Grant-Incong2003AJB.pdf>

or if this URL is too long

<http://tinyurl.com/lrzy55>

Taxacom Aug. 15, 2009:

Disparate congruence of results of different genes (sequences) between the sequences has long been known. Many gene trees have apparently different histories (differential lineage sorting). Some trios (like man, chimp, gorilla) have most genes supporting one tree (man, chimp terminal) and about equal but fewer numbers of genes supporting two alternative full resolutions (man, gorilla terminal) and (chimp, gorilla terminal). All or many gene trees may be well supported, which supports their discrepant histories. But then the distributions become governed by small sample statistics (requiring assumed distributions) in most cases but a few.

The explanation is fairly well-known, but the functional basis as it affects statistics is not understood at least by me. Okay, the null is not that all three trees are equal in probability, but instead the null is that only one tree is possible given shared ancestry. The null is that some process forces some gene trees into wrong configurations, and this process is equiprobable in the two alternative wrong configurations. We then assume that the two least common configurations are probably the wrong ones. I think that works okay.

So what is the process that makes some trees wrong? Why is it equiprobable for all possible trees? Is it "oh, I'm late homogenizing in the population" and two polymorphisms are fixed during speciation instead of one? Or some selection might be involved such that equiprobable wrong configurations are not to be expected?

Someone enlighten us?

Taxacom Aug. 15, 2009:

Interesting. So you are saying that an ancestor that is morphologically polymorphic gives rise to multiple descendants that reflect those polymorphisms variously. AND are you also saying that an ancestor that is molecularly polymorphic also gives rise to multiple descendants with various distributions of those molecular polymorphisms?

THUS are you also saying that any group of, say, three exemplars that are supported in three different ways by different gene lineages are all derived from that same ancestor. SO if there is evidence that there is differential lineage sorting, then molecular analysis cannot be used to distinguish a correct species tree for the taxa involved because there is no one correct species tree and all the taxa are derived from a joint ancestor with polymorphic genes?

So if ---- ----- can find differential lineage sorting with well-supported but different gene trees for configurations of orang, man, chimp and gorilla, then the molecular evidence cannot be used to disprove or decide against a morphological analysis of relationships?

Are you implying this? Are you saying that if there are many gene trees supporting one tree and only are few supporting other configurations, then we should not choose the configuration (topology) of the one supported by the most or the overwhelming number of gene trees from different genes?

This is NOT following dogma, -----! Doubtless one of the excellent phylogeneticists among us will explain why my take (above) on your message is totally wrong.

Taxacom Aug. 16, 2009:

Can I argue here that the genome does NOT include all that is relevant to determining evolution? I suggest that the environment or habitat is a kind of metachromosome or “envirosome” that contributes both direction of evolution and stabilization over time through natural selection. It is shared by all members of a species, and by affecting traits of a genus give coherence to evolution at the genus level.

Given this, morphology is a better clue to evolution than the genome since it is at the interface of genome and environment.

Taxacom Aug. 19, 2009:

Hope no one thought I agreed that differential lineage sorting meant that ancestors were so undifferentiated molecularly that molecular analysis was impossible if there was any evidence of different gene histories. No, no. I tend to subscribe to the common understanding that there is one species history, and that during speciation or at least isolation of two

lineages from one, a process goes on that eliminates all but one of the ancestral polymorphisms in each of the new lineages, a process called reciprocal monophyly. New sets of polymorphisms are created, but these can be distinguished as derivative.

Evidence that polymorphisms are rather random is that when three taxa (e.g. man, gorilla, chimp) are analyzed with multiple genes and differential sorting is discovered, one generally gets one rather frequent number of trees of one sort, and a smaller number of the other two possible resolved trees, and these two are about equal frequency, which is to be expected for this scenario. Thus, the single species tree is preferred over the undifferentiated and unanalyzeable molecular ancestor.

So, for the sempiternal orang/man/chimp/gorilla question, there are several possibilities. One might wonder why the morphological traits of man/orang evolved twice if ((man, chimp) gorilla) orang. Or why the molecular traits of gorilla/chimp evolved twice if ((man, orang) chimp) gorilla. Or maybe some exotic scenario presents itself to the Taxacomers' perfervid imagination: balanced selection for man/organ ancestor followed by wrong gene history. Anybody?

Right now I repeat my take on this, ----- is right for wrong reasons. Molecular history shared by of a vast majority of gene sequences is correct but the traits shared by man and orang were salted away epigenetically in the ancestors of chimp and gorilla. Is there evidence for this? There is a lot of cases in the literature that major traits and trait complexes are conserved for hundreds of thousands of years, then apparently reactivated. I can give examples if anyone wants to investigate. Morphology is the interface with selection, and we cannot ignore it.

Taxacom Aug. 19, 2009:

When phylogeneticists weight all traits alike, is this objective? It's commonly accepted as “wrong” but we kick clods sheepishly and glance about furtively when we admit this. I say “we” since the Laplacian (I think it was who said when nothing is known about weighting, equal weighting is better in some way) fault is everyone's.

I have a paragraph I wrote in an early, early paper: “Weighting highly those characters with best fit as determined after the parsimony analysis, may be done in various ways: Ladiges et al. 1989 used the consistency index (c) over the patristic unit character

length (Farris 1969) and also the product of character consistency and character retention index as was determined in Hennig86 (Farris 1989). Inasmuch as all characters theoretically have different phylogenetic importance (as per discussion by Farris 1983: 11), equal weighting prior to the exact algorithm is equivalent to arbitrary weighting (Swofford & Olsen 1990: 464). Thus, the more the characters are (reasonably) weighted differently, the less arbitrary is their weighting; Kluge and Farris (1969) recommended weighting by degree of variability of a character within OTU's, this being an estimate of the rate of evolution of that character. No method now exists to recommend the best weighting by character fit (Farris' 1969 example works for an artificial data set with a known random element)."

I can give references if asked. So there are objective (as opposed to certain or true) methods of weighting on the basis of evolutionary theory. Convergence is an evolutionary theory. So: In one paper I increased weighting of morphological traits NOT associated with convergence of a particular plant organ to force convergence-related traits high in the tree. All attempts at recovering a one-time historical event are heuristic, and one should not confuse "objectivity" in this context with objectivity in analyzing a universal in physics.

We all get funny results, and those call for considered and reasoned judgment, which can be called "subjective" by those promoting automatic classification or automatic evolutionary relationships, but is the basis for true advances in the field.

Taxacom Sept. 15, 2009:

----- says "Note that high levels of morphological dissimilarity, particularly of genitalia, are EVIDENCE for, but not DEFINITIVE of species boundaries according to BSC. Similarly, high levels of GENETIC dissimilarity are also evidence of species boundaries according to BSC. Only high levels of reproductive incompatibility are DEFINITIVE of species boundaries according to BSC."

I think "genetic" is too vague. The genome can change vastly but if stabilizing selection clamps down on those genes that affect evolution as expressed traits, such as when a species is in expressed-trait-stasis for hundreds of thousands of years, then the only value of what genetic change is tolerated is in tracking lineage continuity, which we do in molecular cladograms. I think what we (each of

us) mean by evolution is critical. As far as I'm concerned, big changes in the genome that do not affect expressed traits are not important in classification, even if they interfere with reproductive compatibility. Using reproductive compatibility as a criterion for species delimitation is okay only when it is practical, such as with birds and other big blundering beasts.

Remember the fuss when Bradshaw and others demonstrated large populations of plants that had no barriers to gene exchange but exhibited rather stable morphological differences based on genetic differences among parts of the population separated merely distance?

Taxacom Sept. 16, 2009:

By resolution of strong disagreements being valuable, I mean it is more than a goal, but a process. Watching how Taxacomers at odds dance around intellectually, ducking and dodging until some clear point emerges at which they actually agree on definitions and (1) decide to agree to disagree by citing something really interesting, maybe different information or methods, or (2) give up, which points out something really interesting about the problem, or (3) agree, rarely and boring unless the reading also agrees.

I visualize this as a stream of well-supported theory traversing time like a path in a dark jungle with battling scientists in a sense chopping a way through the undergrowth for that path.

Define cryptic species. If your definition is basically two or more species that are actually one species, I can't argue for or against, like the Trinity. Of course there are morphologically cryptic species that differ in other expressed traits, different major environmental adaptations, maybe considerably different larvae. If you are thinking two identical populations that differ only in some DNA sequence used to track lineage continuity, again there is a definitional problem about what is important in evolution such that classification should reflect it. In my various readings, nobody in evolution studies has dealt with the problem that one taxon can easily exist in two different molecular lineages, in spite of copious evidence that they often do. Phylogenetic monophyly (direct connection of descendant lineages with a shared ancestor) is quite different from evolutionary monophyly (sometimes gapped connection with a shared ancestor, such as in paraphyly).

How often do you yourself determine that the organisms you study have identical genomes, or genomic differences that are inferentially short of interfering with reproductive compatibility? An interesting point here is that many taxonomists who might not salute the biological species concept when asked about it actually “act as if . . .” in that they look for evidence of no or little gene flow, including gaps that represent gradualistic differential change. Much morphological analysis may well be looking for indirect evidence of little reproductive exchange. This is, of course, wrong. In my opinion. I think strong stabilizing selection is a major aspect of keeping, say, isolated populations of the same species looking, acting, and being alike and being the same taxon. Much the same procedure as looking for indirect evidence of reproductive isolation is involved in looking for evidence of unique stabilizing selection, so only the intent is wrong, not the outcome.

Bryonet Oct. 2, 2009:

--- ---- and ----- ----- have cogent thoughts on nonmonophyly. I will go a bit further.

Reciprocal monophyly after speciation (budding) of a daughter line or splitting of one ancestral line is commonly considered inevitable by those who cannot tolerate surviving ancestors of static phenotype, or who insist on gradualistic evolution of expressed traits through divergence of both resultant lineages after splitting. But there is abundant evidence that taxa that derive from within a population or a group of species or a group of genera do not eventually become a sister-group of that ancestor (i.e. reciprocally monophyletic), but the ancestral species, genus or family remains paraphyletic. Think cryptic species, genera and families that are indistinguishable by robust traits from other species, genera and families.

Given this evidence, insistence on phylogenetic monophyly is counter reality. Phylogenetic monophyly is a “principle” of classification, and is thus an axiom, maxim, or slogan, not necessarily representing a thing in nature (as opposed to evolutionary monophyly, which allows paraphyly). Regression to first principles and Aristotelian logic where any deduction is necessarily true (a syllogism) is crippling systematics. Remember when cladists asked “traditional” taxonomists to examine the basis for their methods, and we all said, hey, wonderful, yes we should analyze what we are doing? Actually, we were doing science, which is rather free-form and

involves induction. When we examined our “principles,” however, we found to our chagrin we had no guiding “principles.” Beyond doing science, I mean.

Yes, using first principles (e.g. species are named by phylogenetic monophyly, some species are not phylogenetically monophyletic, therefore these must be split or lumped with something else -- syllogism) makes things simple, but such axioms are not simplifying. Binomial nomenclature is simplifying, though exact long names are lost. Phylogenetic monophyly is simplistic, because representation of macroevolution in classification is lost.

One more point: If species, genera and families may occur in more than one molecular lineage (as in paraphyly), then molecular analysis does not necessarily determine the sequence of splitting of a lineage. This is because extinct lines of different molecular lineage but same phenotype may have come off earlier than what is given in the molecular cladogram. Again, we have empty precision that is based on assumptions that are, indeed, contradicted by scientific evidence. Thus, molecular systematics is not “easy” as some have said because it is just lab work (that's often quite difficult), but because recourse to axioms makes conclusions about evolution simplistic.

I believe that the long foray of systematics into cladistics and phylogenetics, using both morphological and molecular data, has been a tremendous waste of time because of empty precision, reliance on the “automatic classification” originating in phenetics (e.g. insistence on all traits being equally weighted to eliminate inserting any “phyletic” element), and regression to the authority of first principles. Much labor in the years to come will be necessary to repair the damage.

Bryonet Oct. 3, 2009:

Anent this, something I'd like to bring up is the chromosome number variation within species, and its significance or lack thereof in modern systematics. Remember chromosome numbers, Bryonetters?

An examination of Fritsch, R. 1982. Index to Plant Chromosome Numbers-Bryophyta. Bohn, Scheltema & Holkema, Utrecht & Antwerp shows many species with only one haploid chromosome number, but also demonstrates significant variation of haploid chromosome numbers (many derived, however, from counting meiotic figures) within many species of

various bryophyte families. These are usually aneuploid, but also polyploid.

Examples from Pottiaceae:

Barbula unguiculata usually $n = 13$ or $13+m$, but also 14 , $14+2m$, $12+m$,

$11+m$.

Didymodon rigidulus and *D. tophaceus*, usually $n = 13$, but also 12 .

Hymenostomum microstomum, usually $n = 13$, but also 26 .

Hyophila involuta, usually $n = 13$, but also $n = 7$.

Pottia bryoides, $n = 15$ or 52 .

Pottia lanceolata, usually $n = 26$, but also 13 and 24 .

Pottia truncata, usually $n = 26$, but also 20 , 25 , and 52 .

Tortella humilis $n = 15$ or 26 .

Tortella calycina $n = 13$, 30 or 52 .

Tortula desertorum usually $n = 12$, but also 3 .

Tortula laevipila $n = 12$, 15 or 26 .

Tortula muralis (copiously counted) $n =$ variously $13+m$, 24 , 26 , 27 , 40 , 48 , 50 , 52 , 60 and 66 .

Tortula princeps $n = 12$, 24 , $24+m$, 26 , 28 , $36+2m$.

Tortula robusta $n = 7$ or 12 .

Tortula ruralis $n = 12$ or 26 .

Tortula subulata $n = 14$, 24 , 26 , 48 .

In other families, a similar aneuploid or polyploid variation obtains.

For instance, *Funaria hygrometrica* usually has $n = 14$ or 28 , but also 56 .

None of these species are difficult to identify, and most have a distinctive microhabitat that may provide stabilizing selection on the phenotype for that particular expressed structure and its phyletic constraint, and any characteristic geographic ranges are difficult to infer.

Given that all these intraspecific chromosomal variants doubtless are to a large extent genetically isolated, shall we split each species such that the variants are cryptic species? Clearly not, and this has been the verdict of history regarding chromosome number variation. This is another example of punctuational (initial change followed by stasis) evolution of expressed traits, and gradualist variation of those traits of the genome that are nearly neutral.

Bryonet Oct. 5, 2009:

In fact, assuming few would respond to my comment, I asked R. Rednaz, a reclusive bryologist who is knowledgeable and occasionally supportive if he would comment on my note. He wrote me:

“What's the matter with you, Zander? The aneuploids are either mistakes or will not germinate. The polyploids on the other hand are a great opportunity for describing cryptic species. I'm going to go through Fritsch and describe as a new genetically different but morphologically cryptic species any polyploid that has a geographic distribution different from the type of the species. Thanks for the tip!”

Well, this was rather stern. On the other hand, Rednaz is assuming that

(1) the polyploids will eventually differentiate as a new species, (2) they are the same as any molecular DNA cryptic species that may be distinguished, or if different, then the DNA cryptic species are no good, and (3) people will let him get away with it.

I think he is correct in number (3).

Taxacom Oct. 5, 2009:

Well, ---, “phylogenetically informative” may prove somewhat of an oxymoron. This is because empty precision leads to aleatory classification. This is how: In parsimony of morphology, traits are not necessarily tacked onto a taxon as speciation gradually continues, but an initial linked set may be necessary for selection into a new environment. Thus, if A and B share three traits that are selectively linked, and A and C share two traits that are not (maybe neutral or sequentially added as the environment changes over time), then A and C probabilistically share the latest ancestor, not A and B. Although when dealing with masses of shared traits, main clusters of a parsimony cladogram may be okay, parsimonious decisions about relationships of small groups of closely related OTU's may need additional information, and are otherwise cladogrammed by chance.

In molecular analyses, any sister group pair may have had an extinct lineage identical in phenotype to one of the sister groups occurring below the split. If so, then this is not a sister group relationship but ancestor-descendant relationship instead. If the extinct lineage identical in phenotype to one of the sister groups is even farther down in the tree (phylogenetic polyphyly) then the molecular tracking of splits in the gene history is further compromised. The probability of this being true for any particular sister group on a molecular tree may be estimated by the frequency of paraphyly or phylogenetic polyphyly in that group for its particular gene analysis.

This leads to overly precise results of both morphological and molecular phylogenetic analyses. Not just a little too precise, but so very much more precise that any differences between classical omnispection and numerical analysis by phylogenetic methods must be viewed with considerable dubiety.

Following ---'s communications, the organism has been lost to reductionism. Phylogenetic analyses might be saved with information from chromosome counts, ecology, biogeography, and genomics, but right now most "advances" are a joke. This may be strong, but it comes from my belief that genera and higher taxa do evolve, and just renaming taxa that occur in two or more different lineages is just sweeping significant evolutionary information under the rug to preserve assumptions that are contrary to reality (e.g. "a taxon cannot be in two molecular lineages at once").

Taxacom Oct. 7, 2009:

To be even more cynical, there is a bit of misdirection in the word "gene" in taxonomy, as in "gene tree." If it is a gene tree, then it is subject to selection and convergence between taxa, which will then be reflected in classification as false shared ancestry. If it is not a gene tree, and only a non-coding trait tree, we are basing our taxonomy on the "evolution" of gradually differentiating neutral traits in the genome, but selection is eliminated as a factor in evolution. Classification is then solely based on lineage splits without recourse to any additional information. But the cladogram is then not exactly a gene tree.

Although most publications in molecular systematics do refer to additional information on evolution that may be available, the final classification is almost always based entirely on the molecular tree. Because in real life molecular analysis involves both gene changes (and therefore possible convergence), and non-coding traits that are actually regulators and therefore involved in selection (and therefore possible convergence), and non-coding traits that are okay but insufficient in number or contradictory across sequences studied, and really great molecular traits (I think sines, certain indels) that offer only limited illumination, and horizontal gene transfer, and all the rest, I support the contention of certain Taxacomers that evolution on which classification should be based should include serious consideration of additional traits (autapomorphies, chromosome

numbers, geographic distributions, and the now disreputable population genetics).

The modern taxonomic process (as discussed offline with some others) is twofold. 1. An evolutionary analysis, like phenetics or parsimony and Bayesian phylogenetic study, then 2. classification. The evolutionary analysis is presently highly restricted in data it considers, such data is biased to a large extent, and the results involve a great deal of empty precision regarding real questions. There are some triumphs, but we should not let these give us false confidence in simplistic methods of evolutionary analysis.

Bryonet Oct. 7, 2009:

Well. How to explain this? Perhaps mistrust that there are species and genera "out there" though recognized by botanists since Aristotle is due to an over-focus on pure method leading to the emptying from classifications of biological content.

1. Over-focus on "automatic classification" of pheneticists, where weighting is discouraged because introducing a "phyletic" element is discouraged.
2. Over-focus on narrow types of data (phylogenetic data sets) to exclusion of chromosome numbers, geography, population genetics, etc.).
3. Over-focus on sister-group relationships to exclusion of macroevolution, leading to trees that are just nested parentheses with no named ancestors.
4. Emphasis on importance of extremes of the usual spectrum of degree of group distinction; some species stink, others are different at genus level, most are distinguishable by traits given in floras.
5. Ignoring value to other sciences of basic units of taxonomy; they are of pragmatic value.

Ultimately, phylogenetics leads to anomie. Empty precision leads to aleatory classifications.

Bryonet Oct. 7, 2009:

"Clades are real." Hmmm, polar bears have been shown to have evolved from one group of brown bear. Thus:

((brown1, polar) brown2) . . .

So one of the brown bear molecular lineages and that of the polar bears make a clade.

The clade is based on the interesting fact that they share some non-coding genetic traits that may be taken as tracking generation of the polar bear species.

Real interesting, but are we going to base changes in classification on this? Brown bears and polar bears are quite different even if the brown bear occurs in two separate molecular lineages. I feel that the circumscription of brown bear as a biological entity in nature is far more important than basing classification on information on what group of brown bears the polar bear came from. Clades are real, but not real important.

Bryonet Oct. 7, 2009:

In my case, however, there are lots of studies that show that belief may not be the right word, as it has baggage concerning faith, but rather I have confidence in action that using species both as a rank and to refer to groups “out there” is both useful in everyday taxonomy and advances science in many fields.

So, promoting evolutionary basis for classification, species are, as a rank, basic units of taxonomy, and there is no pre-established definition for species as real entities, but we as taxonomists can make hypotheses about why they seem integral, such as the biological species concept for birds and higher mammals, and other concepts that may apply to different groups or species. Even if every species were a special case, the basic rank of species would be valuable and each species definable.

Trying to define groups and ranks using unreal criteria (phylogenetic monophyly) is bound to lead to nihilism. I can understand your suggestion, -----, that species as a rank be eliminated - only in this context. One species, however, can be found in separate molecular lineages (e.g. paraphyly). Renaming these as cryptic species or just lumping all the taxa into one sweeps the phenomenon under the rug.

There is no problem with species for most taxonomists; it is an artificial problem invented by phylogeneticists because their first principle (axiom, maxim, slogan) of phylogenetic monophyly in classification is on the face of it plain wrong. Species ranks and concepts are your problem, -----, not a major contention in systematics.

Promoting the first principle of phylogenetic monophyly is like defending the Earth is flat by

eliminating all data that concern anything too far away, and relegating any reference to a spherical Earth as “just stories” promoted to enhance cultural hegemony of an established elite of superannuated and unnecessary oldsters. Time is passing for all of us, though. Phylogenetic monophyly is not evolutionary monophyly, it is arbitrary nonsense that creates problems for phylogeneticists. With steely nerve, persistence, and some luck, at least some phylogeneticists, I am sure, can surmount this problem.

Bryonet Oct. 9, 2009:

I suggest you change your poll to phylogenetic monophyly (holophyly) versus paraphyly.

Evolutionary monophyly includes paraphyly. Those who wish to participate in this poll should note that “paraphyly” is a phylogeneticist's disparaging word for what is generally known as ancestors involved in macroevolution. Para implies faulty, wrong, amiss, or similar to the true form. Macroevolution is a real scientific concept supported by plenty of data with no revanchist connotations.

My own poll would be:

1. Creationist-style suppression of macroevolution in classification.

Versus:

2. Recognition that macroevolution should be reflected in classification.

An example of number one is:
Pottiaceae.

An example of number two is:
Pottiaceae. Ephemeraceae. Splachnobryaceae.
Cinclidotaceae.

Bryonet Oct. 9, 2009:

The --- blog's question is now:
“Do species have to be monophyletic?”

Some problems with this. First, why just species? Also “have to be monophyletic” is odd because many species just are paraphyletic, like brown bear versus the autophyletic polar bear. Only later, after recognition of paraphyletic status, do phylogeneticists wreak havoc on classification.

Shouldn't the question be:

“Do taxa have to be

1. split into cryptic species if paraphyletic, or lumped into one huge species with the autophyletic group, or
2. generously permitted to be recognized as a natural paraphyletic taxon versus the autophyletic natural taxon.

I here repeat that recognition of paraphyletic groups will greatly decrease the joss of phylogenetic analysis because the possibility of extinct paraphyletic lineages makes the highly precise results of molecular analysis doubtful. The chance of extinct paraphyletic lineages can be judged from the percentage of extant paraphyletic lineages. Only if paraphyletic lineages are verboten can phylogeneticists simply rename all extinct lineages and so dispose of them administratively. One can expect one or more extinct molecular lineages representing isolated populations for every large taxon, and these lineages may be isolated from the extant molecular lineage by one or more lineages of a different, derived taxon. This is within any reasonable patristic distance judged from phyletic constraint (frogs don't change into foxes right away).

Taxacom Oct. 19, 2009:

To expand on my contention that there is no all-purpose species concept, I think we taxonomists do recognize rather basic groups of organisms “out there” and name them as fundamental taxonomic

units useful to many fields of science. Such groups are, we infer, created and sustained for geological time spans by various natural processes. Species concepts commonly reflect such processes and generally assert one (or two, one for asexual organisms) to be most important or most fundamental.

We don't scramble for an all-purpose species concept because we are lazy. Yes, the lure of simplicity and some kind of general field theory for systematics is always there. I think we cleave to one species concept or another because there IS NO MONEY to do the investigative work to infer origination and sustaining processes for each and every species we come across. Working with evolutionists might help ascertain the scientific processes involved in a particular historical event and its following anagenesis or stasis, but there is no money to do so.

For instance, a species derived from hybridization followed by polypoidy would involve the Polyploidy Species Concept, a bird species might involve the Biological Species Concept, a species consisting of two long-isolated but identical populations might involve the Ecological Species Concept, and spots on the wall might involve the Phylogenetic Species Concept. The species is there, and we do not need a Concept to identify it, but to explain it. An egregious example of taxa not recognized because they do not fit into a Concept are macroevolutionary ancestor-descendant pairs that flout the antiparaphyly laws. Some taxa, would you believe, are outlaws?

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