

Structuralism in Phylogenetic Systematics

Richard H. Zander

Missouri Botanical Garden

St. Louis, MO, USA

richard.zander@mobot.org

Abstract

Systematics based solely on structuralist principles is non-science because it is derived from first principles that are inconsistent in dealing with both synchronic and diachronic aspects of evolution, and its evolutionary models involve hidden causes, and unnameable and unobservable entities. Structuralist phylogenetics emulates axiomatic mathematics through emphasis on deduction, and “hypotheses” and “mapped trait changes” that are actually lemmas and theorems. Sister-group-only evolutionary trees have no caulistic element of scientific realism. This results in a degenerate systematics based on patterns of fact or evidence being treated as so fundamental that all other data may be mapped to the cladogram, resulting in an apparently well-supported classification that is devoid of evolutionary theory. Structuralism in systematics is based on a non-ultrametric analysis of sister-group informative data that cannot detect or model a named taxon giving rise to a named taxon, resulting in classifications that do not reflect macroevolutionary changes unless they are sister lineages. Conservation efforts are negatively affected through epistemological extinction of scientific names. Evolutionary systematics is a viable alternative, involving both deduction and induction, hypothesis and theory, developing trees with both synchronic and diachronic dimensions often inferring nameable ancestral taxa, and resulting in classifications that advance evolutionary theory and explanations for particular groups.

Keywords

classification, conservation, empiricism, evolution, phylogenetics, structuralism

(Author-generated reprint)

January 21, 2011; accepted April 9, 2011

Biological Theory 5(4) 2010, 383–394. © 2011 Konrad Lorenz Institute for Evolution and Cognition Research

Biological systematics does not exist as independent of changing philosophies in other fields. Structuralism (Overton 1975; Matthews 2001) was introduced by Ferdinand de Saussure (1857–1913) to linguistics (Balzer et al. 1987; Barry 2002), and spread as a postmodern “rejection of all things past” to architecture, art, anthropology, literary theory, psychology, psychoanalysis, mathematics, and, as is now evident, to systematics (Rieppel and Grande 1994: 249). It is intended to replace empiricism, which involves observation, data, and experiment leading to testable hypotheses, and empiricism rejects hidden causes and unnameable or unobservable entities. Structuralism emphasizes the importance of irreducible hidden structures that are essentially engraved in the ground of being, exist at all times as axiomatic, and are not properly dealt with by theories of changes or processes in nature (Piaget 1970; Gilbert et al. 1996; Brading and Landry 2006). Such ahistorical and synchronic structure is, in structuralism, the ultimate reality that contributes to the human-mediated appearance of what we observe. Although the word “structuralism” is sometimes used to refer to biological developmental design limitations on evolution, in this article it refers to apparently fundamental nesting patterns of similarity that imply evolutionary relationship.

Science, Mathematics, and Phylogenetics

Science, mathematics, and phylogenetics may be compared with reference to patterns in nature. *Mathematics* is consistent in all dimensions, bounded only by Gödel’s Incompleteness Theorem and certain intuitionist inroads on axioms (Kline 1980). It is axiomatic, using lemmas (proven statements used as logical stepping stones) and theorems (statements proven on the basis of previous true statements). It is entirely deductive (mathematical induction is not the same as inductive reasoning, it is actually a rigorous deduction). It ignores causes and real entities. Moreover, it is doxastic, as we have faith that it is true because a deduction must be true if based on a true first principle (Chesterton [1933] 1956: 154). It is also somewhat magical in that mathematical concepts, no matter how convoluted or pyramidal, can be expected to work well every time in real situations.

Science (including evolutionary systematics as distinct from phylogenetics) is paraconsistent, as there may be contradictory theories but we need them to deal with nature; e.g., wave and particle theories of light, polythetic species descriptions, and different species concepts. It does not, however, ignore any fundamental dimension, i.e., one not reducible to component terms, like length and force. It is non-axiomatic and corrigible because scientific theory is expected to be continuously tested by new facts. It is based on hypotheses and theories involving causal explanations (Frost-Arnold 2010) with a footprint in natural phenomena. It uses both deductive and inductive reasoning (Cleland 2001), say, theory of evolution using

deduction from, e.g., fossils and polyploidy, and induction to extend the theory to all evidence and species. It is founded on empiricism in rejecting hidden causes and unnamed or unobservable entities. Moreover, it is nondoxastic because we require that all theories and assumptions be falsifiable or at least have some demonstrable causal connection with natural phenomena. The only quasi-fundamental patterns in science are certain laws and principles of physics (Giere 2005), and even these are presented in such a way as to be subject to falsification. The magic is in the greatly advanced understanding of nature through scientific theorization based on all available facts, and competition between alternative theories.

Phylogenetics projects an aura of the exactitude and certainty of mathematics. It is, however, not consistent because its apparently fundamental patterns are generated only by sister-group analysis. A whole dimension, accessible through ancestor–descendant analysis, is ignored, yet is critical to evolutionary theory as being directly involved in inferences of “descent with modification.” Phylogenetics is axiomatic in the sense that sister-group trees are taken as lemmas and traits or distributions mapped thereon as theorems (though these are incorrectly called “hypotheses”). It is largely deductive, citing the “hypothetico-deductivism” of Popper (1959) but substituting observed pattern for hypothesis. It rejects empiricism in rejecting or at least relegating non-phylogenetically informative data and in relying on unnameable “shared ancestors” as hidden causes. And it is doxastic, as adherents believe that sister-group analysis of evolution is the only acceptable basis for classification because it reflects facts of present-day evolutionary relationships, not theory. Phylogenetics is neither mathematics nor science because of the categorical prescriptions and proscriptions in axiomatic structuralism (see Giere 2005). A phylogenetic tree is linguistically “pseudo-referencing,” imbuing a representation with import it lacks, and there is no real magic in that.

Classification

Classification is the structured language by which coherent groups in nature are represented. A protothetic classification (based on first principles) may be internally consistent and precise (Rieppel 2011), but is empty without process-mediated content (Gilbert et al. 1996; Rieppel 2010). Axiomatic geometry, for instance, did not replace empiricism when it was discovered, but established empiricism on a firm and regularized basis in both applied and research venues. It is tempting to treat theoretically refractory but otherwise pattern-forming phenomenon as metaphysical Platonic structures, but any set of phenomena can be treated as well-documented observations in search of a theory. Even the almost magical Principle of Least Action now has a well-established theoretical explanation through quantum effects in the mesocosm (Hanc

et al. 2003). Structures discovered in fields other than mathematics and physics are mostly real in some sense (“Meinong’s Jungles” sensu Jacquette 1996), yet, though important to practitioners despairing of subjective or multiple analytic viewpoints, are hardly of the import and demonstrable value of mathematical and physical axioms. There are, however, uses for structuralist forms of analysis in an empirical context (van Fraassen 2007). The structuralist slogan, “theoretical knowledge is knowledge of structure only,” on the other hand, can be pitted, in science, against the long-accepted completeness criterion that science must explain how things manifest themselves as content in reality, namely through an inferred or observed process (Dewey 1950: 12; Giere 2009). Phylogenetics asserts that parsimony, Bayesian, and maximum likelihood-derived patterns of exemplars’ shared ancestry, particularly statistically certain or near-certain molecular cladograms, reflect fundamental structures in nature, and classification should reflect these patterns. I say classification should not, because present patterns of relationship are only evidence of past evolutionary processes in nature. Testing the integrity of a theory of process requires both deduction and induction of a theory from that evidence (Cain 1959). That theory may be as simple as and as fraught as naming a node in a cladogram as a diagnosable species or higher taxon.

Systematics has followed several scholarly fields in reconstructing fundamentals by emphasizing relationships over that which is related (Nelson 1989; Avise 2000: 1830; Brower 2000). The elucidation of structuralist patterns is presently preferred by phylogeneticists (these often pattern cladists; see Scott-Ram 1990; Griffiths 1996) over syncretic classifications based on a multiplicity of theoretic viewpoints (Beatty 1994) in examining aspects of evolution. Saussure and other structuralists also emphasized that language is a complete system at one point in time (synchronic), and historical, diachronic elements should be eliminated to the extent possible (Dosse 1998: 206). Phylogeneticists commonly assert that lineages are diachronic, i.e., have an inherent historical element (Lee and Wolsan 2004), but both cladistic analysis and resulting classifications commonly ignore information leading to theories of macroevolutionary history involving taxa. According to Okasha (2003: 745), “Clades are by definition monophyletic, and as a matter of logic, monophyletic clades cannot stand in ancestor-descendant relations with one another.” Phylogeneticists, in sum, definitionally and axiomatically eschew theory-based reasoning and inference from evidence, all these being well-known attributes of scientific thought. Hull (2005: 17) stated that “treating descent as being prior to similarity with respect to scientific theories results in some extremely counterintuitive groupings.”

Pataphysics is a postmodern “philosophic alternative to rationalism” (Bok 2001: 3) that inserts elements into language arts that are two steps removed from reality. A pataphor (Lopez

1990) is an extended metaphor that creates its own context. Metaphor is established, and is reified as part of the story or image. In phylogenetics, the structuralist problem is demonstrated in the following figures of speech: *simile*: “evolution is like a tree”; *metaphor*: “evolution is a tree”; *pataphor*: “the tree *is* evolution.” A phylogenetic tree is presented as a pataphor. On the other hand, a structuralistically reified metaphor of an evolutionary tree, the cladogram, only represents a set of nested parentheses modeling sister-group relationships of extant taxa. Although phylograms with branch lengths noted on them seem to clothe the tree limbs with information, these distances involve nodes, which are not named (except with the uninformative and somewhat circular term “shared ancestor”) and are treated as a third entity different from the two daughter groups even when phenotypically indistinguishable from one of the daughter species (Okasha 2003). Nonparametric bootstrap and credible intervals are measures of support for the “parentheses of life,” not for a reified tree of life.

The lines forming a cladistic tree are actually no more than visual aids that help sort out the often complex nesting of inferred sister groups of operational taxonomic unit (OTU) exemplars. The nodes (places of dendrogram branching) are of no substance and are much like Leibniz’s monads whose reality is entirely in their relationships or pre-established harmony (Ogrodnik 2004). Nodes on phylogenetic trees are unnameable because to do so would force branch collapse to ensure holophyly (strict phylogenetic monophyly), thus a phylogenetic tree is haecceitistically vacuous; pithily put by Stein (1937: 289): “There is no there there.” A phylogenetic tree as pataphor is indefensible even as a heuristic in the context of extreme scientific realism (Sober 2008: 96) because the tree that is not a tree is also intentionally presented as information about a very limited aspect of evolution (sister-group relationships), this further scrambled in classification (as scientific names given to exemplar specimens post hoc) by enforced holophyly (strict phylogenetic monophyly). Although one-dimensional nested parentheses of the relationships of extant taxa are of interest, even more important is the process-based history of relationships, such as is modeled by ancestor–descendant relationships of taxa in a truly two-dimensional caulogram (Zander 2008b, 2010). An evolutionary tree of both sister-group and ancestor–descendant relationships involving causal or at least historical explanation may be acceptably reified as a pataphor in the context of extreme scientific realism, but many may prefer an instrumentalist view (Sober 2008: 97) that even fully modeled evolutionary entities are simply theories in search of further explication and support.

Structuralism in Phylogenetics

In this article, phylogenetics is considered to reflect structuralism in focusing on the emergence, under analysis, of tree

diagrams of relationships. For instance, according to Williams and Ebach (2007: 260; authors' emphasis): "Patterns can only be discovered if we consider it [sic] to be the primary aim of biology—science as a pattern and not *science as a process*." There is, however, insufficient attention paid to additional empirical aspects involving discursive reasoning about process (Dewey 1950: 12) involved in evolutionarily relevant facts not in the cladistic data set. Phylogenetics uses sister-group analysis as an axiomatic basic framework (Farris et al. 1970; Brower 2000) for classification. It rejects, through application of the principle of holophyly in classification, any hint of macroevolution involving taxa giving rise to taxa of the same or greater rank. This leads to theoretical under-determination by structuralist rejection of empiricism involving elucidation of historical, causal processes. In statistical psychology, diagrams that model phenomena but lack essential information, with the idea of "less is more," are considered problematic (Wilkinson et al. 1999: 605). Rees (2000: 68) has pointed out that a scientifically "bad" theory is one that "is so flexible it can be adjusted to account for any data." Holophyly, an axiomatic principle in classification, is not a fact or theory but provides that flexibility in phylogenetics. The inference of ancestor–descendant taxa at the taxon level from analysis restricted to sister-groups is impossible unless based on arbitrary assumptions (Rieppel and Grande 1994; Rieppel 2011).

Structuralism, perhaps because it is basically a "content-free" methodology (Overton 1975), can introduce an aspect of "hard science" into fields lacking clear axiomatic conceptual foundations. Although definitions are various (Matthews 2001: 1), most generally a structure is an operational set with no defined meaning, grouping elements with no defined content through relationships that are not specified (Aczel 2007). For instance, in mathematics, the Bourbaki group in France reconstructed the foundations of mathematics emphasizing set theory (Giere 2005) as a structuralist framework (Aubin 1997). They are now in eclipse because set theory is inadequate in various respects (paradoxes, inflexibility) compared to, for example, the somewhat more flexible category theory (Bell 1981), though in it, likewise, objects have no meaning of their own, except in the way they relate to each other. Modern chaos theory, fractals, and catastrophe theory are quite important but are not structuralist. The Bourbaki group was responsible for the "New Math" once widely taught in schools. In anthropological alliance theory, Lévi-Strauss ([1949] 1969) included a mathematical analysis (by Bourbakian A. Weil using set theory) of complex incest taboo patterns in Australian aboriginals showing that all subgroups do eventually intermarry (as an irreducible set). Piaget (1970) detailed apparent latent structures in the human mind that he suggested comprise the foundation of all science, the ultimate source, for instance, of neural networks and genetic algorithms.

It is in the structuralist apprehension of apparent reality as human-generated symbols and signs where new scientific discoveries (e.g., macrocosmic relativity, microcosmic uncertainty) may seem to change mesocosmic reality, as popularized in the technological structuralist "connections" of Burke (1995). Empiricism is rejected in favor of a focus on universal hidden patterns. The scientific paradigms of Kuhn (1970) have been viewed as simply politically convenient human constructs on the fundamental cultural syntagm (structured set of paradigms, e.g., in parsed sentences) of Saussurian structuralism (Sardar 2000). In the case of systematics, when evolutionary theory is discussed it is secondary to and necessarily fully dependent on the discovered structure; this implies the lack of substantive theory cautioned against in statistical psychology (Wilkinson et al. 1999: 604). Total subservience of theory to structure obtains even when the structure is probably wrong theoretically, inasmuch as paraphyly and polyphyly have been estimated as widespread in extant taxa (Rieseberg and Brouillet 1994; Funk and Omland 2003) and doubtless occurred widely in ancestral taxa. Phylogenetics commonly attributes heterophyly (particularly phylogenetic polyphyly) to convergent evolution, but a deeply shared ancestral taxon is another explanation. One should be aware that from a structuralist perspective, convergence could be an evolutionary force due to structural attractors (Batten et al. 2008).

By reframing systematics as dependent first and foremost on molecular cladograms, the phenomenon of statistical certainty for some sister-group relationships is philosophically "saved" as global certainty. However, as soon as one adopts a pluralist methodology and looks for additional explanation, for instance concerning a caulistic basis—that is, naming taxa at cladogram nodes when possible—of classification, then certainty is no longer global and we return to empiricism. Saving phylogenetic cladograms from empirical emptiness (Rieppel and Grande 1994: 231), on the other hand, may be accomplished through the historically based and therefore causally based isomorphism between cladograms, one generated from morphological data and another from molecular data. Isomorphism supports the consilient structure hidden in both data sets, both when the cladograms match, and when they do not, being isomorphic in the caulistic dimension. Thus, a taxon shown to be "primitive" in a morphological cladogram but advanced in a molecular cladogram might be proposed as including theoretical progenitors (at that same taxon level) of many clades lower in the molecular cladogram.

Structural realists (e.g., Brading and Landry 2006) assert that what actually arranges phenomena is the world as a series of diachronic events; and, if "structure is all" then the "no-miracles" argument applies in that it would be a miracle for there to be any success in, say, an evolution-based classification, without evaluating process. The "no miracles" argument (Brading and Landry 2006; Frost-Arnold 2010) also applies

in the case of evidence for ancient paraphyly and surviving ancestral taxa (i.e., as causing present-day heterophyly). The principle of holophyly is invoked to lump or split and thus eliminate inconvenient taxic paraphyly or polyphyly, rendering a cladogram miraculously precise and monophyletic. The “measurement problem” in physics also applies here. When more than one perspective is necessarily used on a problem, then there can be no unique solution or precise structure. Thus, a certain amount of imprecision must be tolerated but this provides content beyond the structure that renders theory non-vacuous (Schmidt 2008).

Even if we allow that phylogenetic analysis of data does reveal a fundamental structure in nature, then that revealed pattern (of nested exemplars) is of data about relationships, and does not advance a new process-based theory about causal or timewise connective relationships involving descent with modification among those exemplars. Any implication of causal connections involves “shared ancestors,” which are hidden causes involving unnamed entities, and such reference is not science because not empirical and not corrigible. Thus, phylogenetics involves selected facts about evolution that are commonly well supported, but scramble an evolution-based classification because theory is skipped.

Macroevolution is used here in Jablonski’s (2007) sense as evolution at and above the species level, as opposed to *microevolution*, being minor genetic and phenetic changes within a species, although this may (or may not) lead to speciation through infraspecies in gradualist scenarios. Systematic pattern and evolutionary process are nowadays commonly divorced in the development of phylogenetic classifications (Rieppel and Grande 1994), beyond acknowledgment that shared advanced traits imply shared immediate ancestry. This leads to well-defined sister-group cladograms that are amenable to mathematical and statistical manipulation, the “mechanized knowledge” of Gigerenzer et al. (1989: 211). However, as ancestor-descendant relationships are ignored (O’Keefe and Sander 1999; Mayr and Bock 2002; Grant 2003; Dayrat 2005), it also leads to empty precision (Rieppel 2011). By that I mean it is precise to note “((A,B)C)D,E” but if there is evidence that the taxon represented by exemplar A is the surviving direct ancestor of B, or possibly even of C as well as of B, the precision concerning sister groups is misleading through lack of representation of ancestral taxa when these are inferable, some apparent sister-groups being actually ancestor–descendant series. According to Holton (1993: 164), modern science is underpinned by Galileo’s four great novelties: quantification of nature, mechanization of nature, distancing of science from everyday experience, and from religion. The address of modern systematics through heavy statistics and molecular data appears to fit such criteria, yet treats sister-group diagrams doxastically as first principles.

The essential problems of modern-day phylogenetics are a misunderstanding of traditional methods, phylogenetics’ total focus on sister-group relationships, rejection of appropriately classifying phylogenetically paraphyletic taxa, empty inferences by large leaps in assumptions associated with what an exemplar specimen can represent in molecular analysis, and ultimate rejection of representing macroevolution in classification (Knox 1998; Grant 2003; Bock 2004; Zander 2007b, 2008a, 2009, 2010; Cavalier-Smith 2010). This article is not a defense of paraphyletic taxa (e.g., Sosef 1997; Brummitt 2003, 2006; Hörandl 2006, 2007; Zander 2007b, 2007c) as such, because paraphyly is a phylogenetic, not an evolutionary, concept, it being based on sister-group diagrams lacking ancestor-descendant inferences. Paraphyly is a disparaging (“para”—closely resembling the true form, almost, inadequate) phylogenetic term for what are apparent surviving ancestral taxa reduced to their sister-group structural context on a cladistic tree, even though they are clearly better interpretable as the ancestral element in mother–daughter groups. Paraphyly is a phylogenetic code word for nomenclaturally signaled macroevolution in a sister-group (i.e., nonprogenitor-descendant) context, problematic to phylogenetics because sister-group analysis alone cannot identify macroevolution. For clarity, the term paraphyly is used in the present article in the evolutionary sense for extant ancestral euphyletic (“eu”—perfect, proper, core) taxa. Phylogenetically paraphyletic taxa are surviving ancestors of other extant, apophyletic taxa (sensu Carle 1995, a taxon at the same rank or greater than the paraphyletic taxon in which it is nested, or “autophyletic” sensu Zander 2010), and are diagnosable at a taxonomic level inclusive of all exemplars except those of the apophyletic, descendant taxa.

In addition, according to Mercier and Sperber (2011), a well-established part of critical reasoning is epistemic vigilance, including coherence checking and trust calibration. As to coherence checking, structuralism by its absolutist nature negates integrating new information with old, because the old theoretical context is entirely replaced by the revealed hidden structure; while trust calibration is replaced by mathematization and empty precision.

A Need for a Pluralistic Systematics

There is a need to develop evolution-based classifications that address all available information on evolution of a group (Racheli and Racheli 2006). Such a system would not be “self-sealing,” that is, a system automatically discounting adverse evidence, as with the latter day Freudian psychology as discussed by Oppenheimer (1957) and in systematics by the principle of holophyly. The inclusion of caulistic appraisals provides the ground for conciliation of methods that separately produce rather different results. This conciliation is without

overemphasis on classical systematics, morphological phylogenetics, or molecular systematics, and is compatible with any species concept (e.g., as discussed by Mayden 1997) that operates in both sister-group and ancestor–descendant dimensions. The method of patrocadistics (Stuessy and König 2008) generates classifications based on both taxon divergence (patristics) and tree structure, but incorrectly assumes that phylogenetic trees present fairly accurate sequences of sister-group speciation events, that nodes have ontological substance, and that traits evolve, i.e., estimation of state changes is not affected by surviving progenitor taxa.

The needless splitting and lumping associated with the practice of holophyly (Zander 2007b) cripples the use of phylogenetic classifications by other fields because biases are introduced that may be “discovered” by evolutionists, biogeographers, ecologists, and others as apparent real natural features of evolution even though there is no natural process represented by strict phylogenetic monophyly. There have been no critical problems with the standard Linnaean classification in groups represented in the past as ancestor–descendant “Besseyan cacti” (e.g., Bessey 1915), as exemplified by Wagner (1952) and Zander (2008b, 2009). Given pluralist methodology, the standard classical approach to nomenclature is both appropriate and adequate. Such classification serves as a *well-hooked framework* for a wealth of information from many fields. As there are seldom specimen exemplars (OTUs) in morphological parsimony analysis, which mainly uses taxon descriptions as OTUs, a cladogram based on morphology at best reviews and details the relationships of classical taxonomy. Where classical taxonomy evaluates “local” evolutionary relationships of individual specimens and traits, parsimony can provide a broad-based nested summary of all such evaluations, the goal being a detailed natural key or cladogram equivalent, that is, a key involving natural explanations (see Giere 2005). Problematically, many processes are involved in evolution (Hörandl 2007). For instance, identifying surviving ancestral taxa on the basis of other data than that in the cladistic data set yields a tree that is less parsimonious in length (increasing the number of trait changes) but more parsimonious in having fewer numbers of postulated taxa or entities (nodes). Reviewers of an early draft asserted that I was creating straw-man arguments, but this is not so. One must remember that those used to structuralist “tree-thinking” have difficulty grasping the relevance of scientific theory and of the caulistic dimension in the preliminary evolutionary analysis that leads to evolution-based classifications. Griffiths (1996) has pointed out in a discussion of pattern cladism that phylogenetic systematics is the most successful method of sorting organisms into kinds representing generic forms or “rich clusters of properties that can be relied upon to hold up in unobserved instances,” which I interpret simply as new facts on a subject commonly fit well with old facts whether a causal theory is available or not. Griffiths

(1996) explained that projectable categories (e.g., taxa in natural classifications or keys) are based on members being related by common ancestry, and their “essences” are historical. Such explanations are trivial, circular, or metaphysical. There are better, process-based explanations for recognizing both sister-groups and ancestor–descendant series (Brummitt 2003, 2006; Hörandl 2006; Zander 2007b).

A new syncretic systematics is needed to meld the best features of empiricism and structuralism, and classical taxonomy and phylogenetics. Though theoretically pluralistic (Beatty 1994; Rieppel and Grande 1994: 234; Giere 2009), methodologically and theoretically eclectic, science is not “ontological opportunism” as discussed by van Fraassen (2007). It is also not as inflexible as the principle of complementarity in physics (Oppenheimer 1957), in which two methods that are valid separately simply cannot be combined, e.g., wave and particle theories of light, although both must be separately recognized as part of a complete description of natural processes. The key to conciliation in systematics is examination of the caulistic dimension (the ontological substance of cladogram nodes), heretofore largely ignored in numerical studies in favor of the sister-group context. Ridley (1996: 379) has pointed out that an objective classification must represent unambiguous properties of nature. Although we aim to produce objective classifications, at the present time analysis of ancestor–descendant relationships is less certain (involving the perils of pluralist methods, scientific intuition, and discursive reasoning) than is elucidation of sister-group relationships. The latter ignores major uncertainties contributed by, for example, surviving ancestral taxa (Knox 1998: 38) and ancient extinct paraphyly (Zander 2010) or extant paraphyly not yet sampled in an extant lineage. An euphyletic taxon, whether paraphyletic or not, is ideally the best model of evolutionarily based groups of organisms determined by classical study, numerical analysis of morphological and molecular data sets, and biosystematic work.

A New Framework

Taxonomists may not be professional evolutionists, yet taxonomic and evolutionary studies are closely intertwined. The methodological fundamentals on which a theoretically pluralistic systematics (Gould 2002; Hull 2005; Padial et al. 2010) might be based are as follows: rigorous statistical re-evaluation of published molecular cladograms (Gigerenzer et al. 1989; Cohen 1994; Zander 2007a); recognition that possible surviving ancestral taxa (Lewis and Roberts 1956; Lewis 1962, 1966; Vasek 1968; Mayer and Beseda 2010) may introduce uncertainties in cladistic analyses, as may extinct or unsampled paraphyly (Zander 2007b, 2008b); ancestral taxa may be mapped on a molecular tree through phylogenetic paraphyly or polyphyly on molecular cladograms (Zander 2008a, 2010); and

additional inference of progenitor names is possible through cross-tree heterophyly (superimposition of morphological and molecular cladograms) refereed by Dollo's Rule (Gould 1970).

How does one incorporate new methods (morphological and molecular cladistics) into the standard methodological framework? That is, how can sister-group-only analytic techniques meld with traditional stem-group methods? Details of a method for creating scientific theories reflecting both cladistic and caulistic processes are the subject of another paper, but a short synopsis of the essential elements is given here: (1) Classical alpha taxonomy uses hard-won informal genetic algorithms (Hutchinson and Gigerenzer 2005; Gigerenzer 2007) as a heuristically based expert system focused on both similarities and distinctions of individual specimens and traits to generate general clustering by similarity (Sneath 1995) and therefore by theoretical evolutionary descent. (2) Numerical taxonomy, including morphological parsimony and phenetic analysis (Jardine and Sibson 1971; Hair et al. 1987; Schneider et al. 2009; Mooi and Gill 2010), generates dendrograms that accurately place taxa most dissimilar from an outgroup highest in the tree. As evaluation of traits is clearly specified methodologically, the cladogram is a powerful way to present basic information from which theories of evolution are generated. It is limited by rejection of all information not relevant to sister-group clustering. The cladogram can be used, however, to create a "natural" key (one with embedded evolutionary theory of descent with modification) with the help of additional information about autapomorphies. (3) Molecular cladograms provide good estimates of genetic continuity, but additional information may be used to estimate the caulistic element of the tree. Phylogenetic paraphyly and polyphyly (together heterophyly) on a molecular tree imply a theoretical progenitor-descendant diachronic relationship (i.e., involving nameable nodes on the tree) corresponding to paraphyly-apophyly arrangements on the cladogram. The progenitor taxon is diagnosable at the taxon level that includes all exemplars derived from the previously unnamable nodes involved in heterophyly. (4) Cross-tree heterophyly is basically a comparison of morphological and molecular trees of the same taxa. A taxon low in the morphological tree ("primitive") may be considered as the theoretical progenitor of all lineages between the position of that taxon on the morphological tree and the position of the same taxon on the molecular tree. (5) Application of Dollo's Rule (Gould 1970) in the context of biosystematics allows additional information from other fields (e.g., biogeography, chemistry, cytology, ecology, EvoDevo, fossils, morphometrics, paleontology, population genetics, and other biosystematic indicators of descent with modification of taxa) to help gauge the direction of diachronic, caulistic evolution. The combination of several evolutionarily evaluative dimensions, as suggested above, is clearly an example

of Giere's (2005) "perspectivalism" in constructing scientific models of real things discernable from different objective angles.

Although it is possible for an evolutionary systematist to present to a phylogeneticist an alternative scientific, empirical basis for paraphyletic taxa and for the evolutionary importance of both expressed traits and molecular sequences, and of both divergence and shared ancestry (e.g., Brummitt 2003, 2006; Hörandl 2006, 2007; Zander 2007c; Hörandl and Stuessy 2010), structuralist phylogeneticists would reply, "Yes, yes, that is exactly what we reject" (Brower 2000). Citation of problems with the *results* of phylogenetic classification may have more corrective force; for instance, problems introduced by phylogenetics in biodiversity study and conservation (Zander 2007b). The importance of the recognition of such taxa of concern as polar bears and the cactus family as distinct in classification from their direct ancestral taxa is obvious, though both are apophyletic. Hörandl and Stuessy (2010) have pointed out that isolated island lineages may rapidly become strongly divergent from continental progenitors, yet such lineages are denied proper taxonomic rank because they are often apophyletic. Examples cited for the flowering plants are the genus *Robinsonia* (Asteraceae), of the Juan Fernandez Islands found apophyletic to the widespread *Senecio* (Pelser et al. 2007), and *Lactoris fernandeziana*, of the monotypic island endemic family Lactoridaceae found to be apparently apophyletic to Aristolochiaceae (Qiu et al. 1993; Soltis et al. 1997; Stuessy et al. 1998). Hörandl and Stuessy (2010) indicated that conservation of island taxa is threatened by gradual elimination of their proper taxonomic recognition, caused by apparent recent derivation from paraphyletic continental progenitors, because slowly mutating molecular sequences do not match the rate of rapid and major morphological divergence. Padiál et al. (2010) review problems in estimation of numbers of species involved in biodiversity studies contributed by restriction to single lines of molecular evidence. The reader, if a taxonomist, can probably think of taxa of conservation concern whose status or even apparent reality is affected by structuralist methods. This includes the growing numbers of "cryptic" molecular taxa whose reality is often entirely based on the structure of a molecular tree. These crowd out conservation focuses on endangered taxa of major divergent morphology. Examples of cryptic species are given by King and Hanner (1998); Colborn et al. (2001); and Stuart et al. (2006); and that of cryptic genera by Brown and De Jonckheere (1999); and Gontcharov and Melkonian (2005). Particularly problematic (Rubinoff et al. 2006) when not shored up by supportive expressed traits are structuralistic taxa generated using the presently much touted DNA barcoding (Jarman and Elliott 2000; Hart et al. 2003; Molbo et al. 2003; Lee and Foighil 2004; Hebert and Gregory 2005; Kress et al. 2005; Kuusela et al. 2008; Buhay 2009).

There are practices associated with phylogenetics that must be rejected for a new systematics to truly conciliate taxonomic methods that yield disparate results, especially the following: (1) Shared ancestors are not named at the same rank as their derivative exemplars in phylogenetics because this would result in paraphyletic groups (Knox 1998; Stuessy 2009), and nodes are simply place holders for the next higher inclusive rank. Thus, if followed to an extreme, an alternative view is possible that species do not disappear at all but their lines are bunched as skeins into the “shared ancestor” of a higher rank. There is no evidence in a phylogenetic classification, or a cladogram, or in the evolutionary analysis that generated the cladogram, against a species surviving a speciation event or even of immutability of species. (2) Mapping of traits on cladograms (Cunningham et al. 1998) is commonly referred to as instances of evolutionary change, yet traits do not evolve, species do (Dobzhansky 1956: 340; Bowler 1989: 345; Hickey 2000; Farjon 2007; Jablonski 2007; van Wyk 2007), an extreme reductionism (McShea 2005). Thus, trait changes mapped on cladograms may be used to infer only microevolution and not macroevolution (one taxon evolving from another at the same rank or lower), yielding a microevolutionary rather than macroevolutionary classification. Modeling descent with modification of taxa is avoided. Mapping of morphological traits or biogeographic distributions on cladograms is an attempt to transform evolutionary analysis from hypothesis and theory to lemma and theorem, i.e., from both deduction and induction (Cain 1959) to deduction only. (3) Classification by holophyly (strict phylogenetic monophyly) is artificial and leads to degenerate (as a return to absolutism) nonevolutionary classifications. Holophyly has no ontological basis as a process in nature (Assis and Rieppel 2010), that is, it is not refutable and so is not a scientific hypothesis. It is ostensibly used for simplifying taxonomy, but in doing so requires one to lump and split taxa that in any way appear to represent macroevolution in classification. Holophyly clearly eliminates representation of ancestor–descendant evolution in classification. Curiously, the last three points (apparent immutability of species, microevolution acceptable but not macroevolution, and avoidance of any implication of macroevolution) are quite those of “scientific creationism” (Poole 1990: 106), or phylogenetic baraminology (Gishtick 2006), which uses phylogenetic software to group diachronic skeins of unbranched lineages of single species, and do not instill confidence.

According to Dewey (1909: 90, 92, 96), Darwinian logic and empiricism is opposed to and replaces the ancient but long-regnant Greek philosophy of a transcendent first cause with progressive organization to a final perfect form, where pre-Darwinian science was “compelled to aim at realities lying behind and beyond the processes of nature. . . .” Nowadays, Dewey averred, “in the twilight of intellectual transition” there are new, intellectually atavistic, absolutist technical

philosophies that abstract “some aspect of the existing course of events in order to reduplicate it as a petrified eternal principle to explain the very changes of which it is the formalization.” Likewise, Jaynes ([1990] 2000: 441), in explaining the attractions of modern “scientific mythologies” as opposed to his admittedly controversial psychohistorical inferences, pointed out that “this totality is obtained not by actually explaining everything, but by an encasement of its activity, a severe and absolute restriction of attention, such that everything that is not explained is not in view.” The present article suggests that, for phylogenetics, the ancestor–descendant dimension is that which is neither explained nor is in view.

Summary

This is a call for serious reappraisal of modern systematics. Some decades ago there was a “paradigm change,” and taxonomists were encouraged to reject theories as just-so stories, redefine evolution as relationships on a cladogram, reframe evolution as changes in traits not taxa, abandon scientific induction in favor of hypothetico-deductivism, and revile as mere “intuition” the results of 250 years of taxonomic expertise and discursive reasoning. It is time to consider a total rejection of structuralism in systematics.

Phylogenetics is neither science nor mathematics—it is structuralism. It relies on hidden causes, and unnamed and unobserved entities in its explanations. It does not use hypothesis and theory, but lemmas and theorems. Mathematics is likewise deductively based but is consistent. Phylogenetics is inconsistent in ignoring, in fact, being unable to deal with the ancestor–descendant and diachronic dimension of evolution. An example of inconsistency is the use in classification of holophyly (strict phylogenetic monophyly). In sister-group terms, holophyly is the principle that one taxon cannot be nested within taxa of the same or higher rank; this is almost understandable, as nesting implies a hierarchy of somehow smaller or less significant things. Nevertheless, in ancestor–descendant terms, holophyly is the principle that one taxon cannot give rise to another taxon of the same or higher rank; palpably ridiculous because it goes against fact. Phylogenetics, in addition, bases classifications on patterns of selected data about evolution, not on theories about evolution. Cladograms are neither hypotheses nor theories because they do not directly detail possible causal relationships of natural processes that can be investigated and falsified, or supported by additional facts (Cleland 2001). Phylogenetic patterns are facts, being evidence of processes involved in the natural generation of species and higher taxa for a particular group. Interesting and helpful evidence, but facts are not theories.

Phylogenetics rejects forming theories using evidence and induction. Instead it treats patterns of evidence of the process of macroevolution as the phenomenon of evolution itself, and

uses deduction alone to form what are essentially apodictic theorems, avoiding theories of process in nature. Following Thomas Aquinas, when one has the correct first principles, all deductions must be correct (Chesterton [1933] 1956: 154).

This problem is inherent in structuralism, a “content-free” methodology common in linguistics, anthropology, psychology, and other areas, intended to replace empiricism. Structuralism attempts to introduce an element of “hard science” into non-mathematical and non-physics-based fields. This is done by identifying basic patterns that may be taken as axiomatic or irreducible first principles. In phylogenetics, the well-supported structure of the dichotomous tree is “saved” by rejecting all theory-based ancestor–descendant relationships in favor of a forced sister-group parenthetical nesting of exemplars. Internal consistency of the method is aided by administration of the principle of holophyly (strict phylogenetic monophyly). The statistical certainty or near-certainty of patterns of nested exemplars in molecular systematics is “saved” by ending analysis at the level of the nested exemplars, rejecting induction of process-based theories of ancestor–descendant relationships from those evidential patterns and from other data. Phylogenetic analytic methods of clustering are innocent and can be powerful, but the interpretation of the results (as pattern equals evolution and classification must follow such patterns) is not just flawed but is non-science.

Structuralist thinking necessarily eliminates any reflection of macroevolution in classification. The “tree” of life has no scientific realism or theoretic substance (i.e., cladograms are non-haeccetistic) because nodes are not diagnosably named, and the dendrogram is just a visual aid for often complex evidential patterns of nested exemplars. The introduction of other, less certain data or theories (e.g., from morphometrics, fossils, cytology, biogeography, chemistry, development) as additional evidence for scientific induction of evolutionary process involving descent with modification of taxa would collapse the pattern-based statistical certainty of molecular cladograms. Thus, in cladistics, all data outside the data set that are relevant to macroevolutionary theory are “mapped” on the dendrogram or in some other way relegated to the fundamental structure of the cladogram. This is not science.

Important taxa in conservation and biodiversity research are being synonymized as a kind of epistemological extinction. Their identity is often scrambled intellectually by transfer into disparate and heterogenous groups, or to those that are molecularly diagnosed, or they are buried among molecular cryptic species, genera, and families. Without scientific names for macroevolutionarily significant taxa, conservation efforts are confounded.

An immediate return is urged to the practice of process theory-based evolutionary systematics. This recovery involves using all evidence, including both sister-group and ancestor–

descendant (stem-group) analysis, marking the importance of both similarity and difference, and using both induction and deduction to form theories of evolution of groups upon which a robust and responsible classification can be based. Pluralistic taxonomy is not easy and its results are not certain, but it is scientific. It is a challenge that can be aided by modern methods of non-ultrametric (i.e., parsimony or Bayesian) cluster analysis, but never in the context of structuralism.

Acknowledgments

I dedicate this article to the patient and helpful spirits on the Taxacom listserver, *sine qua non*. I thank P. M. Eckel for her abiding support, *cum qua omnes*. R. Mesibov and E. Hörandl contributed valuable comments on a draft. I appreciate the continued support of the Missouri Botanical Garden for this research. Reprints of the author’s publications cited in this paper are available at <http://www.mobot.org/plantscience/resbot/3Repr.htm>.

References

- Aczel A (2007) *The Artist and the Mathematician: The Story of Nicolas Bourbaki, the Genius Mathematician Who Never Existed*. London: High Stakes.
- Assis LCS, Rieppel O (2010) Are monophyly and synapomorphy the same or different? Revisiting the role of morphology in phylogenetics. *Cladistics* 26: 1–9.
- Aubin D (1997) The withering immortality of Nicolas Bourbaki: A cultural connector at the confluence of mathematics, structuralism, and the Oulipo in France. *Science in Context* 10: 297–342.
- Avisé JC (2000) Cladists in wonderland. *Evolution* 54: 1828–1832.
- Balzer W, Moulines CU, Sneed JD (1987) *An Architectonic for Science: The Structuralist Approach*. Dordrecht: Reidel.
- Barry P (2002) *Structuralism. Beginning Theory: An Introduction to Literary and Cultural Theory*. Manchester, UK: Manchester University Press.
- Batten D, Salthe S, Boschetti F (2008) Visions of evolution: Self-organization proposes what natural selection disposes. *Biological Theory* 3: 17–29.
- Beatty J (1994) Theoretical pluralism in biology, including systematics. In: *Interpreting the Hierarchy of Nature* (Grande L, Rieppel O, eds), 33–60. San Diego, CA: Academic Press.
- Bell JL (1981) Category theory and the foundations of mathematics. *British Journal for the Philosophy of Science* 32: 349–358.
- Bessey CE (1915) The phylogenetic taxonomy of flowering plants. *Annals of the Missouri Botanical Garden* 2: 109–233.
- Bock WJ (2004) Explanations in systematics. In: *Milestones in Systematics* (Systematics Association Special Vol. 67) (Williams DM, Forey PL, eds), 49–56. London: CRC Press.
- Bok C (2001) *Pataphysics: The Poetics of an Imaginary Science*. Evanston, IL: Northwestern University Press.
- Bowler PJ (1989) *Evolution: The History of an Idea*. Berkeley, CA: University of California Press.
- Brading K, Landry E (2006) Scientific structuralism: Presentation and representation. *Philosophy of Science* 73: 571–581.
- Brower AVZ (2000) Evolution is not a necessary assumption of cladistics. *Cladistics* 16: 143–154.
- Brown S, De Jonckheere JF (1999) A re-evaluation of the amoeba genus *Vahlkampfia* based on SSUrDNA sequences. *European Journal of Protistology* 35: 49–54.
- Brummitt RK (2003) Further dogged defense of paraphyletic taxa. *Taxon* 52: 803–804.
- Brummitt RK (2006) Am I a bony fish? *Taxon* 55: 268–269.

- Buhay JE (2009) "COI-like" sequences are becoming problematic in molecular systematic and DNA barcoding studies. *Journal of Crustacean Biology* 29: 96–110.
- Burke J (1995) *The Day the Universe Changed: How Galileo's Telescope Changed the Truth and Other Events in History that Dramatically Altered Our Understanding of the World*. New York: Back Bay Books.
- Cain AJ (1959) Deductive and inductive methods in post-Linnaean taxonomy. *Proceedings of the Linnean Society London* 170: 185–217.
- Carle FL (1995) Evolution, taxonomy, and biogeography of ancient Gondwanian libelluloides, with comments on anisopteroïd evolution and phylogenetic systematics (Anisoptera: Libelluloidea). *Odonatologica* 24: 383–506.
- Cavalier-Smith T (2010) Deep phylogeny, ancestral groups and the four ages of life. *Philosophical Transactions of the Royal Society B* 365: 111–132.
- Chesterton GK ([1933] 1956) *St. Thomas Aquinas*. Garden City, NY: Doubleday.
- Cleland CE (2001) Historical science, experimental science, and the scientific method. *Geology* 29: 987–990.
- Cohen J (1994) The world is round ($p < .05$). *American Psychologist* 49: 997–1003.
- Colborn J, Crabtree RE, Shaklee JB, Pfeiler E, Bowen BW (2001) The evolutionary enigma of bonefishes (*Albula* spp.): Cryptic species and ancient separations in a globally distributed shorefish. *Evolution* 55: 807–820.
- Cunningham CW, Omland KE, Oakley TH (1998) Reconstructing ancestral character states: A critical reappraisal. *Trends in Ecology and Evolution* 13: 361–366.
- Dayrat B (2005) Ancestor–descendant relationships and the reconstruction of the tree of life. *Paleobiology* 31: 347–353.
- Dewey J (1909) The influence of Darwinism on philosophy. *Popular Science Monthly* 75: 90–98.
- Dewey J (1950) *Reconstruction in Philosophy. With a New Introduction*. New York: Mentor Book, New American Library.
- Dobzhansky T (1956) What is an adaptive trait? *American Naturalist* 90: 337–347.
- Dosse F (1998) *History of Structuralism, Vol. 1: The Rising Sign 1945–1966*. Minneapolis, MN: University of Minnesota Press.
- Farjon A (2007) In defense of a conifer taxonomy which recognizes evolution. *Taxon* 56: 639–641.
- Farris JS, Kluge AG, Eckardt M (1970) A numerical approach to phylogenetic systematics. *Journal of Zoology* 19: 172–189.
- Frost-Arnold G (2010) The no-miracles argument for realism: Inference to an unacceptable explanation. *Philosophy of Science* 77: 35–58.
- Funk DJ, Omland KE (2003) Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology, Evolution and Systematics* 34: 397–423.
- Giere RN (2005) Modest evolutionary naturalism. *Biological Theory* 1: 52–60.
- Giere RN (2009) Essay review: Scientific representation and empiricist structuralism. *Philosophy of Science* 76: 101–111.
- Gigerenzer G (2007) *Gut Feelings: The Intelligence of the Unconscious*. New York: Viking Penguin.
- Gigerenzer G, Swijtink Z, Porter T, Daston L, Beatty J, Küger L (1989) *The Empire of Chance: How Probability Changed Science and Everyday Life*. Cambridge: Cambridge University Press.
- Gilbert SF, Opitz JM, Raff RA (1996) Resynthesizing evolutionary and developmental biology. *Developmental Biology* 173: 357–372.
- Gishlick A (2006) Baraminology. *Reports of the National Center for Science Education* 26(4): 17–21. <http://ncse.com/rncse/26/4/baraminology> (accessed September 2, 2010).
- Gontcharov AA, Melkonian M (2005) Molecular phylogeny of *Staurostrum* Meyen ex Ralfs and related genera (Zygnematophyceae, Streptophyta) based on coding and noncoding rDNA sequence comparisons. *Journal of Phycology* 41: 887–899.
- Gould SJ (1970) Dollo on Dollo's Law: Irreversibility and the status of evolutionary laws. *Journal of the History of Biology* 3: 189–212.
- Gould SJ (2002) *The Structure of Evolutionary Theory*. Cambridge, MA: Belknap Press of Harvard University Press.
- Grant V (2003) Incongruence between cladistic and taxonomic systems. *American Journal of Botany* 90: 1263–1270.
- Griffiths PE (1996) Darwinism, process structuralism, and natural kinds. *Philosophy of Science* 63: S1–S9.
- Hair JF Jr, Anderson RE, Tatham RL (1987) *Multivariate Data Analysis with Readings*. New York: Macmillan.
- Hanc J, Tuleja S, Hancova M (2003) Simple derivation of Newtonian mechanics from the principle of least action. *American Journal of Physics* 71: 386–391.
- Hart MW, Byrne M, Johnson SL (2003) *Patriella pseudoexigua* (Asteroidea: Asterinidae): A cryptic species complex revealed by molecular and embryological analyses. *Journal of the Marine Biology Association UK* 83: 1109–1116.
- Hebert PDN, Gregory T (2005) The promise of DNA barcoding for taxonomy. *Systematic Biology* 54: 842.
- Hickey DA (2000) The evolution of sex and recombination. In: *Evolutionary Genetics: From Molecules to Morphology* (Singh RS, Krimbas CB, eds), 314–330. Cambridge: Cambridge University Press.
- Holton G (1993) *Science and Anti-Science*. Cambridge, MA: Harvard University Press.
- Hörandl E (2006) Paraphyletic versus monophyletic taxa: Evolutionary versus cladistic classifications. *Taxon* 55: 564–570.
- Hörandl E (2007) Neglecting evolution is bad taxonomy. *Taxon* 56: 1–5.
- Hörandl E, Stuessy TF (2010) Paraphyletic groups are natural evolutionary units and acceptable in biological classification. *Taxon* 59: 1641–1653.
- Hull DL (2005) The essence of scientific theories. *Biological Theory* 1: 17–19.
- Hutchinson JMC, Gigerenzer G (2005) Simple heuristics and rules of thumb: Where psychologists and behavioural biologists might meet. *Behavioural Processes* 69: 97–124.
- Jablonski D (2007) Scale and hierarchy in macroevolution. *Palaeontology* 50: 87–109.
- Jacquette D (1996) On defoliating Meinong's Jungle. *Axiomathes* 1–2: 17–42.
- Jardine N, Sibson R (1971) *Mathematical Taxonomy*. London: John Wiley.
- Jarman SN, Elliott NG (2000) DNA evidence for morphological and cryptic Cenozoic speciations in the Anaspidae, "living fossils" from the Triassic. *Journal of Evolutionary Biology* 13: 624–633.
- Jaynes J ([1990] 2000) *The Origin of Consciousness in the Breakdown of the Bicameral Mind*. New York: Houghton-Mifflin, Mariner Books.
- King JL, Hanner R (1998) Cryptic species in a "living fossil" lineage: Taxonomic and phylogenetic relationships within the genus *Lepidurus* (Crustacea: Notostraca) in North America. *Molecular Phylogenetics and Evolution* 10: 23–36.
- Kline M (1980) *Mathematics: The Loss of Certainty*. Oxford: Oxford University Press.
- Knox EB (1998) The use of hierarchies as organizational models in systematics. *Biological Journal of the Linnean Society of London* 63: 1–49.
- Kress WJ, Wurdack KJ, Zimmer EA, Weigt LA, Janzen DH (2005) Use of DNA barcodes to identify flowering plants. *Proceedings of the National Academy of Sciences USA* 102: 8369–8374.
- Kuhn T (1970) *The Structure of Scientific Revolutions*, 2nd ed. Chicago: University of Chicago Press.

- Kuusela J, Ziętara MS, Lumme J (2008) Description of three new European cryptic species of *Gyrodactylus* Nordmann, 1832 supported by nuclear and mitochondrial phylogenetic characterization. *Acta Parasitologica* 53: 120–126.
- Lee T, Foighil DÓ (2004) Hidden Floridian biodiversity: Mitochondrial and nuclear gene trees reveal four cryptic species within the scorched mussel, *Brachidontes exustus*, species complex. *Molecular Ecology* 13: 3527–3542.
- Lee M, Wolsan M (2004) Integration, individuality, and species concepts. *Biology and Philosophy* 17: 651–660.
- Lévi-Strauss C ([1949] 1969) *The Elementary Structures of Kinship* (Needham R, trans). Boston: Beacon Press.
- Lewis H (1962) Catastrophic selection as a factor in speciation. *Evolution* 16: 257–271.
- Lewis H (1966) Speciation in flowering plants. *Science* 152: 167–172.
- Lewis H, Roberts MR (1956) The origin of *Clarkia lingulata*. *Evolution* 10: 126–138.
- Lopez PA (1990) Closet pataphysics. <http://www.paulavion.com/pata/cpat.html> (accessed September 2, 2010).
- Matthews P (2001) *A Short History of Structural Linguistics*. Cambridge: Cambridge University Press.
- Mayden RL (1997) A hierarchy of species concepts: The denouement in the sage of the species problem. In: *Species: The Units of Biodiversity* (Claridge MR, Dawah HA, Wilson MR, eds), 381–424. London: Chapman & Hall.
- Mayer MS, Beseda L (2010) Reconciling taxonomy and phylogeny in the *Streptanthus glandulosus* complex (Brassicaceae). *Annals of the Missouri Botanical Garden* 97: 106–116.
- Mayr E, Bock WJ (2002) Classifications and other ordering systems. *Journal of Zoological Evolutionary Research* 40: 169–194.
- McShea DW (2005) The evolution of complexity without natural selection, a possible large-scale trend of the fourth kind. *Paleobiology* 31: 146–156.
- Mercier H, Sperber D (2011) Why do humans reason? Arguments for an argumentative theory. *Behavioral and Brain Sciences* 34: 57–74.
- Molbo D, Machado CA, Sevenster JG, Keller L, Herre EA (2003) Cryptic species of fig-pollinating wasps: Implications for the evolution of the fig-wasp mutualism, sex allocation, and precision of adaptation. *Proceedings of the National Academy of Sciences USA* 100: 5867–5872.
- Mooi RD, Gill AC (2010) Phylogenies without synapomorphies—a crisis in fish systematics: Time to show some character. *Zootaxa* 2450: 26–40.
- Nelson G (1989) Cladistics and evolutionary models. *Cladistics* 5: 275–289.
- Ogrodnik B (2004) The metaphysical dimension of optimizing principles. *Conrescence: Australasian Journal for Process Thought* 5: 1–5.
- Okasha S (2003) Does the concept of “clade selection” make sense? *Philosophy of Science* 70: 739–751.
- O’Keefe FR, Sander PM (1999) Paleontological paradigms and inferences of phylogenetic pattern: A case study. *Paleobiology* 25: 518–533.
- Oppenheimer JR (1957) *Physics in the contemporary world*. In: *Great Essays in Science* (Gardner M, ed), 188–204. New York: Washington Square Press.
- Overton WF (1975) General systems, structure and development. In: *Structure and Transformation: Developmental and Historical Aspects*, Vol. 3 (Riegel K, Rosenwald GC, eds), 61–81. New York: Wiley.
- Padial JM, Miralles A, De la Riva I, Vences M (2010) The integrative future of taxonomy. *Frontiers in Zoology* 7: 1–16. <http://www.frontiersinzoology.com/content/7/1/16> (accessed September 2, 2010).
- Pelster PB, Nordenstam B, Kadereit JW, Watson LE (2007) An ITS phylogeny of tribe Senecioneae (Asteraceae) and a new delimitation of *Senecio* L. *Taxon* 56: 1077–1104.
- Piaget J (1970) *Structuralism*. New York: Basic Books.
- Poole M (1990) *A Guide to Science and Belief*. Oxford: Lion Publishing.
- Popper KR (1959) *The Logic of Scientific Discovery*. New York: Basic Books.
- Qiu Y-L, Chase MW, Les DH, Parks CR (1993) Molecular phylogenetics of the Magnoliidae: Cladistic analyses of nucleotide sequences of the plastid gene *rbcL*. *Annals of the Missouri Botanical Garden* 80: 587–606.
- Racheli L, Racheli T (2006) Phylogenetic hypothesis and classification: Theoretical and methodological issues with reference to some studies on Saturniidae (Lepidoptera: Saturniidae). *SHILAP Revista de Lepidopterología* 34(133): 5–12.
- Rees M (2000) *Just Six Numbers: The Deep Forces that Shape the Universe*. New York: Basic Books.
- Ridley M (1996) *Evolution*, 2nd ed. Cambridge, MA: Blackwell Science.
- Rieppel O (2010) The series, the network, and the tree: Changing metaphors of order in nature. *Biology and Philosophy* 25: 475–496.
- Rieppel O (2011) Willi Hennig’s dichotomization of nature. *Cladistics* 27: 103–112.
- Rieppel O, Grande L (1994) Summary and comments on systematic pattern and evolutionary process. In: *Interpreting the Hierarchy of Nature* (Grande L, Rieppel O, eds), 227–255. San Diego, CA: Academic Press.
- Rieseberg LH, Brouillet L (1994) Are many plant species paraphyletic? *Taxon* 43: 21–32.
- Rubinoff D, Cameron S, Will K (2006) A genomic perspective on the shortcomings of mitochondrial DNA for “barcoding” identification. *Journal of Heredity* 97: 581–594.
- Sardar Z (2000) *Thomas Kuhn and the Science Wars*. Cambridge: Icon Books.
- Schmidt H-J (2008) Structuralism in physics. In: *Stanford Encyclopedia of Philosophy*, Spring ed (Zalta EN, ed) //html: plato.stanford.edu/archives/spr2008/entries/physics-structuralism
- Schneider H, Smith AR, Pryer KM (2009) Is morphology really at odds with molecules in estimating fern phylogeny? *Systematic Botany* 34: 455–475.
- Scott-Ram NR (1990) *Transformed Cladistics, Taxonomy and Evolution*. Cambridge, UK: Cambridge University Press.
- Sneath PHA (1995) Thirty years of numerical taxonomy. *Systematic Biology* 44: 281–298.
- Sober E (2008) *Evidence and Evolution: The Logic Behind the Science*. Cambridge, UK: Cambridge University Press.
- Soltis DE, Soltis PS, Nickrent DL, Johnson LA, Hahn WJ, Hoot SB, Sweere JA, Kuzoff RK, Kron DA, Chase MW, Swensen SM, Zimmer EA, Chaw S-M, Gillespie LJ, Kress WJ, Sytsma KJ (1997) Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. *Annals of the Missouri Botanical Garden* 84: 1–49.
- Sosef MSM (1997) Hierarchical models, reticulate evolution and the inevitability of paraphyletic supraspecific taxa. *Taxon* 46: 75–85.
- Stein G (1937) *Everybody’s Autobiography*. New York: Random House.
- Stuart BL, Inger RF, Voris HK (2006) High level of cryptic species diversity revealed by sympatric lineages of Southeast Asian forest frogs. *Biological Letters* 2: 470–474.
- Stuessy TF (2009) Paradigms in biological classification (1707–2007): Has anything really changed? *Taxon* 58: 68–76.
- Stuessy TF, Crawford DJ, Anderson GJ, Jensen RJ (1998) Systematics, biogeography and conservation of Lactoridaceae. *Perspectives in Plant Ecology, Evolution and Systematics* 1: 267–290.
- Stuessy TF, König C (2008) Patrocladistic classification. *Taxon* 57: 594–601.
- van Fraassen BD (2007) Structuralism(s) about science: Some common problems. *Proceedings of the Aristotelian Society, Supplement* 81: 45–61.
- van Wyk AE (2007) The end justifies the means. *Taxon* 56: 645–648.
- Vasek FC (1968) The relationships of two ecologically marginal sympatric *Clarkia* populations. *American Naturalist* 102: 25–40.
- Wagner WH Jr (1952) The fern genus *Diellia*: Its structure, affinities and taxonomy. *University of California Publications in Botany* 26: 1–212 (pl. 1–21).

- Wilkinson L, Rosenthal R, Abelson R, Cohen J, Aiken L, Appelbaum M, Boodoo G, Kenny DA, Kraemer H, Rubin D, Thompson B, Wainer H (1999) Statistical methods in psychology journals: Guidelines and explanations. *American Psychologist* 54: 594–604.
- Williams DM, Ebach MC (2007) *Foundations of Systematics and Biogeography*. New York: Springer.
- Zander RH (2007a) Nine easy steps for constructing reliable trees from published phylogenetic analyses. *Annals of the Missouri Botanical Garden* 94: 691–709.
- Zander RH (2007b) When biodiversity study and systematics diverge. *Biodiversity* 8: 43–48.
- Zander RH (2007c) Paraphyly and the species concept, a reply to Ebach & al. *Taxon* 56: 642–644.
- Zander RH (2008a) Statistical evaluation of the clade “Rhabdoweisiaceae.” *Bryologist* 111: 292–301.
- Zander RH (2008b) Evolutionary inferences from non-monophyly of traditional taxa on molecular trees. *Taxon* 57: 1182–1188.
- Zander RH (2009) Evolutionary analysis of five bryophyte families using virtual fossils. *Anales del Jardín Botánico de Madrid* 66: 263–277.
- Zander RH (2010) Taxon mapping exemplifies punctuated equilibrium and atavistic saltation. *Plant Systematics and Evolution* 286: 69–90.

This is an author-generated reprint. The text pagination is exact.
For an official journal PDF reprint, contact the author at
richard.zander@mobot.org or visit the journal's Web site.