

Paraphyly and the species concept, a reply to Ebach & al.

Several recent Letters to the Editor and other *Taxon* papers have questioned the evolutionary base of modern phylogenetics (Alexander, 2006; Hörandl, 2006, 2007), promoted the use of paraphyly in classification when appropriate (Sosef, 1997; Brummitt & Sosef, 1998; Brummitt, 2003, 2006; Dias & al., 2005; Nordal & Stedje, 2005), or downgraded the primacy of molecularly based classifications (Lee, 2006). Others have provided rebuttals (Nelson & al., 2003; Potter & Freudenstein, 2005; Williams & al., 2005; Ebach & al., 2006). My comments generally support aspects of what has been written critical of modern phylogenetics and its use in classification, but also expand on questioning the value of monophyly itself when used to extend an inferred genealogy to concepts of taxa.

The traditional species concept is commonly accepted as tripartite: (1) a biological species concept that is appropriate for well-studied species, like birds, with a distinct gene pool or potentially interbreeding populations and generally clearly marked morphological differences associated with habitat, but is problematic in cryptic species; (2) an ecological species concept (van Valen, 1976; Andersson, 1990, 1992; Bremer & Eriksson, 1992) that is appropriate for organisms that may or may not have interbreeding populations but, when taken as a unit, have essentially identical morphotypes, reproductive strategies, and environmental preferences and interactions; and (3) an “alpha taxonomic” concept appropriate for species that are expected by experts to eventually fit a biological or ecological species concept when better studied. All three concepts provide basic taxonomic units that react alike in experimental studies or in nature and are of practical use in science (Raven, 1974).

The ecological species concept as basic taxonomic unit is not the same as the basic evolutionary unit, which is usually considered to be one population as affected by the fitness of its individuals due to (1) selection (selectionistic interpretation of evolution; e.g., Gillespie, 1991; Pianka, 2000), or (2) rapid decline in population size (bottlenecking) followed by genetic drift that changes relative numbers of mutations in the population (neutralistic interpretation of evolution; e.g., Nei, 2005). The second interpretation is supported by the recent discovery of massive though gradual changes in apparently neutral DNA bases over time, suggesting that selection may be less important than neutral exon changes in affecting the phenotype.

The selectionistic and neutralistic theories of evolution have bearing on the different approaches to classification and the paraphyly debate. It is reasonable to assume that classifications should reflect descent with

modification. But, following Alexander’s (2006) arguments, descent of what, and exactly what is modified? Traditional classification is a best attempt at designating as basic units of taxonomy, groups of populations with similar phenotype, reproductive behavior, and manner of interaction with the environment (“biorole”). Morphological traits are important in traditional classification when they are very unusual or differentially functional. Phylogenetic analysis, however, has introduced three new concepts of taxa (presented as OTUs in cladograms), based on evidence from either morphology, nuclear DNA, or organellar DNA.

(1) Phylogenetic analysis of morphology produces a parsimonious tree involving potentially all apparently independent traits of all taxa in the dataset. What descends is not the traditional species but a construct based on all traits used in the tree. Evolutionary modification is expressed by a series of morphological state changes extracted from a miscellany of traits, which may or may not have selective advantages. Note here that if there are surviving ancestors, any morphological autapomorphy needs to be regarded as a synapomorphy with reversal or change in the sister taxon, an increase in tree length with no change in topology. All but one terminal taxon can be, theoretically, a surviving ancestor.

(2) Phylogenetic analysis of nuclear DNA tracks phylogeny by assuming the biological species concept and asking the question: “Of any three OTUs, which two probabilistically share a most recent event of genetic isolation?” With any event of isolation, neutral mutations accumulate in both the newly isolated population and the ancestral population. The two changing populations may be called “sister taxa” as they arise from the inferred condition of the ancestral population prior to the split. This implies monophyly involving three taxa, two new sister taxa and the ancestral taxon when the latter did not disappear (Hörandl, 2006). The OTU, representing that which descends, is either a continuously and gradually mutating ancestral line or the separately mutating newly isolated lineage. Phenotypic interactions with the environment are not tracked except as miscellaneous morphological traits mapped on the molecular tree. The OTU does not represent the traditional species but a freely interbreeding population, in which any recombinant mutation may merge with other lines in the gene pool. Populations of the species that are genetically isolated though remaining nearly identical in phenome and niche are not evaluated or are considered different, cryptic species. In classification, they must be named as separate lineages, otherwise monophyly and the biological species concept are not respected.

(3) Phylogenetic analysis of matrilineally inherited loci of organellar, chloroplast and mitochondrial DNA, involves separately mutating descendents of an individual. All progeny accumulate neutral mutations without recombination and are tracked as to their pedigree. The OTU in this case does not represent the traditional taxon but an inferred line of descent of individuals genetically isolated by birth. Using loci at a high enough rate of mutation, any individual as OTU may be termed a basic unit of classification, reflecting a kind of fractal speciation.

Although the results of the phylogenetic analyses would, of course, be of value in creating a classification reflecting descent with modification of, for instance, inferred biroles, none directly track biroles. Molecular techniques, focusing largely on evolutionarily neutral or nearly neutral nucleotide base changes that occur in all lineages, cannot distinguish between surviving ancestors and new lineages with different functional evolution, nor can they deal directly with intraspecific genetic isolation. Given that new taxa may arise out of any population, and, given that there may be much phylogenetic structure in, at least, plant taxa, then most newly evolved taxa must be phylogenetically embedded within a larger ancestral taxon. Most speciation must therefore involve paraphyly. By extension, paraphyly must be expected among genera and families. For species consisting of many populations, the patristic distance between two isolated populations of that species may in fact be greater than that between one of these and a new species originating from a third population.

Given that OTUs resulting from analysis of morphology, nuclear DNA, or organellar DNA represent three different hypothetical descending entities (apples, oranges, lemons) and changing traits, combining all data as “total evidence” yields OTUs that represent no clear hypotheses of what is descending and what is being modified (fruit salad). Yet, phylogenetic analyses can be valuable when OTUs are interpreted on the basis of what they are or have become. Of greater concern, however, is the chaos in classification caused by modern insistence on avoiding paraphyly, which is ultimately only supported by the wrenching notion of considering taxonomically separate those surviving ancestral populations or even individuals merely showing continuing mutations of neutral loci. Theoretically, they all do or will.

A more valuable classification would reflect an estimate, to whatever extent possible as judged from phenotype and environment, of functional evolution (Pianka, 2000). Abundant mutation of evolutionarily neutral loci is well documented and is convenient for phylogenetic analysis, but descent of populations with modification of traits involving adaptation and fitness, whether conferred by disruptive selection or resulting from bottle-necking and genetic drift, can only be inferred as hypotheses after

combing through all evidence and rigorous testing. Evaluation of descent with modification involving functional evolution is a difficult and intellectually taxing study (e.g., Robinson, 1990; Hearn, 2006), while phylogenetic analysis, perhaps with morphology mapped to the molecular tree, is relatively easy. Even if many organismal structures have unknown function, the morphology as clue to phenome/environment interaction should characterize the taxon. Although the analysis of evolutionary and developmental process has been accused of being assumption- and theory-laden (e.g., Cracraft, 2005), testing theory is the foundation of science. Hörandl (2007) gave a fine comparison of the major features distinguishing cladistic and evolutionary classification.

According to Blomberg (1987), there are two approaches to historical criticism: evidentialism and presuppositionalism. The evidentialist applies accepted historical criteria to demonstrate reliability. The presuppositionalist first assumes reliability of data and method, then attempts to show that the data and method generate a consistent whole, confirming the presuppositions. It is the consistent whole of the cladogram, being the internal simplicity of phylogeny isolated from evolutionary theory, that has been substituted for efforts at understanding evolution that systematists tragically abandoned thirty years ago, namely “biosystematics” associated with the Modern Synthesis. The problem is global in that the evolutionary dimension in systematics should allow biodiversity studies to follow and to some extent predict changes in niches and the taxa that fill them. This is not the case with systematics now often defined as phylogenetics with applications in classification.

In sum, monophyly is convenient for developing a simple, artificial classification from dichotomous trees of a medley of morphological traits parsimoniously distributed in cladograms, or of molecular traits accumulated along lines of inferred individual pedigree or population relationships. In the context of molecular phylogenetic analysis, however, it enforces the biological species concept. Any but the most geographically restricted species and higher taxa can produce new phenotypes with new environmental strategies from anywhere out of a commonly complex internal phylogenetic structure, and evolutionary classification should reflect this natural paraphyly. The present crisis in biodiversity clearly involves strong differential selective pressures. This calls for a return to process-oriented *diagnostic systematics* organized in part by the phylogenetic clustering properties of molecular genealogies of inferred populations and individuals. The theoretical details of evolution of the phenome through selection or even random fixation of traits among extant taxa in the dynamic context of the ecological species concept, is of greatest potential value in studying and preserving biodiversity.

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