

Conservation Systematics: The *Bufo boreas* Species Group

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Systematics and taxonomy play critical roles in conservation (May, 1990; Eldredge, 1992; Systematics Agenda, 2000, 1994a,b; Wheeler, 1995; Koch and Peterson, this volume; Minton, this volume). Taxonomic names are important for recognition and clear communication about the units to be conserved; conservation efforts have been compromised when taxonomy did not accurately reflect systematic relationships (e.g., Greig, 1979; Avise and Nelson, 1989; Daugherty et al., 1990; O'Brien and Mayr, 1991; Mishler, 1995; but see Zink and Kale, 1995). However, new developments in systematics and taxonomy that recognize, describe, and quantify organismic diversity have not been adequately incorporated into conservation programs. Extinction of the divergent island populations of tuataras (Daugherty et al., 1990; Finch and Lambert, 1996) is exemplary. Despite the description of subspecies occupying different islands, this diversity was ignored and several subspecies were allowed to go extinct because divergent tuatara lineages did not have the Linnaean rank of species. Furthermore, the remaining evolutionary diversity within the few extant tuatara subspecies is valuable for the conservation of organismic diversity because tuataras are not simply a distinct species group. In fact, the phylogenetic lineage, of which they are the sole representatives, is sister to a lineage that is represented by about 6,000 species of snakes, lizards, and amphisbaenians (May, 1990).

The major tasks of systematics (which includes taxonomy; Quicke, 1993) are to (1) classify organisms into species; (2) provide species names that are explicit, universal, and stable; and (3) combine species into the more inclusive categories of the Linnaean hierarchy (Futuyma, 1986). The general focus of systematics is to discover the genealogical relationships among the inclusive categories and describe patterns of evolutionary change (Futuyma, 1986). As a conservation biologist interested in systematics, my goals are to identify organismic units for conservation (whether they are species, Evolutionarily Significant Units [Ryder, 1986], or other units), describe and name these units, and quantify the divergence among them to assist in conservation efforts. My focus is similar to other systematists, but differs in the specific intent for conservation. Discovering relationships is critical because quantification of diversity depends on the pattern of evolutionary relationships. Deducing evolutionary processes from patterns of change is critical because it is the processes, as well as the end products (populations and individual organisms),

that must be conserved. Biologists who focus on conservation have coined the terms "conservation biology" (Soulé and Wilcox, 1980) and "conservation genetics" (Shonewald-Cox et al., 1983; Avise and Hamrick, 1996). In that sense, my focus is on "conservation systematics" and "conservation taxonomy."

The purpose of this essay is to describe how systematics and taxonomy can better address conservation issues in both theoretical and utilitarian ways. I begin with a discussion of organismic diversity and how systematics and Linnaean taxonomy have failed to meet the needed description and quantification of diversity for conservation purposes. I then argue that recognizing diversity is more critical than recognizing species, and I suggest how diversity can be incorporated into systematics using measures of phylogenetic diversity and phylogenetic taxonomy. In the final section, I suggest three utilitarian ways conservation systematics can incorporate diversity into management and politics: (1) set priorities for conservation; (2) reconstruct the Endangered Species Act (ESA); and (3) mitigate loss of total diversity by a procedure that identifies acceptable losses. To illustrate problems and solutions, I use examples from North American bufonids, especially the western toad (*Bufo boreas*) species group (Examples 1–3, below).

The Critical Role of Diversity

Diversity

The intent of both systematics and taxonomy is to describe organismic diversity in a general way ("systematics is the study of organismic diversity," Wiley, 1981). However, conservation biologists need to be more specific when quantifying diversity. Conservation biologists frequently are asked: (1) How divergent are two units/taxa from one another—is a subspecies or population of special interest really a different species? (2) Is a particular species/taxon made up of many diverse lineages that should have independent conservation programs or is it a single lineage that lacks diversity and can be managed as a single unit? (3) Are there genetic or taxonomic restrictions to translocating organisms? (4) Are the organisms in a particular U.S. state the same taxon/population as those that have been listed as endangered or threatened by another state or the Federal Government? (5) Is a species/population divergent enough for an expensive conservation program

to be biologically and politically defensible or should the money, time, and credibility of the conservation program be spent elsewhere? (6) Which species/taxa should have the highest conservation priority and how should those priorities be set? The answers to these questions require not only a delineation of the organismic units in question and an assessment of speciation, but also a quantification of diversity within and/or among such units.

Conservation depends on understanding many kinds of diversity, including organismic, ecological, climatic, and landscape diversity (Moss, 2000). However, the purpose of systematics and taxonomy is to describe organismic diversity, which will remain the focus of this essay. Because organismic diversity is a broad term, let me define my use in this essay. Organismic diversity is comprised of the different attributes or traits (e.g., molecular, biochemical, physiological [Spicer and Gaston, 1999], morphological, behavioral, etc.) that are passed down through evolutionary lineages and within individuals and populations. Because such traits are inherited, organisms that are closely related have a high probability of sharing many traits; those that are more distant will share few. Traits evolve through time; novel traits arise through random mutations and rearrangements of existing traits. Diversity is critical because it is the fuel for evolutionary change and essential for adaptation to changing environments. The extinction of any lineage represents not only the loss of novel traits but also the loss of knowledge about what kinds of traits, trait combinations, and evolutionary pathways are possible.

The ability to describe organismic diversity has increased dramatically in the last 10 years with advances in molecular systematics (e.g., Hillis et al., 1996; Smith and Wayne, 1996; Karp et al., 1998; Goebel et al., 1999; Hall, 2001). Unlike frequently used morphological characters, molecular characters not only recognize patterns of inheritance, but also recognize inherited diversity on a continuum from parent-offspring relationships to diversity within and among lineages as well as among higher taxa. Although the connection between specific molecular changes and the presence of a particular physiological, behavioral, or morphological trait is rarely known, the greater the degree of molecular divergence, the higher the probability that unique physiological, behavioral, or morphological traits have evolved by random chance alone. Thus, a calculus of divergence based on independently evolving molecular characters may provide an estimate of the probability of other divergent traits (e.g., physiological) that are not measurable at this time (Faith, 1992a,b, 2002; Crozier, 1997; but see Pearman, 2001). Another advantage of molecular phylogenetic analyses is that they identify genetic diversity even if they cannot unambiguously identify clades as specific taxonomic units in the Linnaean hierarchy (e.g., classes, genera, and species). But molecular data are not a panacea for describing diversity (Pritchard, 1999). For example, discriminating between gene and organismic lineages may be difficult (Neigel and Avise, 1986; Pamilo and Nei, 1988; Quinn et al., 1991; but see also Moore, 1995, 1997; Nichols, 2001) and rates of change may vary among lineages and genes (Wu and Li, 1985; Martin et al., 1992; Zhang and Ryder, 1995). These difficulties result in a discouraging sense that more data will always be needed to correctly identify phylogenetic relationships. However, molecular data continue to provide valuable insights even while better methods to collect, interpret, and analyze data are being developed to circumvent these problems. In spite of an explosion in the ability to identify and describe diversity, the incorporation of measures of diversity into systematics and taxonomy has been slow (Soltis and Gitzendanner, 1999).

Inadequacies in Systematics and Linnaean Taxonomy for Conservation

The Linnaean system (Linnaeus, 1737, and described in the codes of nomenclature: International Commission on Zoological Nomenclature, 1999; International Botanical Congress, 2000; International Association of Microbiological Societies, 1992) applies specific ranks to all lineages (e.g., class, order, family, genus, species, and variety) independent of the diversity within or among them. Ranks are an imprecise measure of diversity because they identify only a few categories in a world that can have a near infinite number of hierarchical levels. Even so, many conservation efforts are based on the species rank—it is seen as the fundamental unit of evolution and therefore as the fundamental unit for conservation (e.g., Wilson, 1992; Caughley and Gunn, 1996). However, conservation efforts based on any rank have resulted (and continue to result) in a critical loss of diversity. For example, conservation efforts have been inhibited by the lack of recognition of species (Greig, 1979; Daugherty et al., 1990), disagreement over the recognition of species (Daugherty et al., 1990; Sangster, 2000; see also Hille and Thiollay, 2000), arguments over the importance of hybridization (O'Brien et al., 1990; Lehman et al., 1991; Wayne and Jenks, 1991; Nowak, 1992; Roy et al., 1994, 1996), and a lack of understanding of the phylogenetic (genealogical) relationships among species (Avise and Nelson, 1989). Conservation efforts may also have been misplaced with programs for poorly defined taxa (e.g., Bowen and Karl, 1999; Karl and Bowen, 1999; Zink et al., 2000; but see also Pritchard, 1999; Grady and Quattro, 1999).

Conservation of diversity grounded on a species-based system is inadequate. Species definitions continue to abound (Mayden, 1997; Soltis and Gitzendanner, 1999; Wheeler and Meier, 2000; Hey, 2001) yet there is little consensus on what a species is (Cantino and de Queiroz, 2000; Barton, 2001). The species category is not defined on the basis of divergence, but frequently on the basis of qualities such as reproductive isolation (Biological Species Concept; Mayr, 1942, 1982, 1996), ability of mates to recognize one other (Recognition Species Concept; Paterson, 1985; Lambert and Spencer, 1995), occupation of an adaptive zone (Ecological Species Concept; Van Valen, 1976), and potential for phenotypic cohesion (Cohesion Species Concept; Templeton, 1989). Other species definitions are based primarily on the historical pattern of evolution including Evolutionary Species (lineages have their own evolutionary tendencies and historical fate; Simpson, 1961; Wiley, 1978), Plesiomorphic Species (lineages identified by a unique combination of characters even if uniquely derived characters have not evolved or are as yet undetected, Olmstead, 1995), and Phylogenetic Species (species are monophyletic groups, Mishler and Donoghue, 1982; or species are the smallest diagnosable clusters of individual organisms within which there is a parental pattern of ancestry and descent; Cracraft, 1983b; see also Goldstein et al., 2000, and Soltis and Gitzendanner, 1999, and references therein). Contention over which qualities or phylogenetic patterns are most appropriate for the delineation of species may further confound species-based conservation programs if accepted definitions change in time or vary among conservation agencies or legislative decisions. However, even if criteria for identifying species were not contentious and were uniformly applied, species-based conservation programs are problematic because the pattern and quantity of diversity are unique to each lineage and are not defined by rank (e.g., Karl and Bowen, 1999).

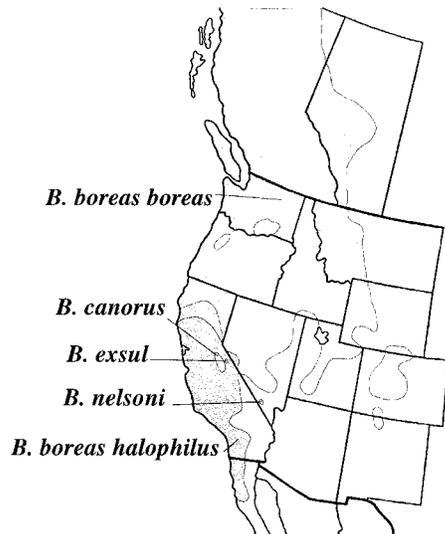


FIGURE 30-1 Distribution of four species of the *B. boreas* group (Blair, 1964b; Blair, 1972a; Schmidt, 1953; Feder, 1973; Stebbins, 1985). Intermediate shading represents range overlap between the subspecies *B. b. boreas* and *B. b. halophilus*.

This is especially apparent for paraphyletic species (e.g., Shaffer et al., 2000).

In real lineages, the amount of diversity within and divergence among species varies widely (Examples 1 and 3). Attempts to describe diversity within ranking systems include the incorporation of the many super-, sub-, and infra-categories (e.g., subspecies, subgenus) to the Linnaean system (Simpson, 1961; Mayr, 1969), as well as definitions for non-Linnaean categories such as Evolutionarily Significant Units (ESU; Ryder, 1986; Waples, 1991, 1995, 1998; Dizon et al., 1992; Rojas, 1992; Vogler and DeSalle, 1994; Karl and Bowen, 1999; Paetkau, 1999; but see Cracraft, 1997; Crandall et al., 2000), Management Units (MU; Moritz, 1994, 1995; Paetkau, 1999), and Evolutionary Units (EU; Clegg et al., 1995). Populations have also been considered the appropriate unit for conservation (Crozier, 1992; Crozier and Kusmierski, 1994; Pennock and Dimmick, 2000). However, these all suffer from the same difficulties as the species rank: (1) criteria can be applied to ranks that have widely differing levels of diversity within and among them and (2) naming specific ranks across lineages will falsely imply similar levels of divergence.

One approach to conservation is a rush to write new species descriptions. Only a small fraction of all species (about 1.75 million of an estimated 13.6 million or more total) have been taxonomically described (Hammond, 1992, 1995). Amphibian species descriptions have increased an estimated 20% in 15 years (4,103 species in 1985 to an estimated 5,000 in 2000 A.D.; Frost, 1985; Duellman, 1993; Glaw and Kohler, 1998). Even this rate, however, may not be enough to document the world's diversity due to increasing rates of species extinctions (Pimm and Brooks, 2000), especially in poorly studied taxa (McKinney, 1999). Furthermore, species descriptions may result in increased conservation efforts for the single species of interest but could ignore conservation of equally divergent and threatened lineages (Paetkau, 1999) because the descriptions rarely identify the diversity of the whole group to which the species of interest belongs. Similar difficulties are seen with bird species (Peterson, 1998) to the point that systematics is seen as

a threat to conservation (Sangster, 2000) due to the lack of taxonomic stability.

An emphasis on conserving diversity rather than a taxonomic rank (e.g., species) will allow the design of conservation programs appropriate for the unique pattern of diversity found in each lineage, at all levels of the evolutionary hierarchy, rather than the sole preservation of the characters or criteria on which a species was determined. Suggestions for such diversity-based conservation programs for bufonids in North America and for the western toad species group are described in Examples 1 and 2.

Using Linnaean taxonomy for conservation is inadequate because the identification of Linnaean species is a slow process and providing a Linnaean species name does not mean that the species is a legal biological entity. An estimated 6 months to several years is needed for documentation of characteristics defining species and for the publication of formal species descriptions in peer-reviewed journals. Even with formal descriptions, only the name is a legal entity and it belongs to a single (or few) type specimen(s). The recognition of species status need not be accepted (Lazell, 1992) and may be contentious for years, due to the many criteria for recognizing species (described above; Goebel et al., this volume, Part Two). A system where diversity is formally recognized from phylogenetic analyses, rather than by recognizing only species from descriptions, may provide a faster and more stable base for conservation programs. Arguments will surely continue about which lineages constitute species (e.g., the disagreements among "splitters" and "lumpers") and which criteria should be used to recognize species, but there will be much less contention about the presence of lineages or clades once they are discovered. Due to the current extinction crisis and limited time and funding, inclusive descriptions of diversity may be more useful than single species descriptions.

Conserving species (or any unit) alone is inadequate because it protects only organisms. In contrast, an emphasis on diversity requires conservation of the evolutionary processes that maintain diversity (e.g., natural selection, mutation, adaptation, gene flow, random drift, vicariance, polyploidy, population and community dynamics, ecological shifts, geological changes, etc.; Dimmick et al., 1999; Crandall et al., 2000; Owens and Bennett, 2000) although the importance of specific processes is debated (e.g., adaptation [Storfer, 1996; Crandall et al., 2000; Young, 2001] versus vicariance [Dimmick et al., 1999; Dimmick et al., 2001]). Conserving diversity requires an understanding of the critical components of diversity, how diversity is apportioned, and how it evolves.

Finally, populations may be the units within which evolutionary processes are most critical. Extinction rates for populations are staggering; if population extinction is a linear function of habitat loss, then about 1,800 populations are being lost per hour in tropical forests alone (Hughes et al., 1997). If populations are the units to be conserved (Crozier, 1992; Crozier and Kusmierski, 1994; Pennock and Dimmick, 2000) then formal recognition of diversity within and among populations, identification of population lineages, and formal names for populations may provide much assistance to the conservation of evolutionary processes.

EXAMPLE 1: PHYLOGENY OF THE WESTERN TOAD (*BUFO BOREAS*) SPECIES GROUP AND MEASURES OF PHYLOGENETIC DIVERSITY.

The *Bufo boreas* species group contains four species distributed across western North America (Fig. 30-1). Three (Yosemite

toads [*B. canorus*], black toads [*B. exsul*], and Amargosa toads [*B. nelsoni*] are thought to be localized relictual isolates from Pleistocene glaciations. (Although the species status of *B. nelsoni* is not recognized by all [Crother et al., 2000], here it is treated as a species.) The fourth and nominal form, *B. boreas*, comprises two subspecies (boreal toads [*B. b. boreas*] and California toads [*B. b. halophilus*] occurring over the rest of the range.

Molecular diversity is not distributed evenly among species (Fig. 30-2). For example, *B. exsul* and *B. nelsoni* compose clades (nodes 5, 7) of closely related individuals. In contrast, specimens of *B. boreas* are found in multiple divergent clades (e.g., 10, 9, 3, 2), some of which may comprise previously unrecognized species (e.g., nodes 2,3). A conservation program based solely on species could result in much loss of diversity within *B. boreas*. Conservation programs based on clades, whether they are currently recognized as species or not, would preserve much more diversity.

The geographic distribution of clades (Figs. 30-2 and 30-3) can identify units for conservation in a hierarchical manner. For example, independent conservation programs could be identified for the species *B. nelsoni* (node 7), the southern clade (node 6), and the species *B. exsul* (node 5). These could work in cooperation with national conservation programs for the entire southwest clade (node 4) and international programs for the entire *B. boreas* species group (node 1).

Priorities for conservation could be identified from phylogenetic diversity calculated from branch lengths (Faith, 1992a,b). Setting priorities based on diversity would provide protection for some populations of *B. boreas*. For example, the southern Utah population, node 2, comprises 8.71% of the total diversity of the species group (Fig. 30-2). Similarly, the previously unrecognized Southern Rocky Mountain clade (node 3) comprises more diversity than the species *B. exsul* or *B. nelsoni*.

Incorporating Diversity into Systematics and Taxonomy

Diversity can be incorporated into systematics and taxonomy by combining phylogenetic taxonomy (de Queiroz and Gauthier, 1992, 1994; Cantino and de Queiroz, 2000) above and below the species level with quantitative measures of phylogenetic diversity (PD) calculated from branch lengths of molecular analyses (Faith, 1992a,b). Phylogenetic taxonomy can identify an infinite number of names based on the hierarchical pattern of relationships, while measures of phylogenetic diversity provide a quantitative measure of the probability that any organism will have unique or divergent traits. By recognizing phylogenetic species (Cracraft, 1983b), more diversity will be identified than species definitions based on other criteria (e.g., ability to interbreed), but phylogenetic species will not identify all of the diversity useful for conservation purposes.

Phylogenetic Taxonomy

Organismic units need name recognition for conservation. As described above, Linnaean taxonomy will always be inadequate because it identifies in a few categories a world that can have a near infinite number of hierarchical levels. Linnaean taxonomy also insists that the same ranks be applied across all lineages, which can be misinterpreted as similar levels of divergence for each rank. For conservation purposes, a taxonomy that provides names for clades that are unique to each lineage and

names on a hierarchical scale from groups of higher taxa down to populations is needed. Because conservation systematics includes conservation of evolutionary processes, a taxonomy that is based on historical evolutionary clades is also desirable.

Phylogenetic taxonomy (de Queiroz and Gauthier, 1992, 1994; Cantino et al., 1999; Pleijel, 1999; Cantino, 2000; Cantino and de Queiroz, 2000, and references therein) differs from Linnaean taxonomy in that it provides names unique to each hierarchical division in a lineage (clade). Names are unique to each clade, are not assumed to be equivalent ranks across lineages, and are based on the pattern of evolutionary descent. Phylogenetic taxonomy was originally described for higher taxa, not for subspecific categories (de Queiroz and Gauthier, 1992). However, the basic tenets can be applied to any clade. Names for some clades may be identical in phylogenetic and Linnaean taxonomy; however, they may differ, because in phylogenetic taxonomy: (1) taxon names always identify clades (Linnaean names are not necessarily clades) and (2) names for all Linnaean ranks are not necessary or sufficient (e.g., names for clades other than order, genus, and species can be included and names for all Linnaean ranks need not be included). Lastly, phylogenetic taxonomy will allow a much more rapid translation of phylogenetic information into taxonomy reflecting the rapid accumulation of phylogenetic information from advances in molecular biology and computer technology (Cantino and de Queiroz, 2000).

Here, phylogenetic taxonomy is applied to the western toad species group with an attempt to identify names for clades, without attempting to identify these clades as species or other Linnaean ranks (Example 2). Applying names to divergent lineages rather than to species alone will have two effects: the burden of identifying which lineages have the characteristics of species is somewhat alleviated, but the burden of identifying diversity is increased dramatically. Both effects will assist conservation efforts by promoting conservation programs that are based on evolutionary hierarchies, are lineage-specific, and incorporate varying levels of diversity.

EXAMPLE 2: PHYLOGENETIC TAXONOMY OF THE WESTERN TOAD (*BUFO BOREAS*) SPECIES GROUP

Linnaean taxonomy currently recognizes four species (Table 30-1). This taxonomic classification does not recognize all the diversity identified in *B. boreas* (Example 1). Even if some of the clades (e.g., nodes 2, 3; Example 1, Fig. 30-2) are eventually identified as species or species groups, the current taxonomy does not recognize clades that comprise multiple taxa (e.g., nodes 8, Northwest clade, and node 4, Southwest clade).

Phylogenetic taxonomy (Table 30-2) can provide names for all the hierarchical clades identified with DNA data (Example 1, Fig. 30-2), whether they are species or multiple supra- or sub-specific categories. Phylogenetic names are identical to Linnaean names when they identify the same clades (e.g., the species Yosemite toads [*B. canorus*], black toads [*B. exsul*], and Amargosa toads [*B. nelsoni*] except that in phylogenetic taxonomy the binomial may be combined with a hyphen [Cantino and de Queiroz, 2000]). Phylogenetic names follow the Linnaean rule of first use, but recognize first use of a clade, not a Linnaean category. For example, clade 3 is identified as Clade Pictus because the name *B. pictus* was first used for a toad collected near Provo, Utah (Cope, 1875c). Names of clades identified with the phylogenetic system that are not recognized as species do not follow all rules of Linnaean nomenclature. They do not have to be binomials and they do not have to be differ-

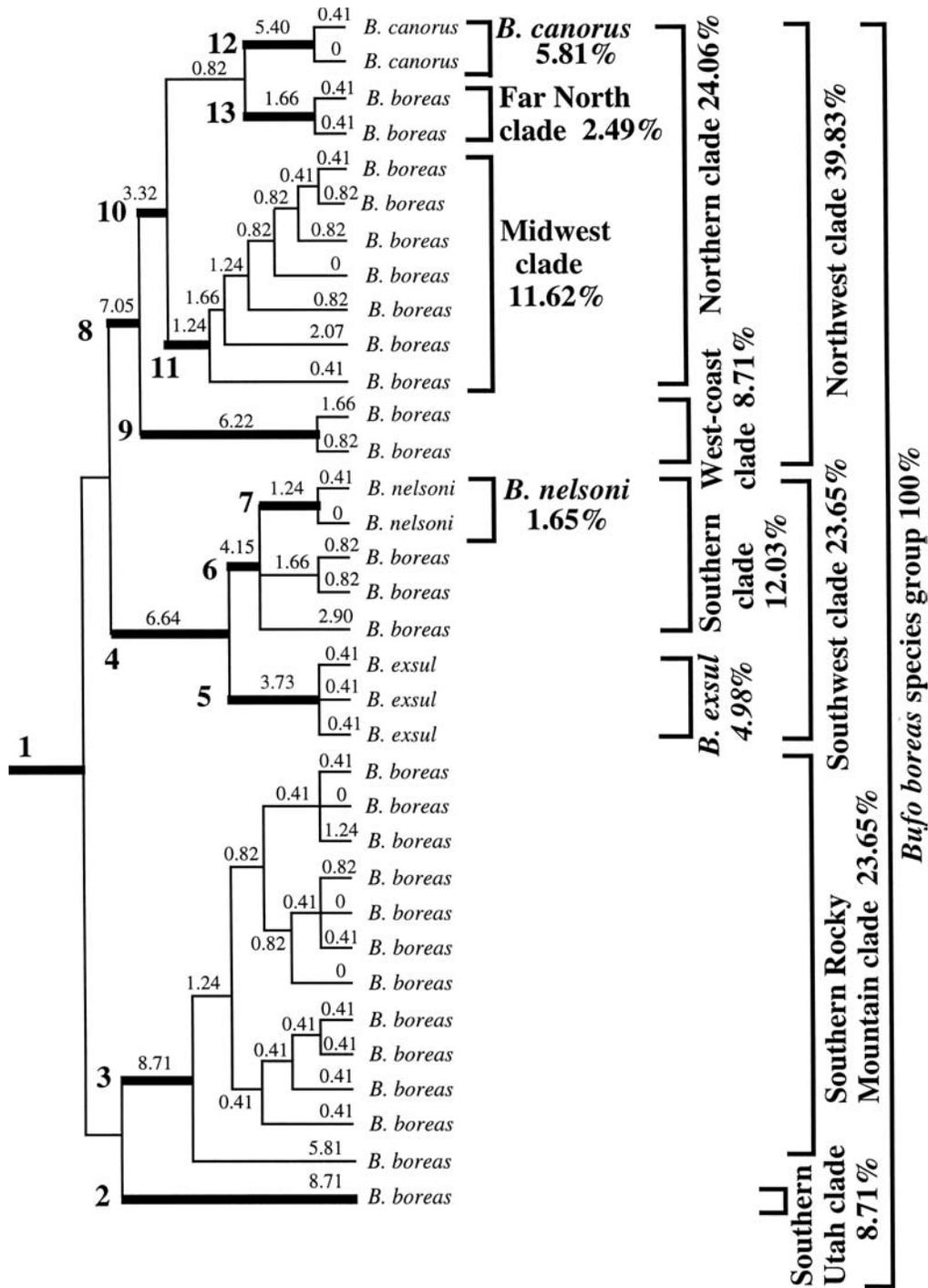


FIGURE 30-2 Phylogenetic analysis of the *B. boreas* species group hypothesized from parsimony analyses (Swofford, 1993) of three mitochondrial DNA regions (12S ribosomal DNA, the control region, and cytochrome oxidase I). Detailed methods, results, and discussion are provided elsewhere (Goebel, 1996a; Goebel, T. Ranker, S. Corn, R. Olmstead and T. Bergren, in preparation). The branching pattern of the phylogenetic tree provides a hypothesis of the genealogical relationships of individual organisms that are represented at the tips (or terminals) of the branches. A clade includes all individuals from the specified node to the tips of the tree (e.g., clade 12 includes the first two terminals only and represents the species *B. canorus*). The branch that identifies each strongly supported clade is indicated by a bold line and names for these clades (based on geographic regions) are identified with brackets to the right of the tree. Strongly supported clades are identified with bold numbers (1–13) whether they are species (e.g., *B. exsul*, node 5, and *B. nelsoni*, node 7) or other units (e.g., 10, 9, 3). Small numbers on the branches are branch lengths, calculated as a percent of the total length of the tree. Phylogenetic diversity (Faith, 1992a,b) is calculated from branch lengths. Measures for whole clades can be identified by summing all the branch lengths within the clade (e.g., phylogenetic diversity of *B. exsul* would be $0.41 + 0.41 + 0.41 + 3.73 = 4.98\%$ of the total value of the species group). Diversity measures for the strongly supported clades are identified to the right of the tree below the names of clades.

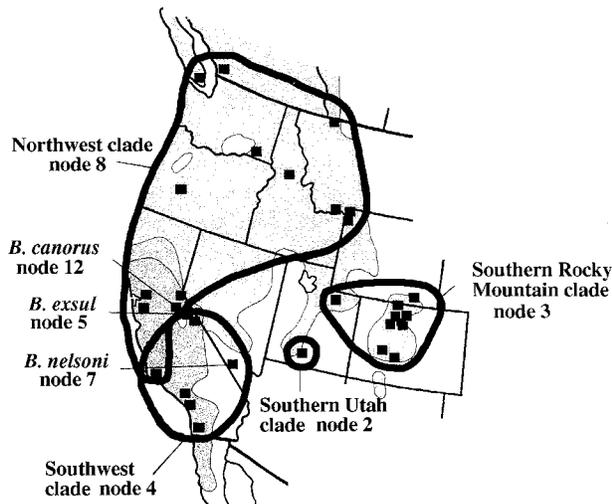


FIGURE 30-3 Distribution of several clades in the *B. boreas* species group. Species identification and shading are as in Figure 30-1. Squares indicate locations of populations sampled in the analysis. Names for clades and node numbers are as in Figure 30-2.

entiated by type font (Linnaean species typically are italicized within non-italicized text). No claim is made that all phylogenetic names refer to species, rather, names are provided for strongly supported clades because the names provide a basis for communication.

Phylogenetic nomenclature will assist conservation efforts by providing names for hierarchical units whether they are species or higher or lower categories. Names can be provided for the full range of diversity; they do not imply equivalent ranks across lineages and they are based on the pattern of evolution of the group. For example, the diversity of Clade Pictus and Clade Bufo-sevieri can be recognized even though one (Clade Bufo-sevieri) is likely a species and the other (Clade Pictus) is likely made of multiple species. In addition, naming “groups” where evolutionary independence is unclear at this time will assist in recognizing diversity before species delimitations are discovered.

Measures of Phylogenetic Diversity

The ability to identify and conserve organismic diversity depends on quantifying the probability that any taxon will have unique traits (also called features or attributes; Faith, 1992a,b). All traits cannot possibly be measured or conserved, nor is it possible to predict which traits should be given the highest value. However, preservation of the greatest number of traits (options) for the future is desirable. IUCN (1980) defined Option Value as “a safety net of biological diversity for future generations,” and the preservation of Option Value (Weisbrod, 1964; Hanemann, 1989; Weitzman, 1992a,b) is seen here as the preservation of the greatest array of diversity.

Measures of organismic diversity have been defined based on species counts (Pielou, 1967; May, 1981; Smith and van Belle, 1984) or on higher taxonomic categories (Gaston and Williams, 1993), where species (or higher categories) are given equal weight. However, these measures are still based on ranks (species, genera, etc.) that may not reflect diversity accurately. Measures based on cladistic analyses, rather than taxonomy alone, include node counts within diversity measures (May,

1990; Vane-Wright et al., 1991; Williams et al., 1991; Nixon and Wheeler, 1992), but these still do not attempt to quantify diversity within and among nodes any more than do species counts. Finally, branch lengths (Altschul and Lipman, 1990) were incorporated into diversity measures based on both genetic distances (Crozier, 1992; Crozier and Kusmierski, 1994) and phylogenetic diversity (Faith, 1992a,b, 1993, 1994a,b). Some methods incorporate both phylogenetic pattern and branch length information (Faith and Walker, 1993; Faith, 1994c) in an attempt to describe phylogenetic diversity within and among clades.

Molecular phylogenetic analyses are especially amenable to quantifying diversity in the form of branch lengths (Faith, 1992a,b). Phylogenetic analyses of gene sequences are used as surrogate data for the evolutionary diversity of many features (e.g., morphological, chemical, or developmental attributes) that cannot be measured independently at this time (Faith, 2002). Because different character suites are likely to follow different evolutionary patterns (Eldredge and Gould, 1972; but see Omland, 1997), DNA analyses of potentially neutral characters on multiple unlinked genes may provide an estimate of the probability of underlying feature diversity. Measures of molecular phylogenetic diversity can be seen within the western toad species group (Example 1, Fig. 30-2) and among North American bufonids (Example 3, Fig. 30-4).

Although it seems intuitive that making decisions about loss of diversity is better than allowing it to proceed at random, Nee and May (1997) suggest that this may not be the case. They suggest that algorithms designed to maximize the amount of diversity (described above) are not much better than choosing the survivors at random, and that 80% of the underlying tree of life can survive even when 95% of the species are lost. However, historical and current extinctions are not randomly distributed among species (Bennett and Owens, 1997; Russell et al., 1998; Purvis et al., 2000, and references therein), which may cause a greater loss of diversity. In addition, it is not clear what level of diversity can be lost before human life cannot be sustained. It may be that the additional 10% of diversity that might be saved with careful planning (Nee and May, 1997) is critical.

EXAMPLE 3: PHYLOGENETIC DIVERSITY AMONG BUFONID TAXA PROTECTED BY THE U.S. ENDANGERED SPECIES ACT

Four bufonid taxa are recognized as endangered in the United States (Wyoming toads [*B. baxteri*], Houston toads [*B. houstonensis*], arroyo toads [*B. californicus*], and Puerto Rican crested toads [*Peltophryne lemur*]; Fig. 30-4). Eight taxa (Colorado River toads [*B. alvarius*], western toads [*B. boreas*], Yosemite toads [*B. canorus*], black toads [*B. exsul*], Amargosa toads [*B. nelsoni*], Arizona toads [*B. microscaphus*], green toads [*B. debilis*], and red spotted toads [*B. punctatus*]; for alternate nomenclature see Crother et al., 2000) are provided some form of protection within individual U.S. states (Frank and Ramus, 1994; Levell, 1995).

Species-based conservation programs for U.S. taxa are inappropriate because phylogenetic diversity is not distributed evenly among species. Twelve of 22 bufonid species in the United States are found in two clades of closely related species (*B. boreas* and *B. americanus* species groups; Fig. 30-4). The threatened taxon (*P. lemur*) is quite divergent and comprises the most basal lineage among U.S. taxa. The remaining three endangered taxa are closely related within the *B. americanus* species group. This pattern of low taxonomic divergence of endangered species

TABLE 30-1
(Example 2) Taxonomy of the *Bufo boreas* Species Group Based on the Linnaean Taxonomic System

<i>Taxon</i> (Common name)	Type Locality and First Description	Distribution
Taxa Currently Recognized		
<i>Bufo boreas</i>	Type locality: Columbia River and Puget Sound, WA; restricted to vicinity of Puget Sound First described by Baird and Girard (1852b)	See subspecies below
<i>B. boreas boreas</i>	Type locality: Mouth of the Columbia River, WA; First described as <i>B. columbiensis</i> (Baird and Girard, 1853a)	Coastal Alaska south to northern CA, east into MT, WY, CO and extreme northern NM
<i>B. boreas halophilus</i>	Type locality: Benicia, Solano Co., CA; First described as <i>Bufo halophila</i> (Baird and Girard, 1853b)	Extreme western NV, central valleys of CA, and mid-coastal CA south into Baja California of Mexico
<i>B. exsul</i>	Type locality: Deep Springs, Deep Springs Valley, Inyo Co., CA; First described by Myers (1942a)	Deep Springs Valley of eastern CA
<i>B. nelsoni</i>	Type locality: Oasis Valley, Nye Co., NV; First described as <i>B. boreas nelsoni</i> (Stejneger, 1893)	Amargosa River drainage of southwestern NV
<i>B. canorus</i>	Type locality: Porcupine Flat, Yosemite National Park, CA; First described by Camp (1916a)	High Sierra Nevada of CA
Taxa Not Currently Recognized		
<i>B. pictus</i>	No locality given; designated as Provo, UT (Schmidt, 1953); First described by Cope (1875c); later determined to be <i>B. boreas</i> (Schmidt, 1953)	
<i>B. nestor</i>	Fossil specimens from La Brea deposits, Los Angeles Co., CA; First described by Camp (1917a); later changed to <i>B. b. halophilus</i> (Tihen, 1962)	
<i>B. politus</i>	Greytown, Nicaragua; First described by Cope (1862); later determined to be <i>B. boreas</i> (Savage, 1967) and locality presumed to be in error	Location assigned to be in the Pacific coast region (Savage, 1967)

NOTE: From Schmidt, 1953; Blair, 1964, 1972; Feder, 1977; Stebbins, 1985. Distributions identified in Figure 30-1.

has also been seen in birds where many endangered taxa are actually peripheral populations when the entire range of the species is considered (Godown and Peterson, 2000).

For comparative purposes, phylogenetic diversity (PD) values were estimated from U.S. taxa alone (Figs. 30-4, 30-5). The United States was chosen as a geo-political unit for evaluation of diversity because laws and funding sources for conservation efforts frequently are geo-politically based. Bufonid taxa nationally listed as endangered include two with low PD values (*B. baxteri* and *B. houstonensis*), one with an intermediate value (*B. californicus*), and the taxon with the highest U.S. PD value (*P. lemur*). On diversity criteria alone, these data provide support for a strong national conservation effort for *P. lemur*, and comparatively less support for *B. baxteri* and *B. houstonensis*.

Phylogenetic diversity values provide baseline measures with which to evaluate conservation needs of North American

bufonids. For example, *B. alvarius* has a high PD value, a limited distribution, and may be a species at risk due to recent over collection. Preservation of this species before it declines would be prudent because it would conserve a high level of diversity both within the United States and globally. In contrast, giant toads (*B. marinus*) have the second highest U.S. PD value but are a common species with near worldwide distribution (due to human translocations) and have closely related taxa outside the United States. Conservation of *B. marinus* within the United States would not preserve a high level of diversity on a global scale.

Individual PD values are very low (0.05–0.74%) among the five taxa of the *B. boreas* group. However, when any one taxon within the *B. boreas* group (labeled *B. boreas* [1 taxon] in Fig. 30-5) is compared to other taxa in the United States outside of the *B. boreas* group, PD values substantially rises to the high category. These results suggest a high conservation value for the species group, but comparatively low values for any particular taxon

TABLE 30-2

(Example 2) Suggested Taxonomy of the *Bufo boreas* Species Group Based on Principles of Phylogenetic Taxonomy

Node Number (Clade Name) (Fig. 30-2, Example 1)	Current Taxon Name	Revised Linnaean (Based on potential species revisions)	Phylogenetic Taxonomy
1. (<i>B. boreas</i> species group)	No name	No name, multiple species	Clade Boreas
2. (Southern Utah)	<i>Bufo boreas boreas</i>	<i>Bufo sevieri</i> *	Clade <i>Bufo-sevieri</i> ^a
3. (Southern Rocky Mountain)	<i>Bufo boreas boreas</i>	No name, multiple species	Clade Pictus
4. (Southwest)	No name	No name, multiple species	Group Nestor
5. (<i>B. exsul</i>)	<i>Bufo exsul</i>	<i>Bufo exsul</i>	Clade <i>Bufo-exsul</i>
6. (Southern)	<i>Bufo boreas halophilus</i>	No name, multiple species	Group Halophilus
7. (<i>B. nelsoni</i>)	<i>Bufo nelsoni</i>	<i>Bufo nelsoni</i>	Clade <i>Bufo-nelsoni</i>
8. (Northwest)	No name	<i>Bufo boreas</i>	Group Boreas
9. (West Coast)	<i>Bufo boreas halophilus</i> and <i>Bufo boreas boreas</i>	No name, not a species	Group Orarius
10. (Northern)	No name	No name, not a species	Group Politus
12. (<i>B. canorus</i>)	<i>Bufo canorus</i>	<i>Bufo canorus</i>	<i>Bufo-canorus</i>

^a This clade may be a species. MtDNA data are consistent with nuclear data (Goebel, unpublished data) and with comments concerning morphological variation within the group. However, the name *Bufo sevieri* is provided for discussion purposes only. I do not provide a formal description, which is needed for recognition within Linnaean and Phylogenetic taxonomy.

NOTE: From de Queiroz and Gauthier, 1992; Cantino and de Queiroz, 2000. Clade names and node numbers are identified in Figure 30-2. Within the phylogenetic taxonomy, names of subordinate clades are indented to indicate hierarchical relationships. For each pair of sister clades, the first listed has fewer subordinate clades than the second. This phylogenetic taxonomy differs from de Queiroz and Gauthier (1992) and Cantino and de Queiroz (2000). First, "Groups" are identified by prefix in the way "Clades" are identified. The designation "clade" infers that the organisms are independently evolving units (e.g., *B. exsul*) or have a historical monophyletic evolutionary pattern (e.g., Clade Boreas). In contrast, "groups" are made up of organisms with divergent but sympatric mtDNAs. Toads in sympatry probably interbreed, although the significance of the interbreeding is not clear at this time. The phylogenetic taxonomy is similar to some suggestions in de Queiroz and Gauthier (1992) and Cantino and de Queiroz (2000) in that clades are identified and named; species names remain identical except that they are joined by a hyphen; not all possible clades are named (clades 11 and 13 are not named); and the taxonomy is presented in a hierarchical fashion. At this time, *Bufo canorus* is not presented as a clade in the phylogenetic taxonomy due to conflicting data presented here and in Shaffer et al., 2000.

within the group. A similar increase is also seen for single taxa in the Sonoran green toad (*B. retiformis*) group.

Examination of comparative levels of phylogenetic diversity can redirect conservation priorities. For example, managers in captive breeding programs in U.S. zoos want to know whether two populations of *P. lemur* should be managed as independent evolutionary units. Phylogenetic analyses identified the two populations as divergent, but more importantly, analyses identified these toads as the most divergent toads covered by the U.S. ESA. Therefore, both populations have extremely high value—not only because they are divergent from one another but primarily because both will be needed to increase the survival probability of the lineage endemic to Puerto Rico.

Ideally, cooperative global conservation strategies, in addition to national and regional priorities examined here, could be established. Phylogenetic diversity values based on taxa worldwide would vary slightly for a few taxa. For example, taxa with the three highest PD values (Gulf Coast toads [*B. nebulifer* (formerly *valliceps*)], *B. marinus*, and *P. lemur*) have sister taxa outside the United States. When these sister taxa are included in PD estimates, PD values decrease from those presented here.

Finally, much of the diversity in U.S. bufonid taxa (47–50%) is not within terminal lineages, but is shared among taxa within the deeper branches of the tree (Fig. 30-4) as may be the case for much of the tree of life (Nee and May, 1997). These data suggest that conservation programs should be coordinated among phylogenetic clusters rather than based solely on the terminal lineages of individual species.

Phylogenetic Species

If phylogenetic species concepts (Cracraft, 1983b) were applied, then many genetically divergent or geographically distinct groups that are currently considered to be subspecies or populations would be elevated to species level (e.g., McKittrick and Zink, 1988; Cracraft, 1992; Peterson and Navarro-Sigüenza, 1999). Further definitions of phylogenetic species (Cracraft, 1987, 1997; Nixon and Wheeler, 1990; Davis and Nixon, 1992; Vogler and DeSalle, 1994; Mayden and Wood, 1995), in which they are diagnosed by a unique combination of traits, would identify even finer units (ESUs).

Adoption of phylogenetic species concepts still may not preserve diversity because the diversity of species varies widely. For example, the western toad species is composed of two subspecies (boreal toads [*B. b. boreas*] and California toads [*B. b. halophilus*]). These two subspecies are not likely to be independent phylogenetic species because of the high probability of interbreeding where they are sympatric. However, recognizing a single species (e.g., western toads) would fail to recognize the unique divergence contributed by the southern populations of California toads. Alternate conservation strategies are appropriate in the regions where diversity is dramatically different. If systematic considerations are fully incorporated into recovery programs, species would neither be considered in isolation nor without information regarding such intraspecific variation.

Phylogenetic species concepts can provide a unique perspective for conservation. For example, 20 years ago, western toads

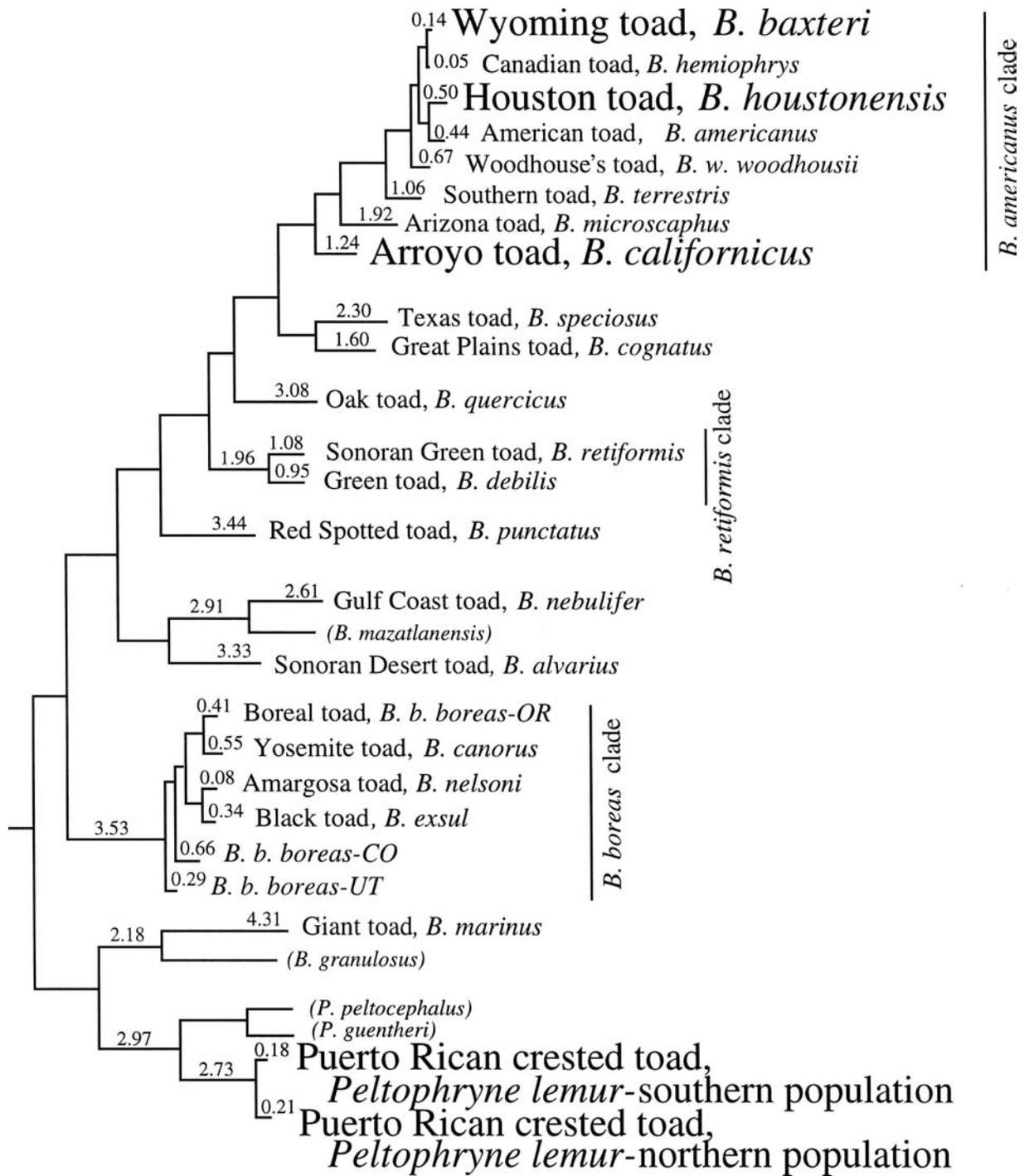


FIGURE 30-4 Phylogenetic relationships among bufonid taxa protected by the U.S. Endangered Species Act. Relationships are based on parsimony analyses (Swofford, 1993) of mitochondrial DNA gene sequences of the 12S ribosomal DNA, control region, cytochrome oxidase I, and cytochrome b regions (details including site-specific and transition/transversion weights are in Goebel, 1996a,b). Taxa listed as endangered or threatened by the ESA are in large print. Taxa that are in parentheses are not protected by the ESA but were included in the analysis because they are closely related (putative sister taxa) to taxa that are protected by the ESA. In the phylogenetic tree, branches are drawn in proportion to their lengths. Numbers on the branches are the percent of the length of a single branch based on the total length of the tree. The tree is rooted; outgroups and taxa not relevant to this analysis were excluded from the figure (details in Goebel, 1996a).

had a near continuous distribution across the high elevations in central Colorado. Recent declines (Goettl and BTRT, 1997) left three viable "populations" in Rocky Mountain National Park, Chaffee and Clear Creek counties, and only scattered individuals across the rest of the state (see Carey et al., this volume). Are these three populations now species? Classifying

them as species under the Phylogenetic Species Concept would provide a better evolutionary perspective to their conservation. If the three populations are considered to be a single species, translocations among the three, as well as translocations from all three (either singly or in combination) to regions where the toads have been extirpated would

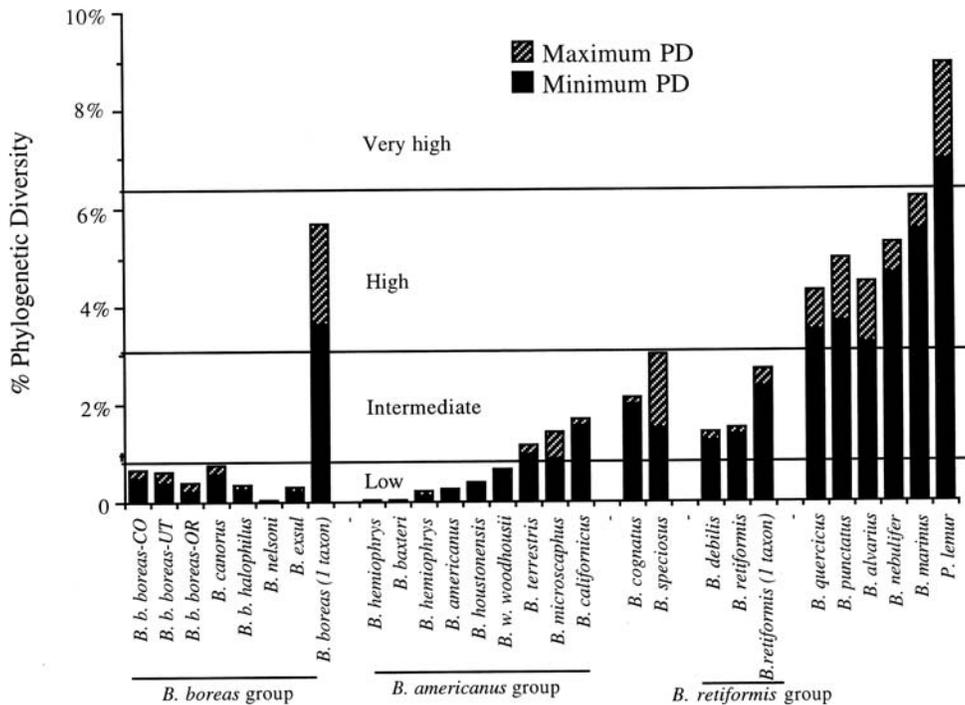


FIGURE 30-5 Comparative phylogenetic diversity values (PD) of taxa protected by the U.S. Endangered Species Act. Phylogenetic diversity values for individual taxa are branch lengths (Faith, 1992a), from the terminal to the first node shared with any other taxon also protected by the U.S. ESA. For example, the PD value for *B. nebulifer* is 5.52 (2.61 + 2.91) where a node is shared with *B. alvarius* (Fig. 30-4). Phylogenetic diversity values are presented as a range (maximum and minimum), based on multiple most-parsimonious trees and alternate weighting techniques in the phylogenetic analysis (Goebel, 1996a,b). Phylogenetic diversity values are classified as low (0–0.074), intermediate (0.88–3.04), high (3.49–6.24), and very high (above 6.24).

be considered to be reasonable conservation alternatives (see Dodd, this volume). However, while gene flow might have occurred through multiple generations along great distances, it is unlikely that gene flow occurred directly among those populations as would be proposed with translocation programs. The distinct evolutionary histories of the three populations may well have allowed unique adaptations to different environmental factors in each region (Crandall et al., 2000). Therefore, a recovery program based on the evolutionary tenets of phylogenetic species would only encourage translocation to expand each population into habitat that previously was accessible to each population. By multiple expansions of each population (until they are once again contiguous across the state) the number of animals can be increased without interfering with evolutionary processes occurring within each population. In addition, by emphasizing a program of “assisted dispersal” rather than long-distance translocations, corridor habitats would be protected, allowing natural levels of gene flow rather than by relying on continued translocations by humans.

Conservation Systematics in Management and Politics

Setting Priorities with Measures of Phylogenetic Diversity

Not all species or lineages have equal value to humans or to ecological and evolutionary processes. Rather than allowing the high rates of human-induced extinctions to proceed haphazardly, humans might be wise to make choices and set priorities

locally and globally. A variety of criteria for setting priorities for conservation have been considered, including ecosystem attributes (Scott et al., 1993), ecological or functional diversity (Williams et al., 1994), the ability to evolve (e.g., giving high priority to species rich groups; Erwin, 1991; Brooks et al., 1992; Linder, 1995), rarity (Gaston, 1994), morphology or phenotype (Owens and Bennett, 2000; but see Crozier, 1992; Williams and Humphries, 1994; Faith, 2002), allelic richness (Petit et al., 1998), and priorities for basal taxa (Stiassny, 1992; Stiassny and de Pinna, 1994). No single criterion should be considered in isolation (Pennock and Dimmick, 1997; Parker et al., 1999; Taylor and Dizon, 1999; Asquith, 2001), but incorporating phylogenetic diversity into all decisions will provide a needed perspective.

While it is critical to conserve lineages with traits of known high value (e.g., human food crops, species with valuable ecosystem functions), humans cannot predict which traits are going to have a high value in the future. However, each lineage has some value representing a unique set of traits. Setting priorities for conservation based on phylogenetic diversity is an attempt to preserve the highest degree of organismic diversity while recognizing that more closely related taxa have a higher chance of sharing traits. Methods for setting conservation priorities based on systematic principles are being developed (Krajewski, 1991, 1994; Vane-Wright et al., 1991; Faith, 1992a,b, 1993, 1994a,b, 1996; Nixon and Wheeler, 1992; Gaston and Williams, 1993; Weitzman, 1993; P. H. Williams et al., 1993; Crozier and Kusmierski, 1994; Forey et al., 1994; Vane-Wright et al., 1994; Williams and Gaston, 1994; Williams and Humphries, 1994; Humphries et al., 1995; Lande et al., 1995; Walker and Faith, 1995). Crozier (1997) reviews methods and

Bininda-Edmonds et al. (2000) suggest directions for future research.

To date, the most common use for systematic diversity measures has been to identify geographic regions that contain the greatest organismic diversity (e.g., methods of reserve design, Humphries et al., 1991; Vane-Wright et al., 1991; Williams, 1996; Moritz and Faith, 1998). The same principles can be used to set priorities for scarce conservation funds, to maximize representation of other features such as environmental diversity (Faith, 1994c, 1966; Faith and Walker, 1995), to assess environmental impacts (Clarke and Warwick, 1998; Warwick and Clarke, 1998), to provide some protection of highly divergent lineages before they become rare (Witting and Loeschke, 1995), and to identify hierarchical management regions based on hierarchical levels of diversity rather than political boundaries alone (Examples 1 and 2).

Reconstruction of the Endangered Species Act (ESA)

The U.S. Endangered Species Act has come under increasing criticism. For example, political and economic forces have fought against the ESA because it costs too much, prevents development, infringes on private property rights, and preserves “useless” plants and animals (Sward, 1990; Rohlf, 1994). Criticisms have also come from those that perceive the ESA as not doing enough to preserve diversity, especially through ecosystem approaches (Losos, 1993; Scheuer, 1993; Murphy et al., 1994; Clegg et al., 1995; Sampson and Knopf, 1996; Yaffee et al., 1996). However, other than attempts to define “distinct populations” (Waples, 1991, 1998; Pennock and Dimmick, 1997), there is little discussion of ESA modifications to protect organismic diversity within and among a variety of hierarchical lineages.

The mandate of the ESA to preserve unique or divergent populations and subspecies, in addition to species (U.S. Forest Service, 1988), provides evidence that diversity, rather than a particular taxonomic rank (e.g., species), was the intended basis for conservation in the ESA (Waples, 1991, 1998; Gleaves et al., 1992; Pennock and Dimmick, 1997, 2000; but see also Rohlf, 1994). Problems have arisen because (1) there is no biological definition of the species category within the ESA and (2) authors of the ESA could not have foreseen the recent usefulness of molecular data in describing and quantifying diversity. In order to utilize new knowledge, measures of phylogenetic diversity should now be included in conservation legislation in the following ways:

Priorities for conservation should include discussions of diversity. Currently, taxa are evaluated as endangered or threatened, with the highest priority given to endangered taxa. New categories that incorporate diversity should be developed. For example, taxa that are listed as threatened but also have a very high phylogenetic diversity (e.g., Puerto Rican crested toads, *P. lemur*; Example 3) could be given priority equal to taxa that are listed as endangered but have less phylogenetic diversity (e.g., Wyoming toads [*B. baxteri*] and Houston toads [*B. houstonensis*]).

Conservation efforts should be based on hierarchical lineages, not primarily on the species category, in order to speed conservation programs and tailor them to each unique lineage. For example, newly discovered but highly divergent lineages (e.g., western toads in southern Utah, Example 1) could be given a high priority long before species descriptions

are published. In addition, clades that contain multiple endangered species could be listed as endangered rather than having to list multiple species independently (e.g., conservation for Clade Pictus [Fig. 30-3; Table 30-2] rather than conservation of *B. boreas boreas* in Colorado only).

Some priority should be given to highly divergent lineages that are not yet listed in order to ensure their survival before a crisis occurs.

Broader systematic analyses (not just species descriptions) should be encouraged for listing on the ESA. Estimates of intraspecific diversity across the range of the group would encourage the discovery of cryptic species/lineages and their inclusion in the listing process. Identification of supraspecific diversity would assist in providing priorities for the most divergent lineages. The ability to list supraspecific categories may be most valuable if extinctions are clustered within certain amphibian genera or families as they are in mammals and birds (Russell et al., 1997).

A national and international effort to identify organismic diversity among all taxa should begin with the cooperation of agencies regulating the ESA. Much like the human genome project, a database for Earth’s diversity would provide both a better understanding of life itself and worldwide priorities for diversity. Such programs are beginning with the “Tree of Life” project (Maddison, 1998) and TreeBASE archive at Harvard, but these are not receiving serious levels of federal attention for funding (like the human genome project).

Defining Acceptable Loss

Not all individuals or populations need to be conserved. Knowledge of phylogenetic diversity can be used to mitigate the loss of diversity if levels of acceptable loss can be identified. While in some cases there may be no acceptable loss (e.g., preservation of rare species may dictate that all lineages and organisms be preserved in order to ensure long-term survival), many species or clades can tolerate some loss. Identification of acceptable loss based on phylogenetic diversity might assist in mitigating losses until the high rates of loss due to the extinction crisis can be stabilized.

Within molecular measures of phylogenetic diversity, there are no inherent criteria for identifying an “acceptable loss” or a value for survival. When faced with calculating a measure of acceptable loss in the absence of biological data, a procedure based on phylogenetic diversity might be used. For purposes of this example, an acceptable loss of 5% phylogenetic diversity will be used; greater loss will be seen as statistically significant and biologically unacceptable. I suggest the following procedure:

1. A clade-specific measure of acceptable loss is defined (either based on 5% phylogenetic diversity or other biological criteria).
2. The value of any clade will be maintained at 100% of the total known diversity. If additional diversity is discovered, the value of less inclusive units will be reduced proportionately but the total value will remain at 100%.
3. If diversity is lost due to extinction, diversity will be subtracted from the whole rather than resetting the total value to 100% (e.g., total known diversity will remain at 100% but total extant diversity may be less).
4. A charge will be levied for loss of diversity and collected funds applied to conservation efforts for the rest of the

clade. An exponential cost scale will be applied, such that low levels of loss (e.g., 0.001–0.10%) have a proportionately low charge but would increase exponentially with higher levels of loss.

Implementing the above produces several desirable effects. First, decisions can be made to allow loss with the least impact on diversity. Pruning short branches of the phylogenetic tree and pruning tips evenly throughout the tree would preserve the greatest dispersion of traits (Williams et al., 1991). Second, an exponential charge scale would discourage the loss of whole clades. In the western toads example, a high value would be placed on the single population comprising the southern Utah clade (8.71%; Example 1, Fig. 30-5), but much lower values would be placed on most single populations throughout the rest of the range. Third, placing a 100% value on the whole group provides an incentive to identify additional diversity. If additional diversity were found, the comparative value for individual clades throughout the tree is decreased relative to the whole. Fourth, priorities could be used by regional planning agencies to determine areas most appropriate for development. A high financial cost of development would prohibit high losses of diversity. Previously developed land without biological diversity might be less costly to develop than pristine habitat. Finally, if an environmental disaster occurred due to human actions, responsible parties could be charged in proportion to the lost diversity. The remaining diversity would automatically increase in value, reducing the risk of future loss that business or managing agencies might be willing to take. For example, in a historical context, tuataras have already lost a high level of phylogenetic diversity (Daugherty et al., 1990); the cost of reducing diversity further should be prohibitively high. Another example is the American bald eagle, which may have lost similarly high levels of phylogenetic diversity when populations declined. Under the current ESA, bald eagles have recently been down-listed due to an increase in the number of individuals. With diversity-based legislation, any agent that might cause a repeated decline would be monitored carefully. This is because a large proportion of the phylogenetic diversity within these species may have already been lost, reducing their evolutionary potential to adapt to future change.

Update

Many of the ideas presented in this chapter were developed almost a decade ago and changed through time. Most were first initiated as a graduate student in the early 1990s and were part of a dissertation (1996). I am encouraged to see some ideas closer to reality such as the implementation of phylogenetic taxonomy (Cantino and de Queiroz, 2000), large phylogenetic projects (Tree of Life [Maddison, 1989]; TreeBASE), and coordinated methods for identifying conservation priorities for geographic regions (WORLDMAP [Williams, 1996]). Other ideas, such as directly modifying the ESA to formally recognize diversity in all its forms, identifying acceptable levels of loss, or initiating financial charges for loss of diversity do not seem close to implementation. A few early ideas, such as an exchange program for “diversity credits” (paralleled after the exchange program for “pollution credits”) now seem so out of favor that they are not included here. Research on biodiversity is being outlined by working groups (Bininda-Emonds et al., 2000; Wall et al., 2001) as the final version of this chapter is submitted. Throughout the decade, and now, I feel sadness for lost lineages (*B. boreas* in Colorado may be lost in the next few years), and I hope that we can conserve more lineages than we can discover relationships for and name.

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