Preface

In 1943 Sherman C. Bishop published his classic treatise, *A Handbook of Salamanders,* which served for many years as the primary reference source on North American salamanders. From 1943 to 1997 researchers published more than 1500 refereed scientific papers on the systematics, ecology, and natural history of North American salamanders. In addition, scientists described more than 30 new species of salamanders from the United States and Canada. Although several state and regional works with accounts of salamander life histories appeared during this period, they did not fulfill the need for a comprehensive summary of the published literature on North American salamanders.

The primary purpose of this work is to provide a reference source for basic researchers, science teachers, naturalists, conservation biologists, foresters, environmental planners, and others who need detailed information on North America's diverse salamander fauna. The focus is on ecology, evolution, biodiversity, behavior, and natural history. For this reason I have excluded most of the voluminous literature on salamander physiology, development, morphology, genetics, anatomy, and infectious disease agents, including parasites. Because of limitations on book length, I have omitted synonymies and highly technical descriptions of species. Instead, I describe key external characters that are useful in determining the sex and species identity of live or freshly preserved specimens.

Rather than present stereotypic descriptions of species and life histories, as is common in many state and regional accounts, I provide summaries of major patterns of geographic variation within species, as well as the general localities where studies were conducted. This approach emphasizes intraspecific differences between local and regional populations and provides a more realistic view of the life history diversity that occurs within each species. In addition, it provides information that can be applied with greater confidence to specific geographic regions that are of interest to resource managers, conservation biologists, and researchers.

One of the most challenging aspects of this work was deciding how many species to recognize. Much of the disagreement among taxonomists regarding current nomenclature applied to salamanders reflects the fact that scientists do not agree on what constitutes a species. Traditionally, the biological species concept has been the primary model for recognizing vertebrate species. This concept uses reproductive isolation as the primary criterion for recognizing species. It is built upon the premise that members of the same species can (or potentially can) freely interbreed with each other in nature, whereas members of different species cannot. The biological species concept can be easily tested when two groups coexist

together locally, and in most instances species can be defined based on whether individuals freely interbreed. In some cases this simple test cannot be applied and scientists must use less direct evidence. Such instances include situations in which species reproduce asexually, populations are allopatric (geographically isolated), genetic divergence of groups is not accompanied by morphological divergence, and populations freely interbreed in certain areas of their range, but not in others.

The biological species concept has been challenged by some researchers because of operational problems as well as on philosophical grounds regarding the goals of systematics and taxonomy. Although many alternative definitions of species have been proposed under the general headings of "evolutionary" and "phylogenetic" species, all pose potential problems in terms of their practical use (for literature most pertinent to salamanders, see Cole 1990; Echelle 1990; Frost and Hillis 1990; Highton 1990, 1995; Larson and Chippindale 1993). The biological species concept recognizes polytypic species consisting of two or more subspecies, but many evolutionary and phylogenetic species concepts would treat currently recognized subspecies as separate species.

Evolutionary species concepts are gaining in popularity. Although several versions have been proposed, these generally view a species as a group of populations or an evolutionary lineage that is evolving along a separate evolutionary pathway from other such groups. Thus, evolutionary species have been characterized as having their own "unitary roles and tendencies" (Simpson 1961) or having their own "evolutionary tendencies and historical fates" (Wiley 1978). Specialists using evolutionary species concepts often attempt to delineate the largest evolutionary units that appear to be on separate phylogenetic trajectories. Phylogenetic species concepts also seek to recognize lineages that are on separate evolutionary trajectories, but these differ in trying to delineate the smallest (rather than the largest) evolving units that appear to be on separate evolutionary pathways. Thus, researchers employing phylogenetic species concepts tend to be extreme "splitters." A group consisting of many weakly differentiated allopatric subgroups might be treated by a researcher using the biological species concept as a single polytypic species consisting of several subspecies. In contrast, a researcher using a phylogenetic species concept might consider each allopatric form to be a separate species, whereas a researcher using an evolutionary species concept might recognize an intermediate number of species.

Evolutionary and phylogenetic species concepts have been criticized because they lack objective criteria for determining whether groups are on different evolutionary trajectories—except, of course, for species that coexist locally without interbreeding. Given the large number of genes and known mutation rates for vertebrates, one could argue from a purely statistical standpoint that most allopatric groups within a species' range contain unique mutations and are following different evolutionary trajectories of sorts. Although recognizing each allopatric form as a separate species would be impractical for highly fragmented species, scientists who employ evolutionary and phylogenetic species concepts must ultimately make subjective decisions on what constitutes a "different" evolutionary trajectory or separately evolving lineage. Unfortunately, there is little agreement among experts about where to draw species boundaries using this or other species concepts. A recent move to raise allopatric subspecies of North American salamanders and other vertebrates to the full species level by

evoking phylogenetic species arguments (Collins 1991) was met with much criticism and debate (Collins 1992; Dowling 1993; Frost et al. 1992; Montanucci 1992; Van Devender et al. 1992). This exchange illustrates the divergent viewpoints on taxonomic philosophies that abound in today's herpetological community.

The problems associated with defining species reflect the fact that our current hierarchical classification system uses discrete taxonomic categories to stereotype the complex genetic and evolutionary patterns that exist in nature. Salamanders have low dispersal rates relative to other vertebrates and are often constrained by physiology and design to cool, moist microhabitats. Biogeographic and molecular data indicate that many species have undergone one or more cycles of geographic expansion, followed by contraction and fragmentation into isolated populations or regional groups (e.g., Highton 1995). Studies of protein variants, mitochondrial DNA, and other molecular information indicate that regional populations are often genetically differentiated from one another. In many cases, however, genetic differentiation between subgroups is not paralleled by conspicuous differences in external morphology, coloration, color patterning, or behavior (Highton 1995; Larson 1984; Wake 1993).

Many salamander species consist of geographic subgroups that evolutionary biologists employing the biological species concept have traditionally treated as semispecies. Such species contain geographic groups that have evolved beyond the level of geographic races or subspecies but have not yet reached the level of full biological species characterized by complete reproductive closure. Where these forms come into geographic contact, they may hybridize freely or nearly so, but the hybrid zones are often narrower than those seen in other vertebrate groups.

Semispecies complexes with narrow hybrid zones are the source of many of the current controversies in salamander taxonomy, and none of the existing species concepts provides a rigorous set of criteria that will result in consistent interpretations by all members of the scientific community. Some researchers have elected to split semispecies complexes into separate species. The most common rationale is that these are well-differentiated genetic groups with narrow hybrid zones. Narrow hybrid zones have often been used as evidence of genetic incompatibility between forms, and to argue that the parental groups that form hybrid zones are on separate evolutionary trajectories. However, the presence of narrow hybrid zones does not necessarily reflect genetic incompatibility. The width of hybrid zones tends to be positively correlated with the innate dispersal abilities of different vertebrate groups. Salamanders have very low dispersal rates relative to almost all other vertebrates, and narrow hybrid zones of only a few kilometers could be produced by a variety of mechanisms regardless of whether the hybrids have lower, equal, or higher fitness than the homozygous parental types from which they are derived (e.g., Hewitt 1989). In addition, hybrid zones often act as semipermeable genetic filters—genes that exhibit negative heterosis (or genes that are epistatically linked to these) may form the hybrid zone, whereas genes that are advantageous may pass readily through the hybrid zone and be incorporated into opposing genomes. Researchers all too often have documented hybrid zones in salamanders without delineating the mechanisms that have produced them. This information is often critical for determining levels of gene flow and for making taxonomic decisions about members of semispecies complexes.

Some scientists have used molecular data to justify naming regionally differentiated groups

as new species—if, in their opinion, genetic divergence (which is indirectly estimated from molecular similarity) is at or above levels that typically occur between closely related species. Unfortunately, molecular similarity is not always a reliable predictor of the degree of reproductive isolation between groups. For that reason, much debate has surfaced as to whether regional groups should be recognized as separate species when molecular similarity is the only criterion used to make such assessments. Scientists have thus far been unable to agree on the validity of this approach. Given the same set of data, certain scientists would split regionally differentiated groups into separate species, whereas others would treat them as members of a single, geographically variable species.

Many changes in North American salamander taxonomy during the last two decades have been controversial. Fewer than 110 to as many as 150 or so species could be recognized in this treatment depending on how a particular scientist interprets taxonomically difficult groups. Here I recognize 127 species (excluding unisexual *Ambystoma*) and rely primarily on the biological species concept for species recognition.

NOMENCLATURE

At this juncture in the evolution of salamander nomenclature, I feel that it is more important to seek nomenclatural stability in the published literature and in field guides than to radically change the existing nomenclature for the sake of being a philosophical purist. In a work of this breadth, it is also important to be as consistent as possible in the treatment of all species. Thus, I have used the following guidelines for interpreting taxonomically difficult groups:

1. In cases in which closely related groups occur allopatrically and show moderate to high levels of genetic divergence, I treat each as a separate species. Examples include *Plethodon idahoensis, Dicamptodon aterrimus,* and *Rhyacotriton olympicus.*
2. In cases in which groups appear to interbreed freely in all areas of geographic contact, I treat them as being conspecific. Examples of described species that are not recognized in this treatment include *Desmognathus santeetlah* and *Plethodon fourchensis.*
3. In cases in which groups form narrow hybrid zones and there is evidence of restricted gene flow or partial reproductive isolation between forms, I treat each form as a separate species. Examples of these species pairs include *Dicamptodon tenebrosus–D. ensatus* and *D. orestes–D. carolinensis.*
4. In cases in which groups extensively interbreed in many areas of a species' range, but are reproductively isolated in others, I treat the complex as a single species. An example is *Ensatina eschscholtzii.* One exception is *Plethodon jordani* and *P. oconaluftee,* for there is evidence that hybridization between these species was triggered by recent anthropogenic disturbance.
5. In cases in which broadly sympatric groups show very limited hybridization, I treat each group as a separate species. Examples of such pairs that occasionally hybridize include *D. ochrophaeus–D. fuscus* and *P. kentucki–P. glutinosus.*
6. In cases involving unisexual *Ambystoma* of hybrid origin, none of the biotypes is formally recognized, and all are referred to by their genomic complements.

7. In cases in which closely related groups that exhibit moderate genetic differentiation occur parapatrically, I do not recognize proposed taxonomic revisions unless zones of contact have been carefully examined and the degree of gene flow between groups has been quantified. In cases in which zones of contact have not been examined in sufficient detail to apply criteria (2) and (3), I retain the older nomenclature and treat these as unresolved species complexes. Examples include the *Eurycea bislineata* complex and most members of the *Plethodon glutinosus* complex.

The common names of certain North American salamanders were unstable prior to 1960. However, the publication of field guides to North American amphibians and reptiles by Conant (1958, 1975) and Stebbins (1966, 1985) largely stabilized the use of English vernacular names applied to North American salamanders. Attempts have been made to formally standardize common name usage for North American salamanders (Collins 1990; Collins et al. 1978, 1982). However, many herpetologists have not fully adopted these names, in part because many of the proposed standard names differ from common names that traditionally have been applied to particular species. Other references for common names, such as the *Catalogue of American Amphibians and Reptiles* and the *Checklist of Vertebrates of the United States, the U.S. Territories, and Canada* (Banks et al. 1987, 1998), are inconsistent with the most recent checklist of standard names (Collins 1990). Instead, these generally follow the traditional names used in the published literature and by Conant (1958, 1975) and Stebbins (1966, 1985). Here, I retain common names that have historically been stable (e.g., red-backed salamander, black-bellied salamander) and that are consistent with the second edition of the *Checklist of Vertebrates of the United States, the U.S. Territories, and Canada* (Banks et al. 1998).

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