SPECIES IN CONCEPT AND PRACTICE: HERPETOLOGICAL APPLICATIONS

DARREL R. FROST[1] AND DAVID M. HILLIS[2]

[1]*Museum of Natural History, The University of Kansas,
Lawrence, KS 66045-2454, USA*
[2]*Department of Zoology, The University of Texas,
Austin, TX 78712-1064, USA*

ABSTRACT: The biological species concept, long entrenched in herpetological taxonomy, has been seriously challenged conceptually and operationally over the past decade. We review alternative concepts and operational approaches as they apply in herpetology, and argue for a concept of species that is consistent with recovered phylogenetic history. We further argue that the entities whose names should be placed in the Linnaean species category can be either largest recovered biparental lineages or uniparental tokogenetic arrays. We also show that any method used for the identification of species is bound to fail with some frequency, and that invoking a particular arbitrary level of genetic distance or morphological divergence as a "species criterion" is neither appropriate nor fruitful. Finally, we present some examples of application of the evolutionary species concept to amphibians and reptiles.

Key words: Species concepts; Amphibians; Reptiles; Herpetology; Genetic distance

"The foundations of systematics lie in ontology, not in subjective epistemology. Systems and their elements should be distinguished from classes; only the latter are constructed from similarities. The term classification should be restricted to ordering into classes; ordering according to systematic relationship may be called systematization". [G. C. D. Griffith, 1974:7]

OUR purpose is to discuss and contrast, within the context of herpetology, the currently popular species concepts as they relate to biparentals, uniparentals (e.g., some species of *Cnemidophorus*), and hybridogens (e.g., many organisms in the *Rana "esculenta"* complex), as well as to discuss species concepts and definitions with respect to operationalism (e.g., the taxonomic partitioning of former *Plethodon glutinosus* by Highton, 1989). Because species, unlike higher taxa, have been considered to be unitary evolving entities (= lineages), they have been regarded with particular interest by evolutionary biologists. However, the nature of species has always been controversial, and recent discussions have been increasingly sophisticated philosophically (e.g., Cracraft, 1987; Ghiselin, 1987; Mayr, 1987; Williams, 1985). This renascence of systematic philosophy has occurred concomitantly with the popularization of the notion that taxonomy, as a set of statements about relationships, must be logically consistent with the recovered history of evolution (Hennig, 1966; Hull, 1964; Wiley, 1981*a*).

In this discussion, we shall distinguish the Linnaean species category from the theoretical class(es) of entities whose names are arguably placed at that rank. Often, this distinction has been obscure, in large part because many authors have not consciously distinguished them. We recognize that our taxonomically biased discussion could result in some misunderstanding; because species concepts must apply across all life, our discussion will be "herpetological" only in the examples noted. Our purpose is not to prescribe a set of operations that will allow the unerring determination of species status. In fact, we shall suggest that any such set of operations or rules will fail at some level [i.e., we will have to accept errors of Type I (recognizing more species than exist) and Type II (recognizing fewer species than exist)] because of the properties of the entities being discovered, and because of the fact that data from any "snapshot" in time provide an inadequate amount of information on which to make decisions about the limits, properties, and fates of dynamically evolving entities. Instead of rules and operations, we offer a view that allows us to

appreciate the limits of our inferential abilities, and thereby to recognize insoluble problems.

REVIEW OF SPECIES CONCEPTS
Biological Species Concept

The genetic or biological species concept (Dobzhansky, 1937; Mayr, 1942, 1957*a*, 1969) has been the dominant concept of species for many years, and although it has been the object of considerable controversy, its staying power cannot be denied. According to Mayr (1969:26), "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups". Mayr considered "species-ness" (reproductive compatibility) to be a "nondimensional" (= relational) property of populations. That is, "species-ness" shared between two populations is an essential property independent of appeal to phylogenetic proximity or distinctiveness of diagnosis. This "nondimensional" aspect of the "biological" species concept depends on sympatry as the critically important test of species distinction. That is, two populations are not parts of the same species if their constituent organisms are reproductively incompatible in sympatry.

Because allopatric populations cannot be evaluated directly under this concept, Mayr developed the "multidimensional" (= polytypic) species concept. Under this concept, separated populations would be ranked as conspecific if they were judged to be reproductively compatible. Because of difficulties in evaluating reproductive compatibility directly, inference of rank of relationship between populations usually has been made by correlation with a subjective measure of overall organismal similarity between populations, although organismal ability to hybridize in laboratory crosses (i.e., gametic compatibility) has been used as an indication of shared "species-ness", or propinquity of relationship, in some studies (e.g., Blair, 1972, in *Bufo*; Moore, 1947, in the *Rana pipiens* complex). Assessment of reproductive compatibility, either by inference or observation, is both a grouping and a ranking criterion under the biological species concept.

Because Mayr and supporters did not regard species necessarily either as lineages or as monophyletic groups, this view renders "biological" polytypic species as essentialist constructs. That is, "species-ness" is an essence, shared among groups, independent of propinquity of descent. Therefore, it is possible (and under this concept, acceptable) that some populations of a biological species are more closely related phylogenetically to other biological species than to populations with which they are reproductively compatible. Although one might assume intuitively that reproductive compatibility between populations should be a reasonably good measure of evolutionary relationship, this belief has not been borne out by data. In frogs of the *Rana pipiens* complex, for example, some of the more distantly related species show high gametic compatibility (a subset of reproductive compatibility) in artificial hybridization experiments, whereas gametic incompatibility is well developed in many pairs of more closely related species (Hillis, 1988).

If reproductive compatibility among populations is seen for what it is, a shared primitive feature, discordance between overall similarity and evolutionary (= phylogenetic) relatedness should not be surprising (Rosen, 1978). Because reproductive compatibility is not an accurate measure of evolutionary relatedness, grouping of populations into taxonomic "species" (= binomials) on the basis of reproductive compatibility must be rejected as logically inconsistent with the study of the underlying process, evolution (Hennig, 1966; Rosen, 1978; Wiley, 1978). Therefore, as a working concept, the biological species concept is worse than merely unhelpful and nonoperational—it can be misleading. Indeed, application of the biological species concept often hinders attempts to recover the history of evolution (Bremer and Wanntorp, 1979; Cracraft, 1983; Donoghue, 1985; Rosen, 1978, 1979; Wiley, 1978, 1981*b*).

In addition to obstructing progress in recovering history, the biological species

concept does not apply to uniparental populations because uniparentals do not have reproductive compatibility with other organisms under normal circumstances. There is no reproductive interaction within uniparental populations, and, therefore, no formation of a plexus of tokogenetic relationships. Although not wrong in principle, a strict application of the biological species concept would require that every individual uniparental organism be regarded as a distinct species, because each is reproductively isolated, both potentially and actually, from other organisms. The problem of uniparentals is not unique to the biological species concept and will be discussed more fully below.

Evolutionary Species Concepts

The biological species concept was, in part, a reaction to the typological (= Aristotelian) concepts of species that had gone before. Real progress was not made in the philosophy and practice of species recognition until the ideas were popularized that (1) taxon recognition must be logically consistent with recovered history (Hennig, 1966; Hull, 1964; Wiley, 1981a); and (2) species cannot be viewed as classes (= sets of organisms), but instead as particulars (= individuals = systems = entities) that have objective reality (Ghiselin, 1966, 1974, 1981, 1987; Griffith, 1974, 1976; Hennig, 1966; Hull, 1976, 1978, 1980, 1981; Mayr, 1976). In response to these philosophical advances, a "family" of concepts has emerged in which the recognition of entities is dependent on, and logically consistent with, the recovered history of evolution.

The evolutionary species concept of Wiley (1978, 1980, 1981b) is rooted historically in the evolutionary species concept of Simpson (1961). Unlike the biological species of Dobzhansky (1937) and Mayr (1942, 1969), the evolutionary species of Simpson is explicitly dimensional. First defined by Simpson (1961:153) as "a lineage (an ancestral–descendant sequence of populations) evolving separately from others and with its own unitary role and tendencies", this was subsequently modified slightly by Wiley (1978:18) to "a single

lineage of ancestral–descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate". Although the views of Simpson and Wiley could be construed as identical, as evidenced by their species definitions, in fact their concepts are considerably different. Simpson believed that the recognition of polytypic species followed logically from his definition; Wiley did not. Simpson did not believe that statements about species were logically reducible to statements about the recovered historical relationships of the constituent populations of polytypic species; Wiley did. That is, Wiley would apply his evolutionary species concept only in ways that are consistent with recovered historical relationships; Simpson would not. Simpson believed that his lineage concept, because of its continuity, required that arbitrary "chronospecies" be recognized; Wiley did not, arguing instead, like Hennig (1966), that species are delimited from speciation to speciation. At least for biparentals, one is hard pressed to find any difference of substance in terms of application between Simpson's (1961) concept of species and the biological species concept of Mayr (1942, 1969).

Both Simpson and Wiley considered the evolutionary species concept to apply equally well to uniparentals and biparentals. However, uniparentals clearly do not form "lineages of populations", forming, instead, historical groups of organism lines (tokogenetic arrays[3]). In uniparentals, phylogenetic and tokogenetic relationships are identical because tokogenetic relationships in these organisms are inherently hierarchical (de Queiroz and Donoghue, 1988; Hull, 1980). However, in biparentals, phylogenetic relationships of lineages (= historical relationships among sexual plexuses) cannot be reduced to tokogenetic relationships of organisms within those

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[3] These are usually referred to as "clones". Because the term "clone" carries an erroneous implication of "identicalness", it has resulted in considerable confusion in discussions of uniparentals (Frost and Wright, 1988).

sexual plexuses, because biparental toko-genetic relationships are not inherently hierarchical (Hennig, 1966: his Fig. 6).

According to Wiley, evolutionary species are the largest evolving entities, as opposed to larger units (i.e., monophyletic groups) that are solely the historical products of speciation. That is, an evolutionary species is the largest lineage on a single phylogenetic trajectory. Relatively small geographic components (sublineages) may evolve through differential reproduction of their constituent organisms, and these components may interact through time, causing the larger system to evolve (Hull, 1980). Whether or not this leaves room for distinctive populations that are nearest relatives to be considered conspecific remains arguable, if not practically untestable. There is clearly no technique, short of very long term observation, that will unambiguously identify "largest" evolving systems. This failure of identification stems in part from our inability to know anything *precisely* about the limits, origin, and fate of historical entities (= individuals in the philosophical sense) (Ghiselin, 1974, 1981; Hull, 1976, 1978, 1980).

Wiley's and Simpson's views share the same operational problem, but to considerably different degrees. As theoretical concepts, they deal with dynamic evolving lineages (possibly composed of interacting sublineages). Some groups of populations judged "paraphyletic" by character analysis under Wiley's view may reconsolidate in the future and prove really to have been temporarily isolated parts of a single Simpsonian evolutionary species. Also, allopatric lineages, whose component organisms are mutually apomorphic but which share reproductive compatibility, would be judged conspecific under the Simpsonian concept, but would be considered distinct species under the Wiley criterion. Further, these allopatric populations may never come back together, but instead continue to differentiate and even develop reproductive incompatibility. Operational difficulties notwithstanding, no one can seriously doubt that there must be "largest" components that evolve, because there clearly is a disjunction between evolving

lineages and the "ghosts of lineages past", those entities called historical or monophyletic groups. Such groups were once species, but they lost their internal cohesion and integration through time, and their parts (component lineages) have continued to evolve (e.g., *Terrapene*, Chamaeleonidae, and Amniota). What makes Wiley's view superior to that of Simpson is that it makes a concerted effort to be logically consistent with recovered history. This is only reasonable, because one can only tell where lineages (or their parts) have been, not where they are going.

Phylogenetic Species Concepts

According to the operational views of Rosen (1978, 1979), Nelson and Platnick (1981), and Donoghue (1985; discussed and amplified by de Queiroz and Donoghue, 1988), and the more theoretical views of Cracraft (1983, 1987; discussed at length by McKitrick and Zink, 1988), species are defined as the smallest detectable samples or populations with unique sets of characters. Rosen would restrict this to geographically constrained populations diagnosed by one or more apomorphies. Donoghue would consider those populations that are diagnosed by apomorphies to be species, and those without apomorphies to be metaspecies, but the intent appears to be the same.

Cracraft (1983:169–170) held that a phylogenetic species is "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent". Although this resembles the definitions of Rosen and Nelson and Platnick, Cracraft separated the concept of species from the character distribution of a species' constituent organisms, because "ancestral" species could not be recognized in any other way. More importantly, however, the characteristics of parts (= organisms) of a supraorganismal entity are clearly irrelevant to the existence of that supraorganismal entity. A phylogenetic species need only have lineage integrity; characters, which are properties of organisms and not properties of higher level entities, are not "defining properties" of lineages, but instead are

simply "symptomatic" of evolutionary relationship, and therefore useful in the inference of evolutionary entities.

What joins the "phylogenetic" species concepts of Rosen (1978, 1979), Platnick and Nelson (1981), Cracraft (1983, 1987), and Donoghue (1985) with the "evolutionary" species concept of Wiley (1978, 1981*b*) is that they all are logically consistent with the recovered history of evolution. The difference of consequence between the "phylogenetic species" of Rosen, Platnick and Nelson, Cracraft, and Donoghue and the "evolutionary species" of Wiley is that a "phylogenetic species" is the *smallest* detectable supraorganismal system. Problems with this view are immediately apparent. Although it might be dismissed as an operational complaint, the time-frame in which phylogenetic species are discerned becomes critically important. Is a jar of fruit flies, with or without apomorphies, a phylogenetic species? If not, what is the justification for excluding entities such as these micro-lineages? Rosen (1978, 1979) and Nelson and Platnick (1981) rejected the utility of a theoretical species concept in favor of an operational concept that would consider terminal taxa in biogeographic analysis to be species. In contrast, Cracraft (1983) explicitly restricted his discussion to biparental lineages, and was looking for the smallest evolving units, the "atoms" of the evolutionary process. Donoghue (1985) took a similar position by equating speciation with the acquisition of apomorphies and, more surprisingly, attempting to reduce phylogenetic explanations to tokogenetic explanations (a position rejected by Hennig, 1966)[4]. Regardless, any attempt to find *the* basic unit of evolution is doomed to failure because *any* cohesive supraorganismal historical system is a lineage, and therefore something that can evolve. If there are "atoms" in evolutionary theory, they must

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[4] More recently, de Queiroz and Donoghue (1988) have accepted the species-as-individuals thesis, but continue to reduce statements about "monophyly" or "paraphyly" of a single population to tokogenetic explanations, a view that requires that populations be treated as sets of organisms.

be replicators and interactors in the sense of Hull (1980, 1988). Species, either evolutionary or phylogenetic, are lineages, but any evidence to support them necessarily as replicators or interactors is lacking. Looking for a general class of entities at the small end of the continuum of organization of evolving supraorganismal entities is not going to be fruitful or helpful. This is not to say that a class such as described by Cracraft does not exist; as with largest entities that evolve, there must be smallest entities that evolve, however transitory.

Although Simpson (1961) and Wiley (1978, 1980, 1981*b*) believed that their concepts applied to uniparentals, this was in error. Only the phylogenetic operationalists, Rosen (1978, 1979), Platnick and Nelson (1981), and Donoghue (1985), provided definitions that were amenable to recognizing uniparental historical groups as species. We will discuss this problem further under "Uniparentals".

Our Concept of Species

Within evolutionary biology, the choices between alternative species concepts and applications of the species category are clear.

(1) The species category could be used to carry names that represent hypotheses of future interactions of parts of evolving lineages, regardless of the phylogenetic relationships of those parts to other evolving lineages [roughly equivalent to the view supported by Simpson (1961) and Ghiselin (1987), and in a relational sense by Mayr (1942, 1969)]. Although no operation can foretell the future, these hypotheses are theoretically testable (one need only live for a very long time to observe the future as it unfolds). The reason for using the species category for estimated "largest *evolving* entities" is to make the species category contain the names of a class of comparable entities. This "comparability" supposedly would enhance making generalizations about the process of "speciation" (i.e., the development of intrinsic isolation of a lineage from other lineages). To accept this position, one needs to adopt the view that knowledge of these "largest"

evolving entities cannot be obtained merely by recovering the history of their parts, because there is no reason to believe that interacting sublineages must appear "monophyletic" at all points in time. Therefore, the species category could be used to depict "paraphyletic" groups of populations, because we hypothesize that these populations will reconstitute in the future. The problem with this view is that "speciation" as a process of developing lineage independence is not studied using a taxonomy. In fact, a taxonomy based on inferences of reproductive compatibility would not be particularly helpful for these studies. Because "speciation" studies depend on relational comparisons, ideally, one would want to study populations that are cladistic nearest relatives. This would be best served by using a taxonomy that was logically consistent with recovered history (i.e., following Alternatives No. 2 or No. 3).

(2) The species category could be used to carry names of lineages whose components (if distinguishable) are not incontrovertibly on different phylogenetic trajectories (i.e., sublineages, if distinguishable, are reproductively compatible), as long as these sublineages do not form a paraphyletic group in recovered history. The species category would carry names of single populations or monophyletic groups of populations that are either unresolved or estimated to be interacting through time. The species category would then not be a class of largest *evolving* lineages; instead it would represent the largest entities that *have evolved* whose parts, if distinguishable, are not likely to be on different phylogenetic trajectories. Instead of being a class of entities reflecting "speciation", the category would be useful for historical investigations (e.g., biogeography, character evolution, ecological evolution, evolution of reproductive incompatibility) and would still represent relatively large entities. Operational problems would remain, but would be minimized in comparison with Alternative No. 1. The subspecies category could be used theoretically for sublineages not incontrovertibly removed from the possibility of interaction with other sublineages, but the use of this category would necessarily follow recovery of the historical relationships of the subpopulations.

(3) The species category could be used for the smallest geographically constrained lineages discovered by character analysis and geographical investigation (i.e., species as the smallest geographically integrated lineages detectable by character analysis). As with Alternative No. 2, this view is logically consistent with historical questions asked of taxonomies. However, although Alternative No. 2 logically has a useful upper limit (i.e., a monophyletic group of reproductively compatible populations), the lower limit of application of Alternative No. 3 could be extremely transitory components (i.e., local demes).

Our concept of entities to be placed in the species category conforms to Alternative No. 2, a view that is reasonably close to that of Wiley (1978, 1980, 1981*b*). We also accept the ontology of Ghiselin (1966, 1974, 1981), Griffith (1974, 1975), and Hull (1976, 1978, 1980, 1981). That is, species (as well as all unitary or historical taxa) are entities (individuals in the philosophical sense of the term). This does not aid in the operational identification of species. In fact, it allows us to walk away from some insoluble problems, because all recent philosophy of individuality predicts that our knowledge about the limits, origins, properties, and fates of historical entities is limited. Because of this, frequently lineages will not be identifiable except within very broad "confidence intervals". We may be wrong that "biological species" (Alternative No. 1) are essentialist notions based on reproductive potential, and that statements about them are not reducible to statements about the recovered history of geographically constrained constituent populations. It seems to us, however, that the biological species concept and its lineage equivalent, the evolutionary species of Simpson, are not useful or philosophically sound concepts, because they obstruct our ability to infer much of the history of evolution (Bremer and Wanntorp, 1979; Cracraft, 1983; Donoghue, 1985; Nelson and Platnick, 1981;

Rosen, 1978, 1979; Wiley, 1978, 1981*b*), and because trying to identify *evolving* lineages, whose existence is not recoverable from history, does not promise any particular payoff.

Any choice of species concepts has operational difficulties. The biological species concept has been most severely criticized on these grounds (e.g., Ehrlich, 1961; Sokal and Crovello, 1970), but Wiley's evolutionary species concept is no exception. However, given the choice of whether to search for "smallest" evolutionary entities (Alternative No. 3—phylogenetic species), which has both operational and theoretical drawbacks (like recognizing ephemeral units), or largest evolutionary entities whose recognition is constrained by evidence of recovered history, we see evolutionary species as preferable.

The standard practical worry about application of evolutionary and phylogenetic species concepts is that they would result in a great increase in the numbers of binomials (Cracraft, 1983). This concern is a case of the tail wagging the dog, since our taxonomy should report on biological diversity, not conceal it. However, as noted by Cracraft (1983) and McKitrick and Zink (1988), application of this kind of species concept would remove all of the "subspecies" denoting sections of clines or other arbitrarily delimited sections of geographically constrained populations and would, in fact, "clean up" our taxonomy significantly.

Conceiving of species as largest lineages, or, in some cases, as monophyletic groups of allopatric populations not likely to be on independent phylogenetic trajectories, does not provide a robust set of operations for the identification of species that are temporarily fragmented, nor can any theoretical concept. Minimally, however, if one thinks that allopatric populations are likely to interact, or be interacting in time, and wants to join them under a single binomial, one should demonstrate that these populations are reproductively compatible (not merely gametically compatible) and together form a monophyletic group. Conversely, general practice has "constructed" many polytypic binomials solely on the basis of overall organismal similarity between populations providing an implication of reproductive compatibility, rather than on evidence of monophyly of, and reproductive compatibility among, the component populations of the polytypic species. We assume that the likelihood of reproductively compatible populations being part of a cohesive lineage is higher if organisms (semaphoronts) are behaviorally, ecologically, and structurally very similar among populations. If the organisms among populations have already diverged strongly, we assume that it is less likely that the populations are influencing each other via immigration or that they will ultimately reconstitute a single population.

As a practical matter, no one wants to name weakly differentiated or undifferentiated allopatric populations if there is no phylogenetic reason (i.e., paraphyly of a group of allopatric populations, or reproductive isolation in the absence of morphological and/or biochemical differentiation) to do so. In fact, to start down this path is to end up imposing the "phylogenetic" species concept with its possible overreductionism.

In cases where allopatric populations have not been demonstrated to be parts of a monophyletic group of very similar populations (e.g., *Bufo m. microscaphus* and *B. m. californicus*), we consider them to be distinct evolutionary species and name them as binomials (i.e., *B. microscaphus* and *B. californicus*). In part, this is because as we have learned more and more about genetic cohesion and integration of sexual plexuses, and more "polytypic" species have been revised taxonomically, we see that there are few examples of widespread genetically integrated and cohesive taxa. It seems that each time that a traditionally viewed polytypic species has been examined closely, it turns out that species (even "biological" ones) have been confounded: see the revision of the *Pseudemys concinna–P. floridana* complex, in which Ward (1984) recognized a restricted *P. floridana*, *P. texana*, and *P. concinna* (containing the distinct allopatric "subspecies" *P. c. gorzugi* and *P. c. suwanniensis*, which should

be considered species, and the broadly intergrading defined "subspecies" *metteri*, *hieroglyphica*, and *concinna*, which have no reality as entities); the partition of *Thamnophis elegans* (sensu Fox, 1951) into *T. atratus*, *T. couchii*, *T. elegans*, *T. gigas*, and *T. hammondii* (Lawson and Dessauer, 1979; Rossman, 1979; Rossman and Stewart, 1987); the partitioning of *Sceloporus aeneus* into *S. aeneus* and *S. bicanthalis* (Guillette and Smith, 1985); and the recognition that former *Nerodia sipedon* really is at least three species (*N. sipedon*, *N. fasciata*, *N. clarkii*) (Lawson, 1987; Schwaner et al., 1980). It seems that we have good reason to be suspicious of all polytypic species and particularly of unusual phenomena, like sympatry of subspecies in *Lampropeltis triangulum* (Williams, 1974) or *Ensatina eschscholtzii* (Stebbins, 1949). For this reason, we predict that most of the large "polytypic" species left (such as *Ambystoma tigrinum*, *Necturus maculosus*, *Sceloporus jarrovii*, *S. undulatus*, *Diadophis punctatus*, *Pituophis melanoleucus*, *Lampropeltis getula*, *Tantilla rubra*, *Thamnophis sirtalis*, and *Crotalus durissus*) will be found to be composed of several evolutionary species.

Nonetheless, because recovered history cannot reject that reproductively compatible populations will interact in time, recognizing monophyletic groups of reproductively compatible populations as species is logically consistent with the evolutionary species concept. Therefore, there is nothing in the evolutionary species concept that necessarily abjures trinomials (= subspecies). However, the subspecies category has been long abused for use in naming arbitrarily defined "slices" of clines (e.g., the arbitrary delimitation of a number of "subspecies" in *Opheodrys aestivus* by Grobman, 1984; and in *Lampropeltis triangulum* by Williams, 1974). These "slices" are clearly not evolutionary entities under any definition of the term (Mayr, 1982; Wilson and Brown, 1953). In part as a result of this long-standing misuse of the subspecies category (as well as for reasons discussed above), it would be better to consider as species the allopatric and clearly

diagnosable populations that were formerly confounded with arbitrarily defined "clinal subspecies" (Wilson and Brown, 1953). As a methodological justification, because intelligent use of trinomials could only follow phylogenetic analyses that demonstrate evolutionary propinquity among populations, their application in alpha taxonomy would be precluded. Additionally, use of the subspecies category would necessitate the hypothesis that the subspecies *will* be subsumed into a larger species in the future, not *could* potentially be subsumed; they would necessarily be seen as temporarily isolated parts of the larger species.

The evolutionary species concept should also give a better measure of "species diversity", which, with the precipitous decline in the world diversity (by any definition or measure), has become such an important topic of discussion. Obviously, the decision to regard a monophyletic group of populations as a single interacting lineage (one species) or as several distinct species is not operational and comes down to traditional inanities of "lumping" or "splitting". We believe that prior to phylogenetic analyses, or studies of geographic variation, it is better to overestimate biological diversity (i.e., to "split"); we see no theoretical or operational advantage in underestimating biological diversity.

APPLICATIONS OF THE EVOLUTIONARY SPECIES CONCEPT

If we take seriously that our taxonomy should report on the recovered history of supraorganismal entities (which in themselves are inferred), we should not shrink from applying this concept, even if the application does not follow traditional practice. To this end, we will discuss several examples of taxonomically troublesome groups of amphibians and reptiles and critique their recent treatment by taxonomists. We do not mean to indicate that any of these authors were "right" or "wrong", only that their taxonomic treatments are either consistent or inconsistent with our belief that taxonomy should reflect evolutionary history.

The Plethodon glutinosus *Complex*

It may be difficult to recover the historical relationships of components of biologically diverse groups that show little morphological differentiation. The *Plethodon glutinosus* complex (slimy salamanders), recently reviewed by Highton (1989), is such a group. In his study, Highton examined allozymic variation among 135 populations formerly recognized as *P. glutinosus*, and suggested that the nominal species actually consists of "16 groups that have achieved the species level of divergence", which he named as species. Although we agree with Highton that many (perhaps all and perhaps more) of these taxa are distinct lineages that should be named, we disagree with his operationalism in identifying lineages. Specifically, he argued that any set of populations that differ in a phenogram by a Nei's genetic distance, Nei's D (Nei, 1972), of 0.15 or higher should be considered distinct species. This kind of arbitrary application of some criterion of overall similarity to the species problem is saddled with all of the same problems as is an arbitrary application of some measure of reproductive compatibility (i.e., as with the biological species concept). Although such an application "solves" the species problem by turning species into artificial class constructs, it moves us further away from producing a taxonomy that reflects evolutionary history.

Highton (1989) agreed that his chosen level of genetic distance (as estimated by Nei's D) was arbitrary, but cited Baverstock et al. (1977), who suggested that if two allopatric populations possess fixed differences at 15% of their loci, then it is probable that they belong to different "biological species". Aside from the fact that one would almost never know if allopatric taxa were different biological species (so we cannot imagine how this probability statement could be formulated), we see no justification for this argument. Taxa need not show 15% divergence to be intrinsically reproductively isolated (an adequate criterion for the recognition of species un-

der all species concepts), and many reproductively continuous clines exceed this limit if the populations at each extreme are compared. This is noted in passing by Highton, who argued that 97–98% of species follow the 15% rule (by citing Thorpe, 1982). Even if this is true, Highton probably overestimated the number of distinct historical lineages in some cases and underestimated this number in other cases. For instance, Highton de-emphasized morphological evidence in delimiting species; in some cases, he ignored morphological evidence of additional species because the levels of genetic differentiation were "too low". As an example, within the nominal taxon *P. albagula*, Highton included two morphologically distinct, parapatrically distributed forms that show no evidence of hybridization, and which apparently are distinct species.

Because Highton (1989) argued that his approach provides an objective operational method for delimiting species, we shall disregard the theoretical objections to his approach for a moment and consider some major operational problems. After arguing in favor of a criterion of 15% fixed differences in allozyme loci (the criterion of Baverstock et al., 1977), he stated that "two populations that have fixed differences at 15 percent of their loci would have . . . [a Nei's] $D < 0.16$". This is not correct; the actual limits on Nei's D for populations with fixed differences at 15% of their loci are 0 and infinity [Fig. 1; see also Hillis (1984) and Tomiuk and Graur (1988) for additional discussion of the problems with Nei's D]. The possible range of Nei's D at a set level of differentiation increases rapidly with increasing levels of polymorphism; in populations with 10 alleles/locus, the theoretical range of Nei's D in populations with 15% fixed differences greatly exceeds the range of Nei distances reported by Highton among all of his samples. Although many studies of interspecific variation concentrate on relatively invariant loci with low polymorphism, Highton scored loci with as many as 36 alleles/locus in his study. His use of highly polymorphic loci highlights another op-
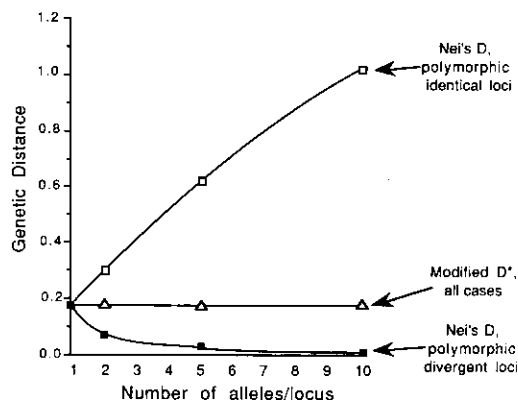
FIG. 1.—Nei's D (Nei, 1972) and Modified D* (Hillis, 1984) at 15% divergence under the conditions of polymorphic identical loci and polymorphic divergent loci. In the case of polymorphic identical loci, 85% of the loci have identical frequencies among alleles within a locus for each population, as well as among populations. The remaining 15% of the loci are fixed for alternative alleles in the two populations. In the case of polymorphic divergent loci, 85% of the loci are fixed for the same invariant allele in the two populations and the remaining 15% of the loci are represented by an array of alleles equally divided in frequency within a species, but with no alleles in common among species. Both conditions represent 15% fixed differences.

erational problem—locus selection is the single biggest determinant of any genetic distance measure. Some loci are extraordinarily variable (such as the esterase and transferrin loci examined by Highton); others evolve very slowly (Sarich, 1977). Therefore, measures of genetic distance can be increased or decreased simply by examining faster or slower evolving loci; the measures, then, are largely arbitrary.

It might be argued that although the theoretical range of Nei's D is great for a particular level of divergence, the range in real populations is more closely related to actual divergence. However, this problem clearly affected Highton's (1989) results. For instance, he chose to make an exception to his D = 0.15 criterion for two subgroups of P. chlorobryonis that differed by a mean D = 0.155, because of the borderline Nei distance and "because these populations are all morphologically similar and come from contiguous areas". However, if one corrects for the polymorphism

bias problem by using a corrected version of Nei's D (= D*) (see Fig. 1 and Hillis, 1984), then these populations differ by D* = 0.184, well above the level of differentiation of some of the taxa recognized as distinct species by Highton. Although we do not know whether these populations are distinct species, we do suggest that the approach of using an arbitrary measure of similarity to define species is doomed to failure on both theoretical and operational grounds.

If all the problems of genetic distance did not exist, and if the problems of using a phenogram to infer phylogeny did not exist, and if one were to accept the arbitrary criterion used by Highton (1989), then there are still problems with the suggested taxonomic changes. If his phenogram does, in fact, reflect phylogeny (which we doubt), then at least one of the taxa recognized by Highton is polyphyletic. One population called P. albagula by Highton clustered more closely to eight other species than it did to other populations called P. albagula. We think (as did Highton) that this reflects a failure of the clustering algorithm to reflect phylogeny accurately, but if this is the case, then it casts doubt on the other clusters as well.

So, what are the evolutionary species in the P. glutinosus complex? The study of Highton (1989) suggests that there are many historical lineages, but it is difficult to tell how many from his analysis. If P. glutinosus were a continuously variable, wide-ranging species, without any sharp contact zones, then the phenogram of genetic distances could be identical to the one presented by Highton. We are not arguing that any of the nominal taxa named by Highton are not evolutionary species; we feel that Highton erred only in trying to construct an artificially defined class concept for species. Additional study and/ or analysis will be required to identify the distinct historical lineages.

The Ensatina eschscholtzii Complex

This complex of salamanders presents a problem similar to that of the P. glutinosus complex, except that the levels of differ-

entiation (allozymic and morphological) are greater than for slimy salamanders (Stebbins, 1949; Wake and Yanev, 1986; Wake et al., 1986). The morphological identification classes in this complex have traditionally been treated as subspecies. However, the taxon known as *Ensatina eschscholtzii klauberi* is sympatric with, and shows only rare hybridization with, the taxon known as *E. e. eschscholtzii* (Wake et al., 1986). The justification for considering *E. e. klauberi* and *E. e. eschscholtzii* to be part of the same species is that they are supposed to be termini of a ring of hybridizing subspecies; however, *E. e. klauberi* contacts only *E. e. eschscholtzii*, with which it is sympatric and nonintergrading, not *E. e. croceator*, to which *E. e. klauberi* is most similar. Clearly, *Ensatina e. klauberi* and *E. e. eschscholtzii* are different evolutionary species, and appeal to "intermediate" populations not in contact with *klauberi* as justification of a single taxonomic species is only thinly veiled essentialism. Minimally, the spotted San Diegan population should be called *Ensatina klauberi*. The remaining "subspecies" in the complex require additional study; however, the existence of narrow, stable hybrid zones and no evidence of effective gene flow among other "subspecies" in the complex (Wake and Yanev, 1986) indicates that additional species should be recognized in this complex. Referring to this nonintegrating series of populations as the *Ensatina eschscholtzii* complex may be the preferable course pending resolution of the problem.

The Adelphicos veraepacis *Group*

An application of the evolutionary species concept to allopatric populations was published recently. Campbell and Brodie (1988) described a new species of snake (*Adelphicos ibarrorum*) from Guatemala and examined the phylogenetic relationships of this species to the other members of the *Adelphicos veraepacis* group in Guatemala and Mexico. All members of this species group are allopatrically isolated in small areas of montane cloud forest. The new species is phenotypically similar to a species (*A. nigrilatus*) in southern Mexico, but phylogenetic analysis shows that it is more closely related to two other species in other montane areas of Guatemala. In the past, taxonomists might have considered the new taxon to be an allopatric population or subspecies of *A. nigrilatus*, but the phylogenetic analysis demonstrates that the *A. ibarrorum* lineage is historically distinct from *A. nigrilatus*, and the new species must be recognized if one is interested in a taxonomy that reflects evolutionary history. Conceivably, the authors could have considered all members of the *A. veraepacis* group to be subspecies of a larger, polytypic *A. veraepacis*. This view, however, would have necessitated the hypothesis that these populations *could* and *would* reintegrate in the future. There is little to recommend this alternative. If the phylogenetic analysis had been based on molecular data, then it would have been appropriate to recognize *A. ibarrorum* even if it were morphologically identical to *A. nigrilatus*.

UNIPARENTALS

In biparental lineages, the sexual plexus is the unit of systematic interest, because the history of evolution cannot be reduced to the tokogenetic histories connecting organisms (Hennig, 1966). This is true in spite of the operational truism that the characteristics of a sexual plexus' constituent parts (= organisms) are used to infer the history of these higher order entities. Unlike organisms, sexual plexuses (like all supraorganismal entities) have as characteristics only their distribution in space and time and the internal cohesion that allows them to form lineages.

Comparison across all historical entities formed by tokogenetic relationships [sexual plexuses (biparental species) and tokogenetic arrays (uniparental species)] would show internal cohesion ranging from extremely high in small panmictic populations of biparentals to extremely low in highly inbred lineages of biparentals, to absent in obligate uniparentals. Even though in some biparental lineages (e.g., highly inbred lineages of rare parasitic

wasps) phylogenetic relationships may approach tokogenetic relationships, only in uniparentals (e.g., asexuals, parthenogens, gynogens, and other monoecious organisms such as obligately self-fertilizing hermaphrodites and cleistogamonts) do phylogenetic and tokogenetic relationships reach identity. Therefore, in obligate uniparentals, there can be no unitary evolving supraorganismal entity, and descent with modification (which still occurs) must be visualized as a between-organism phenomenon (Hull, 1980).

If one takes the phenomenological view that species are merely unresolved terminal sets of organisms on a cladogram (Nelson and Platnick, 1981), there is no problem in the treatment of uniparentals. And, indeed, if one does not distinguish between intrinsic and extrinsic "cohesion" of "populations" then there is no problem (Simpson, 1961; Wiley, 1978, 1981b). Problems arise only because of the ontological difference between biparental lineages and the tokogenetic arrays produced by uniparentals.

Most recent authors agree that uniparentals do not form entities of the same kind as biparentals, and, as we have discussed, so do we. However, Frost and Wright (1988) argued that because descent with modification does occur in tokogenetic lines, to ignore the existence of tokogenetic arrays is to ignore the products of evolution. Their solution, though not particularly elegant or original with them (cf. Mayr, 1957b, 1969; Mishler and Donoghue, 1982), was to maintain that the objective of taxonomy is to store information on the history of evolution, and that this objective is best served by assuming that the Linnaean species category can contain two kinds of entities, lineages estimated to be largest recovered phylogenetic units (evolutionary species) and "significant" tokogenetic monophyletic groups. This may not be satisfying philosophically, but until some *evolutionary* solution to the problem is suggested, they (and we) resist the alternative of excluding tokogenetic arrays from Linnaean nomenclature. If we make the decision to exclude them, we exclude some of the historical entities produced by evolution. Because we do not choose to exclude uniparental historical entities, we must make, therefore, a formal distinction between the Linnaean species category (i.e., binomials) and the kinds of entities that are appropriate to be ranked at that level.

Distinctive tokogenetic arrays are most well known in *Cnemidophorus* (Frost and Wright, 1988) and *Lacerta* (Darevsky et al., 1985), but they have been reported in a few species in Gekkonidae, Pygopodidae (sensu Kluge, 1987), Chamaeleonidae (sensu Frost and Etheridge, 1989), Xantusiidae, Gymnophthalmidae, and Typhlopidae (see Darevsky et al., 1985, for review).

Cole (1985) held that parthenogenetic "populations" should be named as species because they so closely approximate the attributes of biparental lineages (see also Holman, 1987; Mishler and Brandon, 1987). Although Frost and Wright (1988) were sympathetic with Cole's treatment of uniparentals, they disagreed with Cole's treatment of multiple hybrid-origin classes under single binomials, arguing that if taxa are to be evolutionary, they must have unitary origins and limits. Therefore, they held that each discerned hybrid-origin of a uniparental "lineage" constituted the origin of an independent taxon. More recently, Walker (1986), in an attempt to circumvent the inferential and philosophical problems inherent in the recognition of parthenogenetic tokogenetic arrays of *Cnemidophorus*, fell back onto subjective identification classes, outside of the Linnaean hierarchy, to contain these tokogenetic historical groups. Subsequently, Smith (1987) adopted a phenetic stance in favor of "utility" and arranged Walker's subjective classes of parthenogenetic *Cnemidophorus* into species and subspecies equal to Walker's forms within class-complexes. This was in spite of the fact that most of the "subspecies" have demonstrably independent origins in time and space, rendering the "species" polyphyletic (Frost and Wright, 1988). Both Walker's and Smith's approaches are clearly inconsistent with any taxonomy appealing to evolution for its justification and should be rejected.

Frost and Wright (1988) made a number of recommendations with regard to the

recognition of uniparental species. These can be summarized by saying that distinctive monophyletic tokogenetic arrays should be named as species, unless to do so would result in paraphyly of another named species. In the case of most (all?) parthenogenetic species in squamates, particular importance was attached to the historical origin of these tokogenetic arrays as boundaries justifying their ranking as Linnaean species. When the evidence was ambiguous with regard to single or multiple origins of hypothesized taxa, these problematic "taxa" were denoted by referring to them as complexes (e.g., *Cnemidophorus velox* complex), as temporary "solutions" pending resolution.

The hypothesized unisexual reproduction (either gynogenesis or parthenogenesis) in *Ambystoma "platineum", A. "tremblayi"* (Cuellar, 1976; MacGregor and Uzzell, 1964; Uzzell, 1964; Uzzell and Goldblatt, 1967), and *A. "nothagenes"* (Downs, 1978; Kraus, 1985a,b) has been rejected by Bogart et al. (1985) and Bogart and Licht (1986) (summarized in Lowcock et al., 1987). Lowcock et al. (1987) proposed an identificatory nomenclature ("name tags") for the various permutations of known hybrids between organisms in the biparental species *A. jeffersonianum, A. laterale, A. texanum,* and *A. tigrinum.* Their system does not apply to lineages, is strictly identificatory, and is explicitly excluded from evolutionary nomenclature; it is therefore not a topic of discussion here. At this point in time, there is no compelling evidence for the existence of unisexual (either parthenogenetic or gynogenetic) "lineages" in *Ambystoma,* so any discussion of uniparental species in amphibians is premature.

HYBRIDOGENS

One of the most exotic phenomena known in vertebrates is hybridogenesis. Most well understood in fishes of the genus *Poeciliopsis* (Schultz, 1969), hybridogenesis is also known in the *Rana "esculenta"* complex in Europe (Dubois and Günther, 1982; Monnerot et al., 1985; Tunner, 1974; Uzzell and Berger, 1975; Uzzell et al., 1975, 1980). Hybridogenesis is the formation of interspecific hybrids that differentially

produce gametes of one parental type and differentially breed with members of the other parental type, producing new hybrids with each generation. Although several hybridogenetic systems involving different biparental species are known in European green frogs (summarized by Uzzell, 1982, and Dubois and Günther, 1982), the most well-known system is the *R. lessonae–R. ridibunda–R. "esculenta"* system. In most of Europe, members of the class *R. "esculenta"* are formed as hybrids between members of *R. ridibunda* and *R. lessonae,* produce only *R. ridibunda* gametes, but differentially breed with *R. lessonae* to produce new *R. "esculenta".* The *esculenta* phenon was named by Linnaeus (1758) as *Rana esculenta,* and although it has been traditional to refer to the class of organisms that share a *ridibunda–lessonae* genotype as *R. esculenta,* the phenon is clearly a class of hybrids, and thus nonevolutionary except in the sense of reflecting whatever evolution may occur in the parental species.

In the part–whole ontology that we have adopted, there is no supraorganismal entity whose existence could be inferred that we could call *Rana esculenta.* Rather, the name *Rana esculenta* simply represents a class of frogs sharing a class of genotypes. There seem to be unusual processes going on in some of these populations of frogs (e.g., Uzzell et al., 1975, reported diploid and triploid progeny from a single *R. "esculenta"*). However, there are populations in which individuals of *R. "esculenta"* breed with other *R. "esculenta"* to produce *R. "esculenta"* (Dubois and Günther, 1982); this implies that within the class *R. "esculenta"* there may be frogs that are not hybridogens and that these may form lineages. Although we disagree that hybridogens can, by their nature, form supraorganismal evolving entities[5], we think that they should be denoted in some way,

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[5] Although each "hemi-lineage" of hybridophilic DNA in hybridogens can be regarded as forming an historical group, this does not translate to being a lineage of frogs. This would be analogous to regarding males in *Homo sapiens* (possessing Y chromosomes) as forming an evolutionary entity independent of females.

if for no other reason than that they are some of the most abundant vertebrates in Europe. Dubois and Günther (1982) suggested the term "klepton"[6] for these, and, taken as a class construct outside of evolutionary taxonomy, we have considerable sympathy with this notion as a way of keeping the nomenclature of these classes of frogs under the International Code of Zoological Nomenclature (Anon., 1985). However, a more acceptable solution would be to adopt an identificatory nomenclature along the lines of that supplied by Schultz (1969) for hybrid *Poeciliopsis* or by Lowcock et al. (1987) for hybrids in the *Ambystoma jeffersonianum-A. laterale* complex. Regardless of the unpalatability of names like *Rana* (2) *lessonae-ridibunda* or *Rana lessonae-ridibunda*, or the more general *Rana ridibunda-R. lessonae* hybridogenetic complex, these nomenclature systems do not imply that the names apply to evolutionary entities, and would retire names that apply to hybrids as such, like *Rana esculenta*. Again, if we take our system of taxonomy to be nested sets of similarity classes containing idealized phena, there would be no problem with "classifying" hybridogens, nor would there be with mules, or with having different taxa for males and females of a single evolutionary entity. Any evolutionary taxonomy, however, stores names of entities composed of organisms, not sets of organisms.

SUMMARY

Operational difficulties will always exist in trying to discern real historical entities in nature. This is a consequence of the nature of individuals (philosophical sense); they are by nature slippery. However, we see the alternatives to evolutionary species as having an equal or greater number of operational problems and additional theoretical problems. We view the primary aim of taxonomy to recover and describe

evolutionary history. This aim is not compatible with using reproductive isolation as a defining characteristic of a class concept of species, nor is it compatible with any arbitrary operational definition of species. Doubtless, we will be criticized on the grounds that the taxonomy that results from the concept of evolutionary species is too subjective. We see the alternatives as no less subjective, and resulting in much poorer descriptions of historical reality.

LITERATURE CITED

ANONYMOUS. 1985. International Code of Zoological Nomenclature, 3rd ed. International Trust for Zoological Nomenclature, London.

BAVERSTOCK, P. R., C. H. S. WATTS, AND S. R. COLE. 1977. Electrophoretic comparisons between allopatric populations of five Australian pseudomyine rodents (Muridae). Aust. J. Biol. Sci. 30:471–485.

BLAIR, W. F. 1972. Evidence from hybridization. Pp. 196–232. *In* W. F. Blair (Ed.), Evolution in the Genus *Bufo*. University of Texas Press, Austin.

BOGART, J. P., AND L. E. LICHT. 1986. Origins of polyploids in hybrid salamanders of the genus *Ambystoma*. Can. J. Genet. Cytol. 28:605–617.

BOGART, J. P., L. E. LICHT, M. J. OLDHAM, AND S. J. DARBYSHIRE. 1985. Electrophoretic identification of *Ambystoma laterale* and *Ambystoma texanum* as well as their diploid and triploid interspecific hybrids (Amphibia: Caudata) on Pelee Island, Ontario. Can. J. Zool. 63:340–347.

BREMER, K., AND H.-E. WANNTORP. 1979. Geographic populations or biological species in phylogeny reconstruction? Syst. Zool. 28:220–224.

CAMPBELL, J. A., AND E. D. BRODIE, JR. 1988. A new colubrid snake of the genus *Adelphicos* from Guatemala. Herpetologica 44:416–422.

COLE, C. J. 1985. Taxonomy of parthenogenetic species of hybrid origin. Syst. Zool. 34:359–363.

CRACRAFT, J. 1983. Species concepts and speciation analysis. Pp. 159–187. *In* R. F. Johnston (Ed.), Current Ornithology, Vol. 1. Plenum Press, New York.

———. 1987. Species concepts and the ontology of evolution. Biol. Philos. 2:329–346.

CUELLAR, O. 1976. Cytology of meiosis in the triploid gynogenetic salamander *Ambystoma tremblayi*. Chromosoma 58:355–364.

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[6] We do not agree with their other proposal that historical groups of gynogens could be called "kleptons". The tokogenetic historical groups formed by gynogens are ontologically equivalent to those formed by other uniparentals and not to the interspecific classes of hybridogens.

DAREVSKY, I. S., L. A. KUPRIYANOVA, AND T. UZZELL. 1985. Parthenogenesis in reptiles. Pp. 411–526. *In* C. Gans (Ed.), Biology of the Reptilia, Vol. 15. John Wiley & Sons, New York.

DE QUEIROZ, K., AND M. T. DONOGHUE. 1988. Phylogenetic systematics and the species problem. Cladistics 4:317–338.

DOBZHANSKY, T. 1937. Genetics and the Origin of Species. Columbia University Press, New York.

DONOGHUE, M. J. 1985. A critique of the biological species concept and recommendations for a phylogenetic alternative. Bryologist 88:172–181.

DOWNS, F. L. 1978. Unisexual *Ambystoma* from the Bass Islands of Lake Erie. Occas. Pap. Mus. Zool. Univ. Michigan 685:1–36.

DUBOIS, A., AND R. GÜNTHER. 1982. Klepton and synklepton: Two new evolutionary systematics categories in zoology. Zool. Jahrb. Abt. Syst. 109:290–305.

EHRLICH, P. R. 1961. Has the biological species concept outlived its usefulness? Syst. Zool. 10:167–176.

FOX, W. 1951. Relationships among the garter snakes of the *Thamnophis elegans* Rassenkreis. Univ. California Publ. Zool. 50:485–530.

FROST, D. R., AND R. ETHERIDGE. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). Misc. Publ. Mus. Nat. Hist. Univ. Kansas 81:1–65.

FROST, D. R., AND J. W. WRIGHT. 1988. The taxonomy of uniparental species, with special reference to parthenogenetic *Cnemidophorus* (Squamata: Teiidae). Syst. Zool. 37:200–209.

GHISELIN, M. T. 1966. On psychologism in the logic of taxonomic controversies. Syst. Zool. 15:207–215.

———. 1974. A radical solution to the species problem. Syst. Zool. 23:536–544.

———. 1981. Categories, life and thinking. Behav. Brain Sci. 2:268–283, 303–313.

———. 1987. Species concepts, individuality, and objectivity. Biol. Philos. 2:127–143.

GRIFFITH, G. C. D. 1974. On the foundations of biological systematics. Acta Biotheor. 23:85–131.

———. 1976. The future of Linnaean nomenclature. Syst. Zool. 25:168–173.

GROBMAN, A. B. 1984. Scutellation variation in *Opheodrys aestivus*. Bull. Florida State Mus. 29:153–170.

GUILLETTE, L. J., JR., AND H. M. SMITH. 1985. Cryptic species in the Mexican lizard complex, *Sceloporus aeneus*. Bull. Maryland Herpetol. Soc. 21:1–15.

HENNIG, W. 1966. Phylogenetic Systematics. University of Illinois Press, Urbana.

HIGHTON, R. 1989. Biochemical evolution in the slimy salamanders of the *Plethodon glutinosus* complex in the eastern United States. Part I. Geographic protein variation. Univ. Illinois Biol. Monogr. 57:1–78.

HILLIS, D. M. 1984. Misuse and modification of Nei's genetic distance. Syst. Zool. 33:238–240.

———. 1988. Systematics of the *Rana pipiens* complex: Puzzle and paradigm. Ann. Rev. Ecol. Syst. 19:39–63.

HOLMAN, E. W. 1987. Recognizability of sexual and asexual species of rotifers. Syst. Zool. 36:381–386.

HULL, D. L. 1964. Consistency and monophyly. Syst. Zool. 13:1–11.

———. 1976. Are species really individuals? Syst. Zool. 25:174–191.

———. 1978. A matter of individuality. Philos. Sci. 45:335–360.

———. 1980. Individuality and selection. Ann. Rev. Ecol. Syst. 11:311–332.

———. 1981. Metaphysics and common usage. Behav. Brain Sci. 4:290–291.

———. 1988. Science as a Process: An Evolutionary Account of the Social and Conceptual Development of Science. University of Chicago Press, Chicago.

KLUGE, A. G. 1987. Cladistic relationships in the Gekkonoidea (Squamata, Sauria). Misc. Publ. Mus. Zool. Univ. Michigan 173:1–54.

KRAUS, F. 1985a. A new unisexual salamander from Ohio. Occas. Pap. Mus. Zool. Univ. Michigan 709:1–24.

———. 1985b. Unisexual salamander lineages in northwestern Ohio and southeastern Michigan: A study of the consequences of hybridization. Copeia 1985:309–324.

LAWSON, R. 1987. Molecular studies of thamnophiine snakes: I. The phylogeny of the genus *Nerodia*. J. Herpetol. 21:140–157.

LAWSON, R., AND H. DESSAUER. 1979. Biochemical genetics and systematics of garter snakes of the *Thamnophis elegans–couchii–ordinoides* complex. Occas. Pap. Mus. Zool. Louisiana State Univ. 56:1–24.

LINNAEUS, C. 1758. Systema Naturae per Regna tria Naturae secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis, Vol. 1. Stockholm.

LOWCOCK, L. A., L. E. LICHT, AND J. P. BOGART. 1987. Nomenclature of hybrid complexes of *Ambystoma* (Urodela: Ambystomatidae): No case for the erection of hybrid "species". Syst. Zool. 36:328–336.

MACGREGOR, H. C., AND T. M. UZZELL. 1964. Gynogenesis in salamanders related to *Ambystoma jeffersonianum*. Science 143:1043–1045.

MAYR, E. 1942. Systematics and the Origin of Species. Columbia University Press, New York.

———. 1957a. Species concepts and definitions. Pp. 1–22. *In* E. Mayr (Ed.), The Species Problem. Am. Assoc. Adv. Sci. Publ. 50.

———. 1957b. Difficulties and importance of the biological species concept. Pp. 371–388. *In* E. Mayr (Ed.), The Species Problem. Am. Assoc. Adv. Sci. Publ. 50.

———. 1969. Principles of Systematic Zoology. McGraw Hill, New York.

———. 1976. Is the species a class or an individual? Syst. Zool. 25:192.

———. 1982. Of what use are subspecies? Auk 99:593–595.

———. 1987. The ontological status of species: Scientific progress and philosophical terminology. Biol. Philos. 2:145–166.

McKitrick, M. C., and R. M. Zink. 1988. Species concepts in ornithology. Condor 90:1–14.

Mishler, B., and R. N. Brandon. 1987. Individuality, pluralism, and the phylogenetic species concept. Biol. Philos. 2:397–414.

Mishler, B., and M. Donoghue. 1982. Species concepts: A case for pluralism. Syst. Zool. 31:491–503.

Monnerot, M., A. Dubois, and H. Tunner. 1985. Mitochondrial DNA polymerase among *Rana ridibunda, Rana lessonae* and *Rana* kl. *esculenta*: Preliminary study. Alytes 4:101–112.

Moore, J. A. 1947. Hybridization between *Rana pipiens* from Vermont and eastern Mexico. Proc. Natl. Acad. Sci. USA 33:72–75.

Nei, M. 1972. Genetic distance between populations. Am. Nat. 106:283–292.

Nelson, G. J., and N. I. Platnick. 1981. Systematics and Biogeography: Cladistics and Vicariance. Columbia University Press, New York.

Rosen, D. E. 1978. Vicariant patterns and historical explanation in biogeography. Syst. Zool. 27:159–188.

———. 1979. Fishes from the uplands and intermontane basin of Guatemala: Revisionary studies and comparative geography. Bull. Am. Mus. Nat. Hist. 162:267–376.

Rossman, D. A. 1979. Morphological evidence for taxonomic partitioning of the *Thamnophis elegans* complex (Serpentes, Colubridae). Occas. Pap. Mus. Zool. Louisiana State Univ. 55:1–12.

Rossman, D. A., and G. R. Stewart. 1987. Taxonomic reevaluation of *Thamnophis couchii* (Serpentes: Colubridae). Occas. Pap. Mus. Zool. Louisiana State Univ. 63:1–25.

Sarich, V. M. 1977. Rates, sample sizes and the neutrality hypothesis for electrophoresis in evolutionary studies. Nature 265:24–28.

Schultz, R. J. 1969. Hybridization, unisexuality and polyploidy in the teleost *Poeciliopsis* (Poeciliidae) and other vertebrates. Am. Nat. 103:605–619.

Schwaner, T. D., H. C. Dessauer, and L. A. Landry, Jr. 1980. Genetic divergence of *Nerodia sipedon* and *N. fasciata* in South Louisiana. Isozyme Bull. 13:unpaged.

Simpson, G. G. 1961. Principles of Animal Taxonomy. Columbia University Press, New York.

Smith, H. M. 1987. The concepts of species and subspecies in uniparental populations, reflected in the nomenclature of *Cnemidophorus* (Reptilia: Lacertilia). Bull. Maryland Herpetol. Soc. 23:125–127.

Sokal, R. R., and T. J. Crovello. 1970. The biological species concept: A critical evaluation. Am. Nat. 104:127–153.

Stebbins, R. C. 1949. Speciation in salamanders of the plethodontid genus *Ensatina*. Univ. California Publ. Zool. 48:377–526.

Thorpe, J. P. 1982. The molecular clock hypothesis: Biochemical evolution, genetic differentiation and systematics. Ann. Rev. Ecol. Syst. 13:139–168.

Tomiuk, J., and D. Graur. 1988. Nei's modified genetic identity and distance measures and their sampling variances. Syst. Zool. 37:156–162.

Tunner, H. G. 1974. Die klonale Struktur einer Wasserfroschpopulation. Z. Zool. Syst. Evolutionsforsch. 12:309–314.

Uzzell, T. 1964. Relations of the diploid and triploid species of the *Ambystoma jeffersonianum* complex (Amphibia, Caudata). Copeia 1964:257–300.

———. 1982. Introgression and stabilization in Western Palearctic species of water frogs. Pp. 275–295. *In* D. Mossakowski and G. Roth (Eds.), Environmental Adaptation and Evolution. Gustav Fischer, Stuttgart.

Uzzell, T., and L. Berger. 1975. Electrophoretic phenotypes of *Rana ridibunda, Rana lessonae* and their hybridogenetic associate, *Rana esculenta*. Proc. Acad. Nat. Sci. Philadelphia 127:13–23.

Uzzell, T., L. Berger, and R. Günther. 1975. Diploid and triploid progeny from a diploid female of *Rana esculenta* (Amphibia Salientia). Proc. Acad. Nat. Sci. Philadelphia 127:81–91.

Uzzell, T., and S. M. Goldblatt. 1967. Serum proteins of salamanders of the *Ambystoma jeffersonianum* complex, and the origin of the triploid species of the group. Evolution 21:345–354.

Uzzell, T., H. Hotz, and L. Berger. 1980. Genome exclusion in gametogenesis by an interspecific *Rana* hybrid: Evidence from electrophoresis of individual oocytes. J. Exp. Zool. 214:251–259.

Wake, D. B., and K. P. Yanev. 1986. Geographic variation in allozymes in a "ring species," the plethodontid salamander *Ensatina eschscholtzii* of western North America. Evolution 40:702–715.

Wake, D. B., K. P. Yanev, and C. W. Brown. 1986. Intraspecific sympatry in a "ring species," the plethodontid salamander *Ensatina eschscholtzii* in southern California. Evolution 40:866–868.

Walker, J. M. 1986. The taxonomy of parthenogenetic species of hybrid origin: Cloned hybrid populations of *Cnemidophorus* (Sauria: Teiidae). Syst. Zool. 35:427–440.

Ward, J. P. 1984. Relationships of chrysemyd turtles of North America (Testudines: Emydidae). Spec. Publ. Mus. Texas Tech Univ. 21:3–50.

Wiley, E. O. 1978. The evolutionary species concept reconsidered. Syst. Zool. 27:17–26.

———. 1980. Is the evolutionary species fiction?—A consideration of classes, individuals, and historical entities. Syst. Zool. 29:76–80.

———. 1981a. Convex groups and consistent classifications. Syst. Bot. 6:346–358.

———. 1981b. Phylogenetics: The Theory and Practice of Phylogenetic Systematics. John Wiley, New York.

Williams, K. L. 1974. Systematics and natural history of the American milk snake, *Lampropeltis triangulum*. Milwaukee Public Mus. Publ. Biol. Geol. 2:1–158.

Williams, M. B. 1985. Species are individuals: Theoretical foundations for the claim. Philos. Sci. 52:578–590.

Wilson, E. O., and W. L. Brown, Jr. 1953. The subspecies concept. Syst. Zool. 2:97–111.

APPENDIX 1

Glossary of Terms

Apomorphy: An organismal character that is evolutionarily derived with respect to an homologous ancestral character. A relational term. *See* Plesiomorphy.

Character: Any portion of the structure or behavior of an organism that may provide evidence of relationship. *See* Apomorphy, Plesiomorphy.

Cladistic: (1) Referring to the practice of ordering taxonomic entities on the basis of phylogenetic relationships. (2) Referring to a viewpoint that maintains that statements about taxonomic ordering and evolutionary history must be logically consistent.

Cladogram: A branching diagram reflecting phylogenetic relationships. *See* Phenogram, Phylogenetic.

Class: A set of particular things, considered together because of a defining property. Not necessarily localized in time and space. Because defining properties cannot evolve, classes cannot evolve. Definitions may be arbitrary (e.g., not blue) or appeal to natural regularities (e.g., diurnal predators, atoms of gold), but there is no implication that the items gathered in a class make up a working or historical system. *Examples:* stars, ions, predators, herbivores, all paraphyletic or polyphyletic groups. *See* Individual.

Cohesion: The result of the genic integration of a population that forms a tokogenetic plexus and promotes the existence of a unitary lineage. *See* Lineage, Sexual plexus.

Diagnosis: Characters that delimit a set of sample organisms from which the existence of a higher order entity (i.e., species or historical groups) may be inferred. A diagnosis *will always* fail to "identify" some to many members (e.g., developmental monsters, undeveloped zygotes) of a taxon, because taxa, as individuals, cannot be defined, only delimited ostensively. *See* Class, Individual, Ostensive.

Entity: An individual in the philosophical sense. *See* Historical entity, Individual, Monophyletic.

Epistemology: The study of knowledge and the conditions of knowing. Inquires into the justification of knowledge claims. *See* Ontology.

Essentialism: The doctrine that "kinds" are determined by intrinsic, essential properties (= essences). *See* Typology.

Gynogenesis: Unisexual reproduction in which unreduced gametes may be activated by sperm penetration, although the paternal genome is not incorporated into the zygote. *See* Parthenogenesis.

Historical entity: A taxon. *See* Historical group, Individual, Taxon.

Historical group: An entity whose parts form a monophyletic group. An ancestral species and what it has become through evolution (= ancestor and all of its descendants). In uniparentals, an ancestral organism and all of its descendants. Examples: Testudines; *Terrapene; Cnemidophorus exsanguis*; the group composed of *Plica, Uracentron,* and *Strobilurus. See* Individual, Monophyletic, Paraphyletic, Taxon.

Individual: A particular thing; characterized by being localized in time and space, having a unitary origin and fate, and having "fuzzy" limits, both temporally and spatially. Individuals are discovered and named ostensively, because any definition will always fail at some level because of the inherent "fuzziness" of individuals. If cohesion is strong enough, an individual (e.g., a mitochondrion, cell, organism, colony, hive, or kin group) may undergo some process as a unit, i.e., as an interactor, although this is not a requirement of individuality. Examples: the moon, New York, John Wright, Testudines, a cell, a mitochondrion, *Rana bwana. See* Interactor, Replicator, System.

Intensional: In reference to defining by use of a list of descriptive statements allowing one to assign to (or exclude from) membership in a class. *See* Class, Ostensive.

Interactor: An individual with enough integrity to undergo some process as a unit (e.g., an organism, a hive, a kin group). There is no compelling evidence that historical groups or species are interactors. *See* Individual.

Lineage: A sexual plexus (or interacting sexual plexuses) viewed through time. *See* Phylogenetic, Sexual plexus, Tokogenetic.

Logical consistency: Congruence between statements, or, at least lack of disagreement between statements.

Monophyletic: Not excluding from an historical group any descendants of the ancestor of that group. *See* Historical group, Paraphyletic.

Ontology: The branch of metaphysics relating to the nature and relations of being.

Operationalism: Defining the entities or classes to be discovered in a way that extends from the operation used for discovery. A scientific viewpoint that excludes metaphysics. Examples: "A species is the smallest detectable cladistically unresolved cluster of organisms", or "Art is that which sells". *See* Phenomenalism.

Ostensive: In reference to identifying by enumeration or pointing. *See* Diagnosis, Intensional.

Paraphyletic: Referring to an arbitrarily defined group (a class) containing an ancestor and some, but not all, of its descendants. Examples: Reptilia (excluding Aves), Agamidae (excluding Chamaeleonidae), *Fritziana* (excluding *Flectonotus*). *See* Historical group, Monophyletic.

Parthenogenetic: Unisexual reproduction involving the development of unreduced, unfertilized gametes. *See* Gynogenesis.

Phenogram: A branching diagram representing similarity (by some arbitrary measure) between terminal units. Sometimes erroneously considered to depict historical relationships. *See* Cladogram.

Phenomenalism: The doctrine that we should translate theories about physical objects into theories about observations and the techniques undertaken to make those observations. *See* Operationalism.

Phenon: An identification class.

Phylogenetic: Referring to historical relationships among lineages of biparental organisms. In uniparentals, relationships among ancestor–descendant lines. *See* Paraphyletic, Tokogenetic.

Plesiomorphy: An organismal character that is prim-

itive with respect to a derivative homologue. *See* Apomorphy.

Polyphyletic: Referring to an arbitrarily defined group (a class) composed of entities whose common ancestor is not included in the group. Example: Haemothermia (mammals + birds).

Reductionism: The doctrine that it is desirable to interpret a phenomenon in terms applicable to its parts. Sometimes, a doctrine that desires to convert all knowledge of some system into a representation characteristic of (and only appropriate to) a small subsystem of the system. Examples of absurd reductionism: (1) systematic theory can be reduced to population genetics theory; (2) theories of community ecology can be reduced to those of population ecology; (3) all of biology can be explained by DNA sequences.

Replicator: An entity that reproduces itself. *See* Individual, Interactor.

Reproductive compatibility: The condition in which there are no intrinsic premating or postmating factors that would result in reduced successful matings. Unrestricted potential fecundity within or between populations.

Semaphoront: An organism at a particular stage in its life history.

Set: A class. *See* Class.

Sexual plexus: A lineage taken at any section in time. A group of biparental (at least occasionally) organisms inclusively connected by a nonhierarchical "net" of tokogenetic relationships. *See* Lineage.

Speciation: The process of lineage origination. *See* Lineage.

Supraorganismal entity: An historical entity whose parts are organisms. *See* Historical group, Individual, Taxon.

System: An integrated whole composed of parts. An individual in the philosophical sense. *See* Historical group, Individual.

Taxon: An historical entity composed of organisms: either a monophyletic group or an evolutionary species. A taxon may or may not be named. *See* Historical entity, Monophyletic.

Tokogenetic: Referring to ancestor–descendant relationships between organisms. Examples: mother → daughter (uniparental); mother → daughter ← father (biparental).

Typology: A concept in which variation (both ontogenetic and interorganismal) is disregarded and members of a taxon are considered as, or nearly as, replicas of the "type".