Phylogenetic Definitions and Taxonomic Philosophy

KEVIN DE QUEIROZ

Department of Vertebrate Zoology
Division of Amphibians and Reptiles
United States National Museum of Natural History
Smithsonian Institution
Washington DC, 20560
U.S.A.

ABSTRACT: An examination of the post-Darwinian history of biological taxonomy reveals an implicit assumption that the definitions of taxon names consist of lists of organismal traits. That assumption represents a failure to grant the concept of evolution a central role in taxonomy, and it causes conflicts between traditional methods of defining taxon names and evolutionary concepts of taxa. Phylogenetic definitions of taxon names (de Queiroz and Gauthier 1990) grant the concept of common ancestry a central role in the definitions of taxon names and thus constitute an important step in the development of phylogenetic taxonomy. By treating phylogenetic relationships rather than organismal traits as necessary and sufficient properties, phylogenetic definitions remove conflicts between the definitions of taxon names and evolutionary concepts of taxa. The general method of definition represented by phylogenetic definitions of clade names can be applied to the names of other kinds of composite wholes, including populations and biological species. That the names of individuals (composite wholes) can be defined in terms of necessary and sufficient properties provides the foundation for a synthesis of seemingly incompatible positions held by contemporary individualists and essentialists concerning the nature of taxa and the definitions of taxon names.

KEY WORDS: Clade, class, composite whole, definition, defining property, essentialism, evolution, individual, intension, name, ostensive definition, phylogeny, population, set, species, taxon, taxonomy.

I. INTRODUCTION

Traditionally, the names of biological taxa have been treated as if they are defined by sets of organismal traits, that is, material traits of organisms or their parts, including morphology, physiology, behavior, ecology, genetics, and biochemistry. That view has predominated at least since the time of Aristotle (384–322 BC), persisting through the ages of Linnaeus (1707–1778 AD) and Darwin (1809–1882 AD) even into contemporary evolutionary/phylogenetic approaches to taxonomy. In the context of attempts to develop an explicitly phylogenetic system of biological taxonomy (e.g., Hennig 1965, 1966; Eldredge and Cracraft 1980; Wiley 1981a; Ax 1987), several authors have suggested the possibility of basing the definitions of taxon names on phylogenetic relationships (e.g., Wiley 1979, 1989; Ghiselin 1984; Ridley 1986; Rowe 1987; de Queiroz 1988; Gauthier et al. 1988a). Recently, de Queiroz and Gauthier (1990)

described in detail how that can be accomplished, and they explored some of the implications of phylogenetic definitions for taxonomic practices.

Here I review differences between traditional and phylogenetic definitions in the context of the history of biological taxonomy. Although much of that discussion has been presented previously (de Queiroz and Gauthier 1990), it is here modified so as to be neutral with respect to a dispute, discussed later in the paper, between contemporary individualists and essentialists. It also provides background for the subsequent analysis. In that subsequent analysis, I examine the relevance of phylogenetic definitions to several issues in the philosophy of taxonomy, including general methods for defining the names of composite wholes, the categorization of such definitions, and a dispute between contemporary individualists and essentialists concerning the nature of taxa and the definitions of taxon names. In so doing, I hope to illustrate the importance of phylogenetic definitions to taxonomic philosophy and consequently the coherence of the methodological system provided by the phylogenetic approach to taxonomy.

II. TRADITIONAL AND PHYLOGENETIC DEFINITIONS OF TAXON NAMES

Most taxonomists have not distinguished clearly between taxa and taxon names (for exceptions see Hull 1965; Ghiselin 1966a), and some have proposed explicitly that definitions apply to both (e.g., Muir 1968). Biological taxa are sometimes viewed as abstract concepts rather than concrete entities (e.g., Muir 1968; Løvtrup 1986, 1987a, b), and concepts are sometimes said to be defined in the sense of being made distinct or clear. Alternatively, taxa are sometimes viewed as concrete entities, and concrete entities are sometimes said to be defined – or of being self-defining – in the sense of marking out a boundary (e.g., Michaux et al. 1990). In this paper, I use "define" in the sense of specifying the meaning of a symbol, which is to say that definitions apply to words but not to the things symbolized by those words. My restricted use of "define" is not intended to deny the importance of clarifying concepts or of recognizing the boundaries of concrete entities, but only to avoid confusing the meanings of words with either of these other things.

Because they generally do not distinguish between taxa and taxon names, taxonomists have seldom addressed explicitly the issue of how taxon names (as opposed to taxa) are to be defined. And they often use "definition" interchangeably with "diagnosis" (Simpson 1961). Explicit statements treating lists of organismal traits as definitions of taxon names have been made mostly by philosophers (e.g., Hull 1965; Buck and Hull 1966; Ruse 1973). Nevertheless, taxonomists who use "definition" as if it is a synonym of "diagnosis" generally present only the list of characters without an additional statement specifying the meaning of the name. That is to say, either they do not distinguish between diagnoses/descriptions of taxa (i.e., lists of organismal traits) and definitions of taxon names, or else they avoid the issue of definition altogether. Either

alternative represents a failure to devise evolutionary definitions of taxon names.

Phylogenetic definitions represent a fundamental shift in outlook concerning the role of the concept of evolution in taxonomy. Under traditional definitions, that concept is granted the role of an after-the-fact explanation for the order already manifest in taxonomy instead of being taken as a central tenet from which the principles and methods of taxonomy are to be deduced (de Queiroz 1988; de Queiroz and Gauthier 1990). Denying evolution a central role in taxonomy effectively obstructs the development of a truly evolutionary or phylogenetic system of taxonomy, and it explains the delay of the Darwinian Revolution in that discipline (e.g., O'Hara 1988; de Queiroz 1988; de Queiroz and Gauthier 1990). The persistence of traditional definitions of taxon names exemplifies that delay, for such definitions effectively deny the concept of evolution a central role in the definitions of taxon names by granting organismal traits primacy over phylogenetic relationships.

Traditional Definitions

The traditional view that definitions of taxon names are to be stated in terms of sets of organismal traits has held regardless of whether those defining characters were viewed as manifestations of an eternal essence, as they were by Aristotle, and regardless of the precise method of definition. That situation is evident in the history of both the theory and the practice of biological taxonomy. Nevertheless, it is worthwhile to review certain aspects of the post-Darwinian history of taxonomy in order to support that conclusion as well as to highlight the peripheral role that the principle of evolution has played in traditional definitions.

With the acceptance of an evolutionary world view, the assumption that definitions of taxon names were to be based on organismal traits imposed severe constraints on theoretical propositions regarding the nature of those definitions. As noted by Hull (1965), traditional views concerning the definitions of taxon names have their roots in the Aristotelian method of definition. Aristotle's own theory of definitions was tied to the concept of essences; however, his general method of definition can be adopted independent of that concept. According to Hull (1965), what Aristotle advocated, in modern terms, is definition by properties that are severally necessary and jointly sufficient (for taxon membership), that is, definite conjunctive definitions. Taxa whose names are defined in terms of necessary and sufficient properties are called monothetic (Sneath 1962).

Based on organismal traits, definite definitions of taxon names – whether conjunctive or disjunctive – proved to be incompatible with an evolutionary concept of taxa (e.g., Hull 1965; Beatty 1982; Sober 1988). Evolutionary change can result in loss or modification of the very characters that supposedly define the name of a taxon. Therefore, given that the modified descendants are considered to belong to the taxon in question, one must conclude that the so-called defining characters were not truly defining, that is, they were not necessary and sufficient to define the name.

As I will argue below, this problem can be solved by adopting an evolutionary concept of defining properties. That was not, however, the way in which the problem was initially solved. Initially, defining properties were implicitly assumed to take the form of organismal traits, and alternative methods of definition were advocated in order to accommodate an evolutionary concept of taxa. Thus, although he later rejected this view (see below), Hull (1965) proposed that taxon names must be defined as cluster concepts using indefinite disjunctive definitions (see also Beckner 1959). In such a definition, no character or set of characters is necessary and any one of numerous sets is sufficient (for taxon membership). Taxa whose names are defined using indefinite disjunctive definitions are called polythetic (Sneath 1962).

Because no character or set of characters in an indefinite disjunctive definition is necessary for taxon membership, modification or loss of characters during the course of evolution can occur without invalidating such a definition. Indefinite definitions, however, have the unfortunate property of being indefinite (Suppe 1974, 1989), which means that the list of defining characters cannot be completed, even in principle (Hull 1965). Indefiniteness is necessary to accommodate the possibility of future evolutionary change. Although that flexibility makes indefinite definitions compatible with evolution, it also compromises their effectiveness as definitions.

Some taxonomists and philosophers avoided the limitations of cluster concepts by adopting an alternative view of taxa and the definitions of taxon names. Instead of viewing taxa as sets or classes, the names of which were defined by properties of their members, Ghiselin (1969, 1974, 1980, 1981, 1984, 1985) and Hull (1976, 1977, 1978) proposed that taxa be viewed as individuals, that is, composite wholes. Under this view, the names of taxa are proper names, which supposedly cannot be defined in terms of necessary and sufficient properties. Proper names supposedly can only be defined by pointing to the object being named. Lists of organismal traits, formerly treated as definitions, were viewed by individualists not as definitions but as descriptions or diagnoses. In short, definitions taking the form of necessary and sufficient properties were abandoned altogether in order to accommodate evolution.

Constraints imposed by the traditional method of definition are also evident in the history of taxonomic practices. It has been asserted repeatedly that the theory of evolution had little impact on taxonomic practices (e.g., Dobzhansky 1937; Hopwood 1950; Himmelfarb 1968; Stevens 1984). Regardless of the truth of such a broad generalization, the principle of evolution certainly did not immediately take on a central role in governing those practices. That conclusion is evidenced by the long period of time during which ideas about evolutionary relationships had little bearing on the acceptance or rejection of taxa – a phenomenon related directly to prevailing concepts concerning the definitions of taxon names. Because the meanings of taxon names were viewed as being embodied in organismal traits, such traits were effectively granted primacy over evolutionary relationships. Consequently, evolutionary relationships had little or no bearing on the acceptance or rejection of taxa.

For example, theories of polyphyletic origins for various taxa have been popular among evolutionists, and were especially so during the 1950s and 60s. A case in point is the history of ideas concerning the origins of Mammalia (reviewed by Hopson and Crompton 1969). Some authors (e.g., Simpson 1959; Olson 1959) believed that several different lineages had evolved so-called mammalian characters as the result of evolutionary parallelism. As I noted previously (de Queiroz 1988), acceptance of such a theory often did not lead to the rejection of the supposedly polyphyletic taxon, even by professed evolutionists. That situation seems to have occurred because the animals in question all shared certain characters. Given that those characters, rather than phylogenetic relationships, were viewed as defining the taxon's name, then the precise evolutionary origins of the taxon and its characters (i.e., whether they were single or multiple) were irrelevant to questions of its taxonomic validity.

A similar situation exists concerning paraphyletic taxa, those consisting of an ancestor and some but not all of its descendants. Although the situation is changing (see below), paraphyletic taxa have been widely accepted by evolutionists. As in the case of polyphyletic taxa, justifications for recognizing paraphyletic taxa have been implicitly based on shared organismal characters. This has been the case regardless of whether the argument was tied directly to shared characters or only indirectly through appeals to an evolutionary process (e.g., adaptation, anagenesis) intended to explain their existence and/or pattern of distribution (de Queiroz 1988). Because characters, rather than evolutionary relationships, were interpreted as the bases of taxa, the realization that a taxon was paraphyletic was not seen as a reason to reject it.

Evolutionary considerations gained importance in the work of Hennig (e.g., 1965, 1966) and his followers (e.g., Eldredge and Cracraft 1980; Wiley 1981a; Ax 1987), who rejected both polyphyletic and paraphyletic taxa. Nevertheless, for the most part they continued to treat the names of taxa as being defined in terms of organismal traits. This resulted in attempts to redefine the term "character" so that only synapomorphies, the supposedly defining characters of monophyletic taxa, would qualify (e.g., Wiley 1981b; Nelson and Platnick 1981). This reformulation of the concept of defining characters apparently was related to a constraint imposed by the traditional notion of defining properties. In order to reconcile the proposition that only monophyletic taxa warranted taxonomic recognition with the traditional method of definition based on organismal traits, the concept of defining character had to be modified to exclude those characters (plesiomorphies, homoplasies) shared by the organisms of paraphyletic and polyphyletic taxa.

In summary, the historical matters discussed above illustrate that defining properties of taxon names have been assumed to take the form of organismal traits. They also illustrate constraints imposed by that assumption both on the theory of taxonomic definitions and on taxonomic practices. As a consequence of equating defining properties with organismal traits, views on the method of definition of taxon names had to be modified so that they would be compatible with evolutionary concepts of taxa. In order to accommodate the possibility of

evolutionary change, either the lists of defining characters had to be made less definite, or else definition in terms of necessary and sufficient properties had to be abandoned altogether. Neither of those alternatives was able to provide satisfactory definitions of taxon names.

In the case of taxonomic practices, some evolutionists saw no inconsistency in recognizing paraphyletic or polyphyletic taxa, presumably because the organisms of those taxa shared what were judged to be significant characters. As a result, those authors attempted to justify the recognition of such taxa with some form of after-the-fact evolutionary explanation for why organisms shared characters. The importance of phylogenetic relationships was effectively denied in that such relationships could not be used to reject taxa. Some recent taxonomists acknowledged an inconsistency in the recognition of paraphyletic and polyphyletic taxa, but because they also implicitly assumed that defining characters took the form of organismal traits, they were forced to redefine the term "character" so that it would apply only to the characters of monophyletic taxa. Phylogenetic relationships were acknowledged as being important, but they did not become central to the definitions of taxon names. Instead, the concept of a defining character was reformulated so that it would be compatible with modified views about taxa. In summary, although evolutionary considerations have become increasingly important during the post-Darwinian history of taxonomy, they have until recently been denied a central role in the definitions of taxon names.

Phylogenetic Definitions

As a fundamental departure from traditional methods of definition, de Queiroz and Gauthier (1990) described three classes of phylogenetic definitions, that is, three means by which a name can be explicitly defined as referring to a particular clade (Figure 1). Phylogenetic definitions were formulated in the context of an explicitly phylogenetic approach to taxonomy – one that identifies common evolutionary descent as the underlying process from which the taxa of interest derive their existence. Common descent thus takes on the role of a central tenet from which the principles and methods of taxonomy are to be derived or deduced (de Queiroz 1988). It was from this perspective that the method of defining taxon names was reformulated so that definitions would no longer be based on organismal traits but on phylogenetic relationships. Phylogenetic definitions are thus firmly rooted in the concept of evolution, that is, of common descent. In contrast with the situation under traditional definitions, the possession of particular organismal traits is neither necessary nor sufficient for an organism to be considered part of a taxon. *What is both necessary and sufficient is being descended from a particular ancestor.*

Phylogenetic definitions, like definitions in many sciences, serve to synonymize shorthand symbols or labels with longer expressions (e.g., Popper 1950). Specifically, phylogenetic definitions are used to give names to clades, which otherwise must be identified by lengthy expressions.[1] For example,
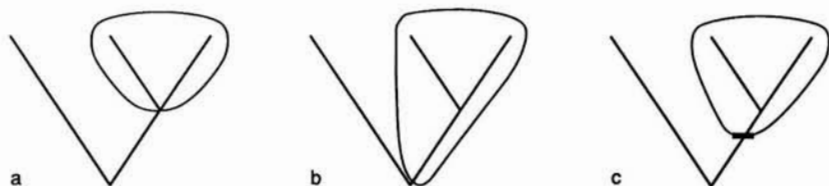
Fig. 1. Three different ways of defining taxon names phylogenetically, that is, of associating a name with a clade. a) Node-based definition (e.g., "Lepidosauria" refers to the clade stemming from the most recent common ancestor of *Sphenodon* and Squamata); b) Stem-based definition (e.g., "Archosauromorpha" refers to the clade of all saurians sharing a more recent common ancestor with Archosauria than with Lepidosauria); c) Apomorphy-based definition (e.g., "Tetrapoda", as traditionally conceived, refers to the clade stemming from the first vertebrate with limbs). After de Queiroz and Gauthier (1990).

Gauthier et al. (1988a) defined the name "Archosauria" as a shorthand symbol for the longer expression "the clade stemming from the most recent common ancestor of birds and crocodiles" (for other examples see Gauthier 1986; de Queiroz 1987; Gauthier et al. 1988a, b; Estes et al. 1988; Rowe 1988). This definition is stated in terms of common descent and the genealogical entity (clade) resulting from that process. Not only does it ignore the particular organismal traits formerly considered to define the name "Archosauria", it rejects the very premise that taxon names are to be defined in terms of organismal traits.

As a consequence of their basis in relationships of common descent, phylogenetic definitions remove conflicts between definitions of taxon names and evolutionary concepts of taxa. Thus, phylogenetic definitions resolve the conflict between evolutionary change and definitions stated in terms of necessary and sufficient properties. Under phylogenetic definitions, characters permit biologists to make inferences about whether an organism belongs to a particular taxon, but the meaning of the taxon's name is specified by relationships of common ancestry, not by characters. Consequently, evolutionary modifications and/or losses in descendant lineages can affect any or all of a taxon's diagnostic characters without invalidating the definition of its name.

Similarly, phylogenetic definitions obviate redefinitions of the term "character" that were forced by trying to reconcile traditional concepts of defining properties with the demand that only clades be recognized as taxa. Because shared organismal traits are no longer viewed as defining properties, there is no need to redefine the concept of a character so that it excludes plesiomorphies and homoplasies, thereby denying the names of paraphyletic and polyphyletic groups from having defining characters. Indeed, phylogenetic definitions can be used to eliminate paraphyletic and polyphyletic taxa in a more

direct way: they can be worded in such a way that the entities with which taxon names are associated are necessarily monophyletic (see de Queiroz and Gauthier 1990).

Phylogenetic definitions of taxon names thus represent a fundamental change in outlook. Not only do they shift the basis of taxonomic definitions from the traits of organisms to common ancestry, but in so doing they reorient the larger context of those definitions away from one in which the concept of phylogenetic relationship is peripheral to one in which that concept is a central taxonomic principle.

III. GENERAL METHODS FOR DEFINING THE NAMES OF COMPOSITE WHOLES AND THE CLASSIFICATION OF TAXONOMIC DEFINITIONS

Philosophers of taxonomy traditionally treated taxa as classes or sets (e.g., Gregg 1950, 1954, 1968; Jardine 1969; Suppe 1974, 1989; Caplan 1981) and the definitions of taxon names as intensional, rather than extensional, definitions (e.g., Buck and Hull 1966, 1969; Ruse, 1973). "Extension" and "intension" correspond approximately with "denotation" and "connotation", respectively, the former referring to the class or set of objects referred to by a term, and the latter to the property or properties something must have to belong to that class or set. Derivatively, an extensional (denotative) definition specifies the meaning of a term by enumerating the members of the class denoted by the term, and an intensional (connotative) definition specifies the meaning of a term by identifying the property or properties that something must have to be considered a member of that class.

In contrast, some authors have preferred to view biological taxa not as classes or sets but as individuals or composite wholes (Woodger 1952; Hennig 1966, 1975; Ghiselin 1969, 1980, 1981, 1984, 1985; Griffiths 1974; Hull 1978; Patterson 1978; de Queiroz 1988; de Queiroz and Donoghue 1988, 1990). The names of individuals are proper names, which supposedly can only be defined ostensively (e.g., Ghiselin 1966b, 1974, 1981, 1984; Hull 1976). Ostensive definitions specify the meaning of a term by pointing either to the object being named, in the case of a proper name, or to a member of the class being named, in the case of a common noun.[2] According to Ghiselin (1974, 1981, 1984) and Hull (1976, 1977), the proper names of individuals do not have intensions and thus cannot be defined intensionally. Hull (1976) considered ostensive definitions to be analogous to baptismal acts, which are not definitions in the traditional sense; consequently, he proposed that the proper names of individuals cannot be defined at all.

De Queiroz and Gauthier (1990; see also Ghiselin 1984) treated phylogenetic definitions as ostensive definitions of the proper names of individuals/wholes rather than extensional or intensional definitions of the names of classes/sets. Phylogenetic definitions represented a means of pointing to clades, analogous to literally pointing to diagramatic representations of clades on phylogenetic trees (Figure 1). That position, however, does not appear to be necessary for the use

of phylogenetic definitions, nor do conclusions about the significance and consequences of phylogenetic definitions (see de Queiroz and Gauthier 1990) depend on it. Examining the basis of phylogenetic definitions suggests alternative interpretations and possibilities, including a general method of definition that can be used to formulate definitions for the names of populations. Those considerations bear on the general classification of definitions as ostensive versus intensional.

Definitions of Clade Names

Although phylogenetic definitions have been viewed as ostensive definitions of the names of individuals, it is also possible to interpret them as intensional definitions of the names of classes. Once freed from the constraint of assuming that defining properties take the form of organismal traits, definition in terms of necessary and sufficient properties can be applied more generally. Thus, being the clade stemming from a particular ancestor could be interpreted as the property that something must have to be a member of the class denoted by a particular taxon name. Because of the singular nature of the clade, however, that class would have but a single member. Although conceptualizing a class for a single thing may seem procrustean, it suggests that phylogenetic definitions can at least be reconciled with the intensional method of definition. Moreover, the composite nature of clades suggests the possibility of formulating definitions of their names that conform more closely with the usual notion of intensional definition.

Viewing taxa as individuals implies that organisms are parts of composite wholes (Hull 1976, 1977; Ghiselin 1981). Therefore, monophyletic taxa, that is, named clades, are wholes made up (at one organizational level) of organisms as their parts. Composite wholes are like classes in one important respect that is critical to formulating intensional phylogenetic definitions of their names: the part/whole relation of individuals is like the member/class relation of classes or sets in that both are relations of inclusion. I do not mean to imply that the relations of classes and their members are identical to those of individuals and their parts. For example, the part/whole relation is said to be transitive whereas the member/class relation is intransitive (Gregg 1950; Hull 1976). The respect in which class/member and whole/part relations are comparable is that of inclusion in a general sense: that of containing and being contained within, of being made up of and making up, of being constituted of and constituting.[3]

This correspondence between member/class and part/whole relations permits the formulation of intensional phylogenetic definitions using phylogenetic relationships as defining properties. For example, the name "Mammalia", defined ostensively as "the clade stemming from the most recent common ancestor of monotremes and therians", could be defined intensionally as a class of organisms, for example, "those organisms comprising the most recent common ancestral population of monotremes and therians and all organisms descended from them".

Such a definition is intensional to the extent that it specifies the properties that are necessary and sufficient for taxon membership. It identifies as the intension of the taxon name those common ancestry relationships that an organism must have if it is part of the clade denoted by that name. So-called ostensive and intensional phylogenetic definitions of the same taxon name differ in their emphases on whole and parts, respectively. The former points to the whole, the clade itself, whereas the latter focuses on the parts and the relationships that unite them to form the whole. Consequently, both definitions have the same extension in terms of organisms. Put another way, the set of organisms specified by the intensional definition corresponds precisely with the organism-level parts of the composite whole specified by the ostensive definition.

In order that both ostensive and intensional phylogenetic definitions refer to the same entity, the intensional definition must be based on the property or properties uniting the component organisms to form the clade. Those properties are the relationships of common descent from which the clade derives its unity. The concept of phylogenetic relationship, that is, of common descent, is thus fundamental to formulating both ostensive and intensional definitions of clade names.

Definitions of Population Names

Until now, I have confined my discussion of taxonomic definitions to the names of clades, which are often equated with the so-called higher taxa. However, by far the greatest body of literature and the greatest controversies surrounding taxonomic definitions concern the names of species taxa. The possibility of formulating definitions of clade names in terms of necessary and sufficient properties suggests the possibility of generalizing that method of definition so it can be applied to other classes of entities that exist as composite wholes. Of obvious interest here are population-level entities, including the species taxa of many authors.

Phylogenetic relationships are fundamental to the formulation of phylogenetic definitions, because they represent the process that unites the parts of a clade to form a whole (e.g., de Queiroz and Donoghue 1988). Populations are also composite wholes, but they are members of a different class of wholes than are clades. These considerations suggest that definitions of the names of populations can also be formulated in terms of necessary and sufficient properties and that such definitions are to be based on the process from which populations derive their existence as wholes, that is, the process uniting organisms to form popula-tions. Although other processes might be invoked under different species concepts, for the purposes of the following discussion I will assume that the species category is a subclass of the class of populations and that the process responsible for the unity of a population is interbreeding.[4]

Phylogenetic definitions of clade names use the names of other biological entities (subclades, populations, or organisms) as reference points. In the case of the definitions of population names, organisms that are parts of the population

being named provide analogous reference points. If a species name is to be given to a population level entity, a convenient point of reference is the type specimen. For example, the name "*Bufo blombergi*" (the name of a species of toad) might be defined ostensively as "the most inclusive population level lineage of which CAS-SU 10419 [the holotype] is a part". The same name could also be defined intensionally as "CAS-SU 10419 and all other organisms related to that organism through interbreeding to form an inclusive population level lineage". In both cases, the nexus of interbreeding relationships delimits a population lineage – a group of anastomosing organism lineages that extends through time. A species name can be defined as referring to such an entity by specifying either particular interbreeding relationships or the population level lineage resulting from those relationships.

The preceding analysis illustrates that phylogenetic definitions are examples of a more general method of definition. To the extent that the appropriate relationships can be identified, precise verbal definitions of the names of other kinds of composite wholes, such as populations, can be formulated in a manner analogous to that used to formulate phylogenetic definitions of clade names.

The classification of Taxonomic Definitions

My prior categorization of certain taxonomic definitions as intensional versus ostensive raises issues concerning the basis for that distinction. What I have called intensional definitions of both clade and population names require pointing to one or more concrete entities (see above). That ostensive element does not, however, compromise the intensional nature of such definitions, which is to say that the definitions are stated in terms of necessary and sufficient properties. Furthermore, although an integral part of such a definition is ostensive, the ostensive component is not, by itself, defining. The entity or entities being pointed to are not the entity whose name is being defined, but only parts of it. Therefore, pointing to those parts does not define the name of the whole; it only specifies a point of reference. A particular relationship to the reference point, not the reference point itself, is the necessary and sufficient property. For these reasons, such definitions can be legitimately classified as intensional.

Although it is possible to justify the classification of certain taxonomic definitions as intensional, the distinction implied by classifying others as ostensive is problematical. That classification rests on considering a necessary criterion of an intensional definition to be the interpretation of the named thing as a class or set *of organisms*. If that criterion is dropped, so that definition in terms of necessary and sufficient properties is the sole criterion of intensional definition, then what I have called ostensive definitions of clade and species names can also be classified as intensional definitions. As noted above, even the interpretation of the named entity as a class or set may be applicable in that case, although such a class would have but a single member – one particular clade or species. Furthermore, both general classes of definitions have an ostensive

component and might therefore be classified as mixed ostensive/intensional definitions. The difficulty of categorizing phylogenetic definitions as exclusively ostensive or exclusively intensional suggests a potential need for reevaluating the general classification of definitions, but that is beyond the scope of the present analysis.

IV. DEFINITIONS, INDIVIDUALISM, AND ESSENTIALISM

The possibility of formulating definitions of the proper names of individuals in terms of necessary and sufficient properties bears on a dispute between contemporary individualists and essentialists. Those categories need not be viewed as mutually exclusive. For example, Kitts (1984), a self-proclaimed essentialist, argued that even if species are individuals, that does not count against their having essences. Nevertheless, individualists and essentialists are sharply divided in their views concerning the definitions of taxon names. As noted above, individualists argue that species and other biological taxa are not spatiotemporally unrestricted classes but spatiotemporally restricted individuals (composite wholes), the names of which cannot be defined, at least not intensionally (e.g., Ghiselin 1974, 1981, 1984; Hull 1976, 1978).

Opposing those views, contemporary essentialists (e.g., Kitts and Kitts 1979; Kitts 1983, 1984; Bernier 1984) argue that the organisms of a particular (species) taxon possess some common property or properties, which they call an essence, that can be used to define the name of that taxon. Essentialism is often viewed unfavorably (e.g., Popper 1950; Hull 1965; Mayr 1982), but at least some of the views of some contemporary essentialists appear to be compatible with the goals of taxonomists. For example, Kitts (1983, 1984) argued that for the name of a species to be useful in biological discourse, it must refer to an entity possessing theoretically significant properties that distinguish it from other entities of the same kind (i.e., other species). He also argued that such a property would have to be some kind of biologically determined relationship that must be invoked to explain the unity of a species. Thus, the essence of a species is not some eternal form or idea but simply a property that explains the unity of that species and distinguishes it from other species. If it is possible to articulate properties of that kind, then it should be possible to formulate definitions of species names in terms of defining (necessary and sufficient) properties.

Traditional definitions of taxon names are based on organismal traits, but according to Kitts (1983), neither organismal traits nor spatiotemporal location qualify as theoretically significant properties. Furthermore, as noted above, the potential for organismal traits to be modified during the course of evolution makes them unsatisfactory properties for specifying the meanings of taxon names. But these conclusions do not necessarily imply that the definition of taxon names in terms of necessary and sufficient properties is impossible, for it assumes that defining properties take the form of organismal traits. As I argued

above, if common ancestry and interbreeding relationships are considered to be defining properties, then it is possible to formulate definitions of the proper names of clades and populations in terms of such properties. This seems to satisfy Kitt's (1983) demand that the defining properties of taxon names must be biologically determined relationships that explain species (and clade) unity.

An essentialist might choose to call such biological relationships "essences"; an individualist probably would not. Others might invoke the concept of "individual essences" (e.g., Losonsky 1987). That difference notwithstanding, the interpretation of relationships as defining properties helps to resolve the conflict between contemporary individualists and essentialists concerning the nature of taxa and the definitions of their names. This interpretation enables one to formulate definitions of clade and population names in terms of necessary and sufficient properties. In so doing, it confirms the essentialist position concerning definitions, and it also implies that taxa are classes or sets. Although it contradicts the individualist position that taxon names cannot be defined in terms of necessary and sufficient properties, that error can be seen as resulting from the assumption that defining properties take the form of organismal traits. In any case, the defining properties of clade and population names are compatible with the individualist thesis that biological taxa are spatiotemporally restricted individuals, rather than spatiotemporally unrestricted classes.

These seemingly contradictory propositions are not, in fact, contradictory. In contrast with the strict dichotomy between classes and individuals presented by Ghiselin (1974, 1981) and Hull (1976), others have suggested that taxa have properties both of classes and of individuals and hence can be viewed as either or both (e.g., Cohen 1974; Van Valen 1976; Wiley 1980, 1981a; Kruskal 1981; Nelson 1985). Given that the relationships unifying the parts of a composite whole have been identified, the name of a class can be defined so that the members of that class correspond precisely with the parts of the whole in question. Consequently, any composite whole can be viewed either as an individual or as a class. This conclusion accounts for the difficulty of categorizing the definitions of clade and population names as strictly ostensive or strictly intensional.

Defining the names of composite wholes as classes implies that the taxa thus recognized are members of an unusual class of classes (compare Hull 1977, 1978; Kitcher 1984). Composite wholes, which are spatiotemporally restricted individuals, are often contrasted with spatiotemporally unrestricted classes (e.g., Hull 1976, 1978). Even if viewed as classes, however, biological taxa are spatiotemporally *restricted*. That is because the very properties used to define their names are relationships to reference points or foci that are restricted in space and time.

The synthesis attempted here does not therefore compromise the thesis that taxa are individuals. Even if viewed as classes, taxa are still composite wholes. Indeed, what I have called intensional definitions of the names of composite wholes *effectively define the name of a class as the set of parts that form an individual.* Similarly, what I have called ostensive definitions of the names of

composite wholes *effectively define the name of a class as a set consisting of one particular individual*. This is not mere semantic trickery. The advantage of being able to formulate precise verbal definitions of taxon names is sufficiently great that it outweighs objections to interpreting taxa as classes.

Such an objection was raised by Hull (1976, 1977), who argued against the interpretation of spatiotemporally restricted complexes as classes for the very reason that it collapses the distinction between classes and individuals. At issue here is the definition of the term "class". If that term is defined generally as a group whose members belong to that group because they possess some property or properties, then classes can be either spatiotemporally restricted or unrestricted, depending on the defining properties. This is the definition adopted in the present paper. Hull was concerned with the distinction between individuals and spatiotemporally *unrestricted* classes, because of the different roles that they play in scientific laws. Under the definition of "class" adopted here, that distinction is not compromised, because entities such as taxa are spatiotemporally *restricted* regardless of whether they are interpreted as individuals or as classes. As Hull himself (1978) noted, it is the distinction that is important, not the terms used to mark it. Furthermore, inasmuch as the term "universal" seems to be roughly equivalent to "spatiotemporally unrestricted class", adopting the more general definition of the term "class" does not leave the more restricted concept without a name.

Phylogenetic definitions thus provide a key to the synthesis of seemingly divergent philosophical perspectives. By treating relationships as defining properties, phylogenetic definitions provide an escape from a constraint imposed by the implicit assumption that defining properties take the form of organismal traits. Removing that constraint permits the formulation of definitions of the names of clades and other composite wholes in terms of defining properties. Such definitions represent a synthesis of what were formerly seen as fundamentally incompatible views concerning the nature of taxa and the definitions of taxon names, that is, whether taxa are classes or individuals and whether or not their names have defining properties.

V. CONCLUSION

Contrary to the opinion of some authors (e.g., Hull 1965, following Popper 1950), the preceding analysis implies that the Aristotelian method of definition was not itself a major impediment to the development of a phylogenetic system of taxonomy. Instead, the development of such a system has been hindered by the implicit assumption that the defining properties of taxon names are to be sought in the traits of organisms. Thus, the fundamental change represented by phylogenetic definitions is not one from intensional definitions to ostensive ones, nor is it a change from viewing taxa as classes to viewing them as individuals. Instead, the fundamental change represented by phylogenetic definitions – a change that is critical to the development of a phylogenetic

system of taxonomy – is a shift in the basis of taxonomic definitions from organismal traits to phylogenetic relationships. It is in this sense that phylogenetic definitions are truly evolutionary. In contrast with its role in the traditional taxonomic system, the concept of common ancestry is not merely an after-the-fact explanation for why organisms share the characters that supposedly define taxon names; instead, the principle of common ancestry is fundamental to the very meanings of those names.

Phylogenetic methods for defining taxon names were not developed until the end of the twentieth century. Although the principle of common evolutionary descent came to be widely accepted much earlier, it did not immediately lead to a revolution in biological taxonomy. Now, more than 130 years after the publication of Darwin's (1859) *Origin of Species*, taxonomists are finally freeing themselves from the bonds of ancient traditions and bringing about a reorganization of the very core of biological taxonomy (e.g., de Queiroz and Gauthier 1991). This revolution is being accomplished by taking the concept of evolution seriously. No longer is evolution being treated merely as an after-the-fact explanation for the order already manifest in taxonomy; now it is being granted the role of a central tenet upon which a new taxonomic system is being built. Phylogenetic definitions are an important manifestation of that change. As such, they are significant to both biology and philosophy.

NOTES

[1] De Queiroz and Gauthier (1990) pointed out that use of phylogenetic definitions need not be restricted to the names of clades (monophyletic taxa); they can also be applied to the names of paraphyletic and polyphyletic taxa. Thus, phylogenetic definitions are general in their basis in common ancestry, which is to say that their use is not dependent on any particular (cladistic) taxonomic philosophy. Nevertheless, phylogenetic definitions of the names of paraphyletic and polyphyletic taxa reveal the artificiality of such taxa by the manner in which they must be worded (see de Queiroz and Gauthier 1990).

[2] One may question whether ostensive definitions can truly be applied to the names of classes. Simply pointing to a member of a class is insufficient to specify the meaning of

the name, because most things that can be pointed to are members of more than one class. Pointing to a member of a class could be used in conjunction with a qualifying phrase (e.g., "green object" might be defined as "all things having the same color as that thing"), but such a definition would be intentional in that it gives necessary and sufficient properties for membership in the class; pointing merely shortcuts a more extensive description of those properties.

[3] Inclusion in the sense of comprising or containing within or being made up of should not be confused with a more restricted definition of that term used to distinguish the transitive relations of classes to their subclasses (class inclusion) from the intransitive relations of classes to their members (class membership) (see Hull 1976, p. 181). I have adopted the general use because it is common among biologists (e.g., in their reference to more and less inclusive taxa).

[4] Other phenomena that have been suggested as conferring cohesion/individuality/whole-ness on populations/species commonly are based on the presumed effect that they have on organismal similarity (de Queiroz and Donoghue 1988). However, in order to qualify as something from which an entity derives its existence as a whole, a phenomenon must actually unify the parts to form the whole. Although similarity or sameness may *permit* unifying interactions to occur, this potential alone does not confer wholeness. Further-more, the parts of a whole need not be and often are not similar (Hull 1976). To the extent that so-called phylogenetic species concepts (e.g., Cracraft 1987; Mishler and Brandon 1987) associate species names with monophyletic entities, the definitions of those names are phylogenetic definitions based on the process of common descent.

BIBLIOGRAPHY

Ax, P.: 1987, *The Phylogenetic System. The Systematization of Organisms on the Basis of Their Phylogenesis*, John Wiley, Chichester.
Beatty, J.: 1982, 'Classes and Cladists', *Systematic Zoology* 31, 25–34.
Beckner, M.: 1959. *The Biological Way of Thought*, Columbia University Press, New York (reprinted by University of California Press, Berkeley, 1968).
Bernier, R.: 1984, 'The Species as an Individual: Facing Essentialism', *Systematic Zoology* 33, 460–469.
Buck, R. C. and D. L. Hull: 1966, 'The Logical Structure of the Linnaean Hierarchy', *Systematic Zoology* 15, 97–111.
Buck, R. C. and D. L. Hull: 1969, 'Reply to Gregg', *Systematic Zoology* 18, 354–357.
Caplan, A. L.: 1981. 'Back to Class: A Note on the Ontology of Species', *Philosophy of Science* 48, 130–140.
Cohen, I. J.: 1974, 'Professor Hull and the Evolution of Science', *British Journal for the Philosophy of Science* 25, 334–336.
Cracraft, J.: 1987, 'Species Concepts and the Ontology of Evolution', *Biology and Philosophy* 2, 329–346.
Darwin, C.: 1859, *On the Origin of Species by Means of Natural Selection*, John Murray, London (reprinted by Harvard University Press, Cambridge, 1964).
Dobzhansky, T.: 1937, *Genetics and the Origin of Species*, Columbia University Press, New York.
Eldredge, N. and J. Cracraft: 1980, *Phylogenetic Patterns and the Evolutionary Process*, Columbia University Press, New York.
Estes, R., J. Gauthier, and K. de Queiroz: 1988, 'Phylogenetic Relationships within Squamata', in R. Estes and G. Pregill (eds.), *Phylogenetic Relationships of the Lizard Families*, Stanford University Press, Stanford, pp. 119–281.
Gauthier, J.: 1986, 'Saurischian Monophyly and the Origin of Birds', in K. Padian (ed.), *The Origin of Birds and the Evolution of Flight*, California Academy of Sciences, San

Francisco, pp. 1–55.

Gauthier, J., R. Estes, and K. de Queiroz: 1988a, 'A Phylogenetic Analysis of Lepidosauromorpha', in R. Estes and G. Pregill (eds.), *Phylogenetic Relationships of the Lizard Families*, Stanford University Press, Stanford, pp. 15–98.

Gauthier, J., A. G. Kluge, and T. Rowe: 1988b, 'Amniote Phylogeny and the Importance of Fossils', *Cladistics* 4, 105–209.

Ghiselin, M. T.: 1966a, 'An Application of the Theory of Definitions to Systematic Principles', *Systematic Zoology* 15, 127–130.

Ghiselin, M. T.: 1966b, 'On Psychologism in the Logic of Taxonomic Controversies', *Systematic Zoology* 15, 207–215.

Ghiselin, M. T.: 1969, *The Triumph of the Darwinian Method*, University of California Press, Berkeley (reprinted by University of Chicago Press, Chicago, 1984).

Ghiselin, M. T.: 1974, 'A Radical Solution to the Species Problem', *Systematic Zoology* 23, 536–544.

Ghiselin, M. T.: 1980, 'Natural Kinds and Literary Accomplishments', *The Michigan Quarterly Review* 19, 73–88.

Ghiselin, M. T.: 1981, 'Categories, Life, and Thinking', *The Behavioral and Brain Sciences* 4, 269–313.

Ghiselin, M. T.: 1984, '"Definition", "Character", and Other Equivocal Terms', *Systematic Zoology* 33, 104–110.

Ghiselin, M. T.: 1985, 'Narrow Approaches to Phylogeny: A Review of Nine Books of Cladism', *Oxford Surveys in Evolutionary Biology* 1, 209–222.

Gregg, J. R.: 1950, 'Taxonomy, language and reality', *The American Naturalist* 84, 419–435.

Gregg, J. R.: 1954, *The Language of Taxonomy. An Application of Symbolic Logic to the Study of Classificatory Systems*, Columbia University Press, New York.

Gregg, J. R.: 1968, 'Buck and Hull: A Critical Rejoinder', *Systematic Zoology* 17, 342–344.

Griffiths, G. C. D.: 1974, 'On the Foundations of Biological Systematics', *Acta Biotheoretica* 23, 85–131.

Hennig, W.: 1965, 'Phylogenetic Systematics', *Annual Review of Entomology* 10, 97–116.

Hennig, W.: 1966, *Phylogenetic Systematics*, University of Illinois Press, Urbana.

Hennig, W.: 1975, '"Cladistic Analysis or Cladistic Classification?" A Reply to Ernst Mayr', *Systematic Zoology* 24, 244–256.

Himmelfarb, G.: 1968, *Darwin and the Darwinian Revolution*, Norton, New York.

Hopson, J. A. and A. W. Crompton: 1969, 'Origin of Mammals', *Evolutionary Biology* 3, 15–72.

Hopwood, A. T.: 1950, 'Animal Classification from Linnaeus to Darwin', in *Lectures on the Development of Taxonomy*, Linnean Society, London, pp. 46–59.

Hull, D. L.: 1965, 'The Effect of Essentialism on Taxonomy – Two Thousand Years of Stasis (I)', *British Journal for the Philosophy of Science* 15, 314–326.

Hull, D. L.: 1976, 'Are Species Really Individuals', *Systematic Zoology* 25, 174–191.

Hull, D. L.: 1977, 'The Ontological Status of Species as Evolutionary Units', in R. E. Butts and J. Hintikka (eds.), *Foundational Problems in the Special Sciences*, D. Reidel, Dordrecht, pp. 91–102.

Hull, D. L.: 1978, 'A Matter of Individuality', *Philosophy of Science* 45, 335–360.

Jardine, N.: 1969, 'A logical basis for biological classification', *Systematic Zoology* 18, 37–52.

Kitcher, P.: 1984, 'Species', *Philosophy of Science* 51, 308–333.

Kitts, D. B.: 1983, 'Can Baptism Alone Save a Species', *Systematic Zoology* 32, 27–33.

Kitts, D. B.: 1984, 'The Names of Species: A Reply to Hull', *Systematic Zoology* 33, 112–115.

Kitts, D. B. and D. J. Kitts: 1979, 'Biological Species as Natural Kinds', *Philosophy of*

Science **46**, 613–622.

Kruskal, J. B.: 1981, 'What Does Ghiselin Mean by "Individual"?', *The Behavioral and Brain Sciences* **4**, 294–295.

Losonsky, M.: 1987, 'Individual Essences', *American Philosophical Quarterly* **24**, 253–260.

Løvtrup, S.: 1986, 'On the Existence and Definition of Taxa', *Rivista di Biologia* **79**, 265–268.

Løvtrup, S.: 1987a, 'On Species and Other Taxa', *Cladistics* **3**, 157–177.

Løvtrup, S.: 1987b, 'On the Species Problem and Some Other Taxonomic Issues', *Environmental Biology of Fishes* **20**, 3–9.

Mayr, E.: 1982, *The Growth of Biological Thought*, Belknap Press, Cambridge.

Michaux, B., C. S. White, and D. M. Lambert: 1990, 'Organisms not Species Evolve: A Reply to Ghiselin', *Systematic Zoology* **39**, 79–80.

Mishler, B. D. and R. N. Brandon: 1987, 'Individuality, Pluralism, and the Phylogenetic Species Concept', *Biology and Philosophy* **2**, 397–414.

Muir, J. W.: 1968, 'The Definition of Taxa', *Systematic Zoology* **17**, 345.

Nelson, G.: 1985, 'Class and Individual: A Reply to M. Ghiselin', *Cladistics* **1**, 386–389.

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

O'Hara, R. J.: 1988, 'Homage to Clio, or, Toward an Historical Philosophy for Evolutionary Biology', *Systematic Zoology* **37**, 142–155.

Olson, E. C.: 1959, 'The Evolution of Mammalian Characters', *Evolution* **13**, 344–353.

Patterson, C.: 1978, 'Verifiability in Systematics', *Systematic Zoology* **27**, 218–222.

Popper, K. R.: 1950, *The Open Society and Its Enemies*, Princeton University Press, Princeton [Fifth Edition, 1966].

de Queiroz, K.: 1987, 'Phylogenetic Systematics of Iguanine Lizards. A Comparative Osteological Study', *University of California Publications in Zoology* **118**, 1–203.

de Queiroz, K.: 1988, 'Systematics and the Darwinian Revolution', *Philosophy of Science* **55**, 238–259.

de Queiroz, K. and M. J. Donoghue: 1988, 'Phylogenetic Systematics and the Species Problem', *Cladistics* **4**, 317–338.

de Queiroz, K. and M. J. Donoghue: 1990, 'Phylogenetic Systematics or Nelson's Version of Cladistics', *Cladistics* **6**, 61–75.

de Queiroz, K. and J. Gauthier: 1990, 'Phylogeny as a Central Principle in Taxonomy: Phylogenetic Definitions of Taxon Names', *Systematic Zoology* **39**, 307–322.

de Queiroz, K. and J. Gauthier: 1991, 'Principles of Phylogenetic Taxonomy: Reorganizing the Taxonomic System around the Central Tenet of Common Descent', submitted to *Systematic Biology*.

Ridley, M.: 1986, *Evolution and Classification. The Reformation of Cladism*, Longman, London.

Rowe, T.: 1987, 'Definition and Diagnosis in the Phylogenetic System', *Systematic Zoology* **36**, 208–211.

Rowe, T.: 1988, 'Definition, Diagnosis, and Origin of Mammalia', *Journal of Vertebrate Paleontology* **8**, 241–264.

Ruse, M.: 1973, *The Philosophy of Biology*, Hutchinson University Library, London.

Simpson, G. G.: 1959, 'Mesozoic Mammals and the Polyphyletic Origin of Mammals', *Evolution* **13**, 405–414.

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

Sneath, P. H. A.: 1962, 'The Construction of Taxonomic Groups', in G. C. Ainsworth and P. H. A. Sneath (eds.), *Microbial Classification, 12th Symposium of the Society for General Microbiology*, Cambridge University Press, Cambridge, pp. 289–332.

Sober, E.: 1988, *Reconstructing the Past. Parsimony, Evolution, and Inference*, MIT Press, Cambridge.

Stevens, P. F.: 1984, 'Metaphors and Typology in the Development of Botanical Systematics 1690–1960, Or the Art of Putting New Wine in Old Bottles', *Taxon* **33**, 169–211.

Suppe, F.: 1974, 'Some Philosophical Problems in Biological Speciation and Taxonomy', in J. A. Wojciechowski (ed.), *Conceptual Basis of the Classification of Knowledge*, Verlag Dokumentation, Pullach/München, pp. 190–243.

Suppe, F.: 1989, *The Semantic Conception of Theories and Scientific Realism*, University of Illinois Press, Urbana.

Van Valen, L.: 1976, 'Individualistic Classes', *Philosophy of Science* **43**, 539–541.

Wiley, E. O.: 1979, 'An Annotated Linnaean Hierarchy, with Comments on Natural Taxa and Competing Systems', *Systematic Zoology* **28**, 308–337.

Wiley, E. O.: 1980, 'Is the Evolutionary Species Fiction? – A Consideration of Classes, Individuals, and Historical Entities', *Systematic Zoology* **29**, 76–80.

Wiley, E. O.: 1981a, *Phylogenetics. The Theory and Practice of Phylogenetic Systematics*, John Wiley and Sons, New York.

Wiley, E. O.: 1981b, 'Convex Groups and Consistent Classifications', *Systematic Botany* **6**, 346–358.

Wiley, E. O.: 1989, 'Kinds, Individuals, and Theories', in M. Ruse (ed.), *What the Philosophy of Biology Is*, Kluwer Academic Publishers, Dordrecht, pp. 289–300.

Woodger, J. H.: 1952, 'From Biology to Mathematics', *The British Journal for the Philosophy of Science* **3**, 1–21.