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Definition and Diagnosis in the Phylogenetic System

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Ghiselin (1984 and elsewhere) has pointed out that in taxonomy different operations have often been confused under the term 'definition.' These operations are performed so that we may distinguish between taxa. In conventional logic a definition states the attributes that are both necessary and sufficient for a name to apply; the thing must have the attribute(s) if it is to be properly called by the name. The various operations confused under the term 'define' may indeed yield proper definitions, but whether this is true depends upon the particular theoretical view of taxa under which the operations are performed.

In one commonly employed sense of 'define,' a group of characters that might be useful for identifying a particular taxon is assembled. If taxa are viewed as nominal classes, as in phenetic systems, they may then possess defining attributes such as morphological or biochemical characters. Provided that such characters are both necessary and sufficient for membership in the class, the statement of characters constitutes a proper definition. However, if taxa are viewed as individuals in the phylogenetic system, Ghiselin (1984) quite rightly pointed out that they may not possess defining characters because characters may transform without affecting the individuality of the taxon. The notion of defining characters cannot be reconciled with the concept of phylogenetic individuality. As Ghiselin argued, if taxa are individuals, a statement of characters does not yield a proper definition. An assemblage of characters to be used in identifying a taxon might more appropriately be referred to as a 'diagnosis' (but see below); it does not properly constitute a 'definition' because individuals may not be defined in terms of characters.

Another sense of 'define' has to do with delimiting boundaries between entities. If

taxa are viewed as nominal classes, they can be delimited and properly defined by a statement of the necessary and sufficient characters for membership as just described. However, taxa cannot be defined in this way if they are viewed as individuals. Ghiselin argued:

If taxa are individuals, then they do not and cannot, in principle, possess defining properties. Their names can be defined, but not in terms of defining properties. They are defined ostensively, connecting the symbol with the thing as at a christening. That taxa are defined ostensively is clear from the standard procedure. Type designation fixes the reference, and nothing more. The names of species are proper names, just like your name or mine. They designate 'that thing' and entail no properties whatsoever. That the names of organisms and species are proper follows from the fact that individuals can change. So far as phylogenetic classification goes, nobody ever provided anything but an ostensive definition for a taxon, and nobody ever will. Names of clades can be ostensively defined by reference to the common ancestor and all of its descendants. Polyphyletic and paraphyletic taxa have to be treated as classes of wholes or parts of wholes, but the wholes themselves have no defining properties [Ghiselin, 1984:106].

Ghiselin appears correct that if taxa are individuals they can have no defining characters and that their names can be only ostensively defined. But it is not clear that taxa themselves can be defined only ostensively; on the contrary, proper definition of individuals would appear to be an important goal in phylogenetic analysis. The standard procedure of type designation fixes the name of a taxon, but it plays no direct role in perceiving or delimiting the boundaries of an individual. Although type designation may constitute a proper definition in some sense in phenetic systems, it does not provide a proper definition in the phylogenetic system. In the latter, however, common ancestry is one criterion that is both necessary and sufficient for membership in a monophyletic taxon, and it thus constitutes more than a mere ostensive def-

initiation. If taxa evolve and have histories, then common ancestry is an attribute that allows their proper definition. Ancestry is the only proper defining attribute that taxa possess in the phylogenetic system. The taxon Mammalia, for example, may be properly defined as comprising the most recent common ancestor of its two principal divisions, Monotremata and Theria, and all of its descendents (Rowe, 1986a). Whether or not a taxon is a member of Mammalia depends on whether it shares that ancestor; sharing such ancestry is both necessary and sufficient for a taxon to be a part of Mammalia. The individual and its parts may transform indefinitely, but its ancestry cannot. Mammalia may continue to diversify, but as long as an organism is born to a mammal it is by definition a mammal whether or not it has hair and mammary glands. The ancestry of Mammalia (or any other genealogical individual) delimits it from all other taxa. The attachment of the name 'Mammalia' followed its recognition as a group.

The distinction between defining taxon names and defining taxa is not trivial. Defining taxon names is clearly important for precise communication, and inappropriate nomenclature has often been the source of misdirection at a variety of hierarchical levels (e.g., Stevens, 1984; Rowe, 1986b). However, naming individuals is subsidiary to defining the individuals themselves. In many cases there is no difficulty in distinguishing the boundaries of individuals and proper definition becomes a trivial exercise. For example, one may easily delimit individuals such as Michael Ghiselin from other *Homo sapiens* or Mammalia from other living taxa without reference to ancestry. However, in many other cases the boundary delimiting one individual from another is not manifest. As Mishler and Donoghue (1982) described, there are many kinds of discontinuities in nature and there is no necessary correspondence among these discontinuities in delimiting the same groups of organisms. They note that species, for example, are equivalent only by their designation as species, and not by virtue of the nature or extent of their evolutionary

differentiation (see Daves and Heywood, 1963:92). They rightly point out that "... comparative biologists must not make inferences from a species name without consulting the systematic literature to see what pattern of variation the name purports to represent" (Mishler and Donoghue, 1982:500; see also Stevens, 1984). This advice applies to hierarchical levels besides species. For example, despite its distinctness from other living taxa, numerous conflicting criteria and boundaries have been proposed to delimit Mammalia from its closest extinct relatives. These in turn have yielded conflicting measurements of such properties of Mammalia as its membership, its distribution in time and space, its diagnosis, and others. The name 'Mammalia' has nevertheless been applied to each of the various entities recognized by the disparate methods (Rowe, 1986a, MS). In the phylogenetic system, only ancestry provides a means of defining monophyletic taxa. Precise delimitation of taxon boundaries is essential if the evolutionary properties of taxa are to be studied at the level at which they arose and compared among taxa in a consistent way (e.g., Greene, 1986). Such definitions are prerequisite to the development of anatomical nomenclature that reflects homology (e.g., Rowe, 1986b) and taxonomic nomenclature that is based on phylogeny (e.g., Stevens, 1984).

Hull (1976) pointed out that populations, species, and higher taxa need not be made up of similar organisms, but that in a genealogical system they must be made up of related organisms. He also pointed out that taxonomists traditionally have not imposed this requirement upon taxa; rather it has followed from the nature of the evolutionary process itself. However, if we follow the suggestion of deQueiroz (1985) to view evolution as a first principle from which to deduce phylogenetic systematic methods, ancestry may be regarded as a proper definition that describes a fundamental property of all monophyletic taxa.

To the extent that this is correct, in the phylogenetic system, as in phenetic systems, taxa may be properly defined by a

statement of their defining attributes. In all of these systems the definitions serve to delimit the boundaries of taxa and thereby distinguish them from all other taxa. In phenetic systems, taxa are defined in terms of characters so that their definitions and diagnoses may be identical. This point underscores how poorly suited such systems are for studying the evolutionary history of Life, because defining characters are in effect forbidden to evolve. In a phenetic system, snakes by definition cannot be tetrapods. In contrast, as Gauthier (1984, 1986) and Gauthier et al. (1988) have argued, ancestry rather than overall similarity must be the basis for a phylogenetic system. Thus, because snakes were born of Tetrapoda, they remain tetrapods despite their lack of limbs. In this way taxa are properly defined by the only attribute they possess that cannot change during the course of evolution, their ancestry. No constraints are placed on the form of descendents, but they cannot escape their histories. Characters may be assembled to diagnose a taxon once it has been defined, but ancestry alone is both necessary and sufficient for taxon membership in the phylogenetic system.

This distinction helps to further clarify the term 'diagnosis.' In phenetic systems, diagnoses are often regarded as listings of characters that may be useful in identifying taxa, but there is no requirement that the level of generality of such characters be specified. As a result, diagnostic characters are not necessarily synapomorphies of the group being diagnosed. For example, ovipary (egg-laying) is often considered diagnostic of Monotremata (e.g., Gingerich, 1984), but there can be little question that ovipary is plesiomorphic at the level of Monotremata. When used in this way, diagnoses are merely abbreviated descriptions or identification keys. Characters in such diagnoses lack the historic information inherent in the relationship between a character and its hierarchical level, and they are thus poorly suited to studying phylogeny. In contrast, in the phylogenetic system the diagnosis of a taxon is a listing of those characters that are

hypothesized to have been evolutionary novelties in its most recent common ancestor. Both the character and its hypothesized level of generality are stated, and thus diagnoses serve to precisely and testably identify taxa. It is difficult to see how else 'diagnosis' could usefully be employed in studying genealogy.

Before the development of phylogenetic systematics, a taxon could be both defined and diagnosed using one set of characters. Because these operations were confused and the characters they identified were not required to specify a hierarchic level, little precision or reproducibility was achieved in either the definitions or diagnoses of taxa. This prompted such statements as Crowson's grand rationalization, "The species is no exception to the rule that the concepts and categories employed in natural history are never susceptible to precise, rigorous or final definition; any scientist who is not content to operate with more or less vague and inexact basic principles and ideas is temperamentally unsuited to the study of natural history" (Crowson, 1970:37). Or, in keeping with this view, Simpson pondered, "Is it possible to define a monophyletic Mammalia including the unknown one ancestral unit and all its descendents but no other species? I submit that this is also obviously impossible and that this concept of monophyly as applied to taxonomy and nomenclature is simply quixotic" (Simpson, 1971:192). In the phylogenetic system, however, statements such as these that conflate definition and diagnosis have little merit. Contrast them with Brundin's view (1966:21; cited in Schoch, 1986:ix): "To be able to do well in reconstructing phylogeny, a difficult task under all circumstances, we must use sharp definitions and strict reasoning without any compromise, the best tools ever." In the phylogenetic system, taxa are monophyletic by definition and diagnoses are explicitly testable measurements of one of their evolutionary properties.

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Size and Time

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The differences in opinion expressed by Strauss (1987) and Blackstone (1987a) will be resolved not by further commentary but rather by empirical data. Nevertheless, to encourage the synthesis of developmental and allometric studies, I will comment on Strauss' major points. (I believe that Strauss' minor points are adequately addressed

elsewhere, e.g., Blackstone, 1985, 1986, 1987b).

Biological Time, Chronological Time, and Size

Strauss' (1987) major premise is that "chronological time does not have theo-