The definitions of taxon names: a reply to Stuessy

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Phylogenetic nomenclature (e.g., de Queiroz & Gauthier, 1990, 1992, 1994; Cantino & de Queiroz, 2000) is an alternative to the traditional system of nomenclature described in the bacteriological, botanical, and zoological codes (e.g., Sneath, 1992; Ride & al., 1999; Greuter & al., 2000). The most fundamental difference between phylogenetic and traditional nomenclature concerns the manner in which taxon names are defined (de Queiroz & Gauthier, 1994; de Queiroz, 1997). Stuessy (2000), however, has questioned whether taxon names are defined at all. In his view, the three types of phylogenetic definitions that have been described—node-based, stem-based, and apomorphy-based (not crown-based, contra Stuessy)—are not definitions of names but methods or concepts for taxon circumscription that have nothing to do with nomenclature (i.e., names). Stuessy's view is incorrect; it misrepresents the function of phylogenetic definitions and fails to account for how existing taxon names are applied in new taxonomic contexts under both traditional and phylogenetic systems.

Stuessy did not present any evidence to support his conclusion that phylogenetic definitions are methods for taxon circumscription rather than definitions; he simply asserted his conclusion and described his view of how taxa are named under the traditional system. According to Stuessy (p. 23), "...taxa are first circumscribed (or delimited or recognised) by some stated criteria. Taxa are then referred to categories of the modern taxonomic hierarchy. Through the process of referral of a taxon to a category, it receives a name by 'christening' or 'baptism'. These names are given in the fashion we name our own children, John Smith or Jane Jones; they are not defined—they are just labels to allow for effective communication". Except for the statement that taxon names are not defined, this is a more or less accurate description of how the traditional system operates. The phylogenetic system operates similarly in some respects and differently in others. One important difference is that in the phylogenetic approach, taxa need not be referred to categories in a taxonomic hierarchy; consequently, they do not receive their names through categorical referral.

Contrary to Stuessy's view, taxon names are defined in both traditional and phylogenetic systems of nomenclature (de Queiroz, 1997). In the traditional system of nomenclature, taxon names are defined in terms of types and taxonomic categories. For example, the definition of the name Asteraceae is "the taxon containing the genus Aster that is assigned to the family category". In the phylogenetic system, taxon names are defined in terms of specifiers and their common ancestry relationships. For example, a node-based phylogenetic definition of the name Asteraceae might be "the clade stemming from the most recent common ancestor of Barnadesia and Aster". Perhaps the reason Stuessy thinks that taxon names are not defined is that definitions under the traditional system are taken for

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granted. That is to say, the bacteriological, botanical, and zoological codes do not explain how taxon names are defined (de Queiroz & Gauthier, 1994; de Queiroz, 1997). Nevertheless, taxon names have implicit definitions of the kind described above.

Definitions are critical to both traditional and phylogenetic systems of nomenclature, because they allow taxon names to be applied unambiguously in the context of any relevant taxonomic proposal or hypothesis. For example, the traditional definition of Asteraceae specifies the taxon to which that name is to be applied: the family that contains the genus Aster. Similarly, the phylogenetic definition of Asteraceae used in the example above specifies the taxon to which that name is to be applied: the clade stemming from the most recent common ancestor of Barnadesia and Aster. Definitions in biological nomenclature thus function the same way that definitions function in normal language. Just as definitions in normal language specify how words are to be used, definitions in biological nomenclature specify how names (which are words) are to be applied (which is how they are used). Specifying how words are to be used allows those words to be used in different contexts, which in taxonomy means that it allows taxon names to be applied in the context of different taxonomic arrangements. In the case of explicitly phylogenetic approaches, node-based, stem-based, and apomorphy-based statements allow taxon names to be applied in the context of different phylogenetic hypotheses. Because node-based, stem-based, and apomorphy-based statements function in this manner, contrary to Stuessy's view, it is appropriate to refer to those statements as definitions.

Stuessy is also incorrect in viewing the definitions of taxon names, whether traditional or phylogenetic, as methods for taxon circumscription that have nothing to do with nomenclature. On the one hand, neither traditional nor phylogenetic definitions circumscribe taxa in the sense of determining which entities (other than the types or specifiers) are to be included in, or excluded from, a taxon. Using Asteraceae as an example, the traditional definition indicates only that this name must be applied to a family and that this family must contain the genus Aster. It neither requires nor prohibits inclusion of other genera (than Aster) in Asteraceae, and hence the circumscription of that taxon can differ among taxonomic hypotheses. Similarly, the node-based phylogenetic definition of Asteraceae used in the example above indicates only that this name must be applied to a clade and that this clade must contain both Barnadesia and Aster. It neither requires nor prohibits inclusion of other taxa (than Barnadesia and Aster) in Asteraceae, and hence the circumscription of that taxon can differ among taxonomic (phylogenetic) hypotheses. Thus, neither traditional nor phylogenetic definitions are methods for circumscribing taxa in that a definition does not specify the composition of a taxon in the absence of a taxonomic hypothesis (see Bryant, 1997). Instead, taxa are circumscribed by whatever methods are used to generate taxonomic hypotheses-that is, to recognise groups (e.g., phenetic clustering, phylogenetic analysis)—and those methods are very different from the statements that advocates of phylogenetic nomenclature call definitions.

On the other hand, both traditional and phylogenetic definitions might be considered to circumscribe taxa in the sense of determining, in the context of a

particular taxonomic hypothesis, which taxa (and thus their components) are to be associated with particular names. However, contrary to Stuessy's view, this kind of circumscription has everything to do with nomenclature. For example, applying the traditional definition of the name Asteraceae in the context of a taxonomic proposal that assigns one of the many nested taxa containing the genus Aster to the family category might be considered to circumscribe the family Asteraceae in that it determines which group of genera is to be designated by that name. Similarly, applying a phylogenetic definition of the name Asteraceae in the context of a phylogenetic hypothesis describing the relationships among relevant taxa might be considered to circumscribe the clade Asteraceae in that it determines which group of terminal taxa is to be designated by that name. In both traditional and phylogenetic systems, definitions associate particular names with particular groups. The groups themselves are circumscribed by other methods, but a definition may be said to circumscribe a taxon in the sense that it determines which one of many possible groups is to be designated by a particular name. But regardless of whether this phenomenon is considered a form of circumscription, definitions determine how names are to be applied to groups, and contrary to Stuessy's view, this function is unequivocally nomenclatural (i.e., about names).

It should be noted that my conclusions about the function of certain statements and their status as definitions are not at odds with Stuessy's description of the process of naming taxa and the function of taxon names. Specifically, my conclusions are fully consistent with his propositions that taxa are circumscribed before they are named, that taxa are named through acts similar to christening, and that taxon names are labels to allow for effective communication. On the other hand, Stuessy's mistaken conclusions about definitions may stem from his failure to distinguish between two different aspects of naming. The systems of nomenclature developed by biologists consist of rules both for generating new names for taxa and for applying previously generated taxon names in the context of new taxonomic hypotheses. Definitions, which specify how taxon names are to be applied, are primarily important in the second aspect of naming. The rules in question ensure both that the application of taxon names will be straightforward and, within the context of a given taxonomic hypothesis, that any particular application of a name will be agreed upon by all biologists. Definitions form the foundation of these rules, and thus they are fundamental to both traditional and phylogenetic systems of nomenclature (de Queiroz, 1997).

Stuessy also criticised advocates of phylogenetic nomenclature for referring to the present system of botanical nomenclature as the "Linnaean system". His reason was that the modern *International Code of Botanical Nomenclature* (Greuter & al., 2000) differs in many ways from the rules of nomenclature outlined in Linnaeus' (1737) *Critica Botanica*. Although there are certainly differences between the nomenclatural system described in the modern botanical code and the system proposed by Linnaeus, the modern system is referred to as "Linnaean" because it is based on a method of definition similar to the one used by Linnaeus, which is in turn based on the categories of a taxonomic hierarchy that derives largely from his work (see de Queiroz, 1997 for a discussion of terminology). In this sense, it is appropriate to refer to the system of nomenclature embodied in the modern botanical code as "a

Linnaean system," though I agree with Stuessy's criticism in acknowledging that it would be appropriate to reserve use of "the Linnaean System" for reference to the system used by Linnaeus himself.

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