

POINTS OF VIEW

The use of apomorphies in taxonomic defining

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Nixon & Carpenter (2000: 306) describe the procedure of a “good Linnaean taxonomist” for defining as being “... equivalent to a formal phylogenetic definition based on diagnosis, i.e., the largest inclusive group bearing the designated homologies”.

Nixon and Carpenter’s “homologies” are presumably synapomorphies, following Patterson (1982) who defined homology in terms of synapomorphies. The “phylogenetic definition” of Nixon and Carpenter is not following Phylogenetic Nomenclature (PN); they advocate “Linnaean” taxonomy. Lee (2001), commented that Nixon & Carpenter (2000), contrary to their intention, do not discredit PN’s apomorphy-based definition and unintentionally argue in favour of the superiority of those definitions to others, including “Linnaean”. Lee furthermore correctly remarks that Nixon and Carpenter’s procedure is not the Linnaean practice of defining names, but instead identical to the phylogenetic apomorphy-based definition. Then, what are Linnaean definitions? Lee (2001: 176) mentions that they “...delimit taxa very vaguely, by specifying a rank and type....” This statement fits the way in which Linnaean *names* are defined. Before discussing whether Lee or Nixon and Carpenter are right or wrong, I will consider what constitutes defining.

A feature of PN is that *names* are defined according to tree topology (see de Queiroz & Gauthier, 1992, 1994). Stuessy (2000, 2001) argues that clades can be defined, but names not. Thus, while “Pinaceae are the family that includes genus *Pinus*” sounds like a definition of the name Pinaceae, it is not. The name Pinaceae is then merely a label to communicate about the family that contains *Pinus* as its type. Stuessy’s arguments receive replies by de Queiroz (2000) and de Queiroz & Cantino (2001). De Queiroz (2000) argues that even according to the *Codes of Nomenclature* names are defined, since family “Asteraceae” is defined by the type genus *Aster*. Stuessy (2001) argues back that de Queiroz mistakes christening for defining. De Queiroz and Cantino (2001) agree that names serve to facilitate communication and that they are given to taxa in a process of christening, but still insist that names can be defined. They point out that under the Linnaean system names are

defined ostensibly by pointing, for example to type genus *Aster*. In general, biologists seem of the opinion that names can and should be defined (Härlin & Sundberg, 1998). I question this, and am sure that I am not the only one.

Härlin & Sundberg (1998) and Härlin (1998) point out that in traditional taxonomy as well as in PN, names are viewed as having the same meaning as the defining descriptions. In other words, names have intension. However, Härlin & Sundberg (1998) and Härlin (1998) support the view that taxa are historical entities. Thus, a name and its meaning are not the same, since the meaning is subject to historical change. A name would thus not have intension (meaning) and cannot be defined. Since a taxon changes through history, the only way to fix the reference to its name is by pointing, i.e., ostensibly (Härlin & Sundberg, 1998; Härlin, 1998). To thus fix a reference, one could point to, for example, specifiers in PN. However, in doing this, the name is not defined. References to names are fixed to facilitate communication. This means that “Pinaceae” is a label without intension. By fixing the reference of the name “Reptilia”, the historical content of this taxon may change (e.g., Dinosauria appear and disappear, but they will always be called “Reptilia”). Consider the difference between “The name Reptilia is defined by specifiers A and B in cladogram X” and “We christen this taxon ‘Reptilia’, a name fixed by type A”. I concur with the latter view. If taxonomic names are not defined, then what is a taxonomic definition? According to Stuessy (2001), *taxa* are defined through circumscription. Can taxa, as historical units, be defined by characters? Can constantly changing units be defined by synapomorphies and hence delimited by a list of characters? That seems highly illogical. However, Griffiths (1999: 220) makes the point that while taxa are subject to historical change, they are also “natural kinds” with fixed identities: “...heredity acts as a sort of inertial force, maintaining organisms in their existing form, until some adaptive force acts to change that form. This *phylogenetic inertia* is what licences induction and explanation of a wide range of properties...using kinds defined purely by common ancestry”.

Thus, species can be circumscribed by a list of char-

acters. Examples of such character lists are taxon diagnoses. Hence, systematists consider the “traditional” diagnosis as a way of defining using characters (Kluge, in press). From this, it follows that a Linnaean diagnosis equals taxon definition. However, in practice, Linnaean diagnoses regularly contain a mix of apomorphies and general differential characters. Often, it is not stated whether characters are apomorphic and/or plesiomorphic (e.g., Powell & al., 2000; Leakey & al., 2001). With “general differential characters” I mean those that fall into two categories. First, those that are phylogenetically undetermined, because their evolution is not understood or their states sometimes unknown. Second, those that are used to distinguish the taxon from its relatives, even though they are plesiomorphies that do not define the taxon. Linnaean definitions, in a cladistic framework, should thus include only synapomorphies. Some systematists produce clade diagnoses that include apomorphies only, e.g., Tyler & al. (1989), and Gago (1997). These can be considered clade definitions. However, the diagnoses that include other characters besides synapomorphies are to be considered “soiled” definitions. Since some have started to include only apomorphies in diagnoses, this should become standard practice, and diagnosis can hence be equalled to definition.

One of the proposals of Nixon & Carpenter (2000: 315) entails definitions (of names) by apomorphies plus a type. Taxa under phylogenetic definitions are not assigned types: species, specimens and synapomorphies are, as part of these definitions, called specifiers. These supposedly function similarly to Linnaean types, giving reference points to taxa (Cantino & de Queiroz, 2000). However, if the type concept is used correctly, the type is not part of a taxon definition. If a Linnaean taxon definition contains only apomorphies, it is similar to PN’s apomorphy-based definition of names, although the Linnaean definition does not need to include a type. Types are not formally part of Linnaean diagnoses, and it is obvious that under any sort of definition the type is part of the clade considered. It is also evident that under Linnaean definitions all members of the clade (type included) are consistent with the apomorphies that diagnose it (snakes for example are not inconsistent with Tetrapods: it is assumed they are an evolutionary offshoot of four-legged lizards, having taken the extra evolutionary step to lose those legs). From [*ICZN, International Code of Zoological Nomenclature*, 1999, Arts. 61–76] it is clear that the type concept was established to fix the reference of names, not to diagnose taxa. See for example *ICZN* (1999, Art. 61.1): “The fixation of the *name-bearing* type of a nominal taxon provides the objective standard of reference for the application of the *name* it bears” (italics mine).

Types function as reference points for taxon defini-

tions, but are not part of these. Types are also designed to remind us what a taxon is biologically (see also Stuessy, 2001). Types are necessary to make “dead” descriptions alive, since one can always consider (or consult) the type. The claim could be made that a definition with only synapomorphies is susceptible to homoplasy: it is possible that a key apomorphy evolved convergently elsewhere. Can this be avoided by including types in definitions? In this way, the precise nature of the apomorphy that defines cannot be mistaken. Normally, however, taxa are diagnosed by multiple apomorphies. I think it unlikely that all considered synapomorphies of a taxon have evolved convergently in another. It is required that characters are rightly interpreted. Endothermy has evolved three times in different ways in scombroid fishes (see e.g., Block & al., 1993). Hence, considering endothermy as an apomorphy here means the characters are not well considered.

I view a diagnosis that consists only of apomorphies as equal to a taxon definition. Linnaean diagnoses often incorporate “other characters” besides apomorphies. In order to define in the strict cladistic sense, diagnoses should include only apomorphies, and “other characters” are to be mentioned elsewhere. In order to define a taxon, types are not needed. The statement, however, that apomorphies that define the clade are homologous to those in the type, is correct and convenient for the reader. The type is thus not part of the definition, but it is referred to. Apomorphy-based definitions of PN may be seen as the phylogenetic alternative of defining by Linnaean diagnosis. However, if names cannot be defined, a view that I follow, the basis of PN is invalid. Instead, strict apomorphy-based diagnoses, equaling taxon definitions, might be formalised in the next *Codes*, or should at least become universal practice amongst systematists. If defining by apomorphies can be done in a Linnaean framework, I do not see the need for introducing a new nomenclatural system. In general, I agree with reviews of PN (e.g., Benton, 2000; Nixon & Carpenter, 2000; Dyke, 2002), which imply preference of the current “Linnaean” system over PN.

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