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METACLADISTICS

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Donoghue (1985: 177) observed incomplete resolution when constructing cladograms of single organisms as terminal taxa, and he used the metaspecies convention to designate certain sets of individuals in those unresolved assemblages (e.g. A–C in Fig. 1).[1] He proposed annotating a metaspecies binominal with an asterisk (e.g. *Archaeopteryx lithographica**; Gauthier, 1986), in order to distinguish it from demonstrably monophyletic species taxa (e.g. D–F in Fig. 1). Donoghue (personal communication) would create a new binominal for unnamed metaspecies, although he has yet to do so in his research on *Viburnum* (Caprifoliaceae s.l.; Donoghue, 1982), where he developed an awareness for the problem of incomplete resolution.

Polytomies result whenever synapomorphies are absent or incongruent, and Donoghue (1985: 186; also personal communication) intended metaspecies for the former situation. For example (Fig. 1), (A, B, C) is a metaspecies if, and only if, the evidence is confined to characters 1–2 in Table 1. As soon as a synapomorphy is discovered that delimits all or some of the members of a metaspecies, the metaspecies convention no longer applies, at least as it was originally attributed. Similarly, metaspecies no longer applies whenever a synapomorphy is discovered that links one or more of the members of the metaspecies to another clade. For example (Fig. 1), (A, B, C) is not a metaspecies if any of the other synapomorphies (3–8) in Table 1 are observed.

Mishler and Brandon (1987: 412; see also Gauthier, 1984, 1986) suggested generalizing the concept of "metaphyly" to higher taxa "that are not known to be either paraphyletic or monophyletic", and Estes et al. (1988), Etheridge and de Queiroz (1988), and Gauthier et al. (1988) formally applied the convention to various squamates (Kluge, 1989a). Mishler and Brandon's proposal is significantly different from Donoghue's (1985) metaspecies formulation, and it seems that most, if not all, of the higher metataxon examples are already provided for by one of Wiley's (1981) taxonomic conventions.

As I noted above, a metaspecies does not include any recognized clades, nor any recognized evidence for such relationships (e.g. characters 6, 7 or 8 in Table 1; see Fig. 1), whereas each monophyletic higher taxon in a polytomy is expected to be delimited by at least one synapomorphy. This distinction is important, because "the recognition of subdivisible unresolved [higher taxonomic] groups is arbitrary"[2] (Gauthier et al., 1988: 16). For example, in their studies of squamate relationships, Estes et al. (1988) stated that Iguania is an unresolved assemblage, consisting of Acrodonta (agamid and chamaeleonid squamates) and eight monophyletic higher taxa referred to as Iguanidae* (see also Etheridge and de Queiroz, 1988). According to Gauthier et al.

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[1] de Queiroz and Donoghue (1988) recommended using populations as terminal taxa when studying species, and they would apply (p. 332) the metaspecies convention to "single basal entities, or groups of basal entities, whose monophyletic status is uncertain".

[2] One could argue that the application of Donoghue's (1985) metaspecies convention is not arbitrary, because each included terminal taxon is an individual organism and all excluded taxa at the same level of generality form at least one diagnosable clade (A–C and D–F, respectively: Fig. 1).

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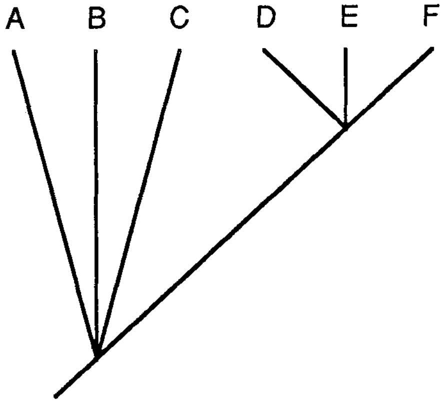

Fig. 1. A cladogram of six terminal taxa (A–F). See Table 1 for evidence.

(1988: 16), the basis for subdividing an unresolved group of higher taxa is name availability, "taxa that have *already been given* formal names". In the example cited above, Iguania is divided into acrodonts and the metataxon Iguanidae because the latter family group name is already available (Gray, 1827). Other formal names that partition Iguania differently are available (e.g. Fitzinger, 1843), although they are not in current use nor have they been used as often as Iguanidae.

Estes et al. (1988: 191) noted that "Iguanids* possess the diagnostic synapomorphies of Iguania but lack either some or all of the diagnostic synapomorphies of Acrodonta". Thus, the authors admit the possibility that "some" of the lines of evidence, although mutually incongruent, point to paraphyly of the "metataxon" Iguamidae. Unlike Donoghue's definition of metaspecies, the evidence is distributed like characters 3–5 in Table 1 (Fig. 1), and incongruent characters pointing to paraphyly, in the absence of overriding evidence for monophyly, do not constitute evidence of "possible" monophyly. Moreover, when characters are so distributed (3–5 in Table 1), as I believe they are in the iguanid* example (also in their Agamidae and Gekkonidae examples of metataxa; see Estes et al., 1988, pp. 193–194, and 205 and 256, respectively), the resulting unresolved polytomy is due to character incongruence, not absence of evidence. That being the case, Wiley (1981) has already provided conventions for classifying those polytomies completely (convention 4; *sedis mutabilis*), or in part (convention 6; the taxon is placed in shutter quotes and marked *incertae sedis* at the level in the taxonomic hierarchy at which the assemblage is grouped). I urge that only

Table 1
A hypothetical data matrix.

Taxa	Characters							
	1	2	3	4	5	6	7	8
A	1	0	1	0	0	1	0	1
B	1	0	0	1	0	1	1	0
C	1	0	0	0	1	0	1	1
D	1	1	1	1	1	0	0	0
E	1	1	1	1	1	0	0	0
F	1	1	1	1	1	0	0	0

0 = plesiomorph; 1 = apomorph.

monophyletic higher taxa be recognized, and that Wiley's (1981) *sedis mutabilis* convention (4) be used to flag all parts of unresolved higher taxonomic polytomies.

The primary goal of cladistics is to reconstruct phylogeny and when other matters, such as stability and convenience in classification, obstruct that purpose they must be set aside (Kluge, 1989b). The criterion of name availability, as the basis for delimiting higher metataxa, can have the effect of perpetuating the *status quo*, and in that way it is counterproductive to our science. For example, Estes et al. (1988) denied themselves the opportunity to test the monophyly of Iguanidae, and Etheridge and de Queiroz (1988), in studying Iguanidae* as if it was a monophyletic ingroup, also failed to identify particular sister group relationships within Acrodonta (in contrast, see Schwenk, 1988: figs 12, 14). Such conservative actions also run the risk of being interpreted as authoritarian.

The need for a metaspecies convention (Donoghue, 1985) seems to follow from the assumption that all specimens must be classified binominally, because they are part of genealogy. And Hull's (1987: 179) analogy that "every library book must be placed on some shelf somewhere in the library" supports that perspective. However, the force of this operational imperative depends on other issues. In particular, it depends on the general theory in which phylogenetic systematics is imbedded, and the species concept is particularly critical (Kluge, in preparation). For example, lack of resolution is a likely outcome of a phylogenetic analysis of tokogenetic relationships among biparental organisms, which are inherently non-hierarchical, and especially where the units of comparison are semaphoronts. However, according to Hennig (1966, fig. 6), reticulate tokogenetic relationships are not within the domain of phylogenetic inference. Moreover, in the context of at least some evolutionary models (e.g. Danser, 1950; see also Kluge, 1988), it is entire life cycles that are replicated (Hull, 1980), not semaphoronts, and, just as these units may be more appropriate sources of evidence for phylogenetic inference, their relationships are not so likely to be unresolved. Those who designate parts of unresolved groups of higher terminal taxa as metataxa face more difficult explanations, such as why they advocate non-monophyletic higher taxa, and employ arbitrary actions and assumptions in those deliberations. In any case, metataxon is just another label for unresolved relationships, and lack of resolution merely describes a fact about our ignorance. Being unresolved is not an objective property of natural entities.

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