The Logical Basis of Phylogenetic Taxonomy

PAUL C. SERENO

Department of Organismal Biology and Anatomy, University of Chicago, 1027 E. 57th Street, Chicago, Illinois 60637, USA;
E-mail: dinosaur@uchicago.edu

Abstract.—Phylogenetic taxonomy, like modern Linnean taxonomy, was modeled on a phylogenetic tree rather than a cladogram and, like its predecessor, perpetuates the use of morphology as a means of recognizing clades. Both practices have generated confusion in graphical representation, operational terminology, and definitional rationale in phylogenetic taxonomy, the history of which is traced. The following points are made: (1) cladograms, rather than trees or hybrid cladogram-trees, provide the framework for the simplest graphical depiction of phylogenetic definitions; (2) a complete notational scheme for phylogenetic definitions is presented that distinguishes symbolic notation from shorthand and longhand versions; (3) phylogenetic definitions are composed of three components (paradigm, specifier, qualifier) arranged in two fundamental patterns—node and stem; (4) apomorphies do not constitute a fundamental definitional pattern but rather serve to qualify a stem-based definition (as do time and geographic range); (5) formulation of phylogenetic definitions involves three heuristic criteria (stability, simplicity, prior use); (6) reasoned definitional revision is encouraged and better defined (textual substitution, first- and second-order revision); and (7) a database, *TaxonSearch*, allows rapid recall of taxonomic and definitional information. [Content; definition; node; notation; PhyloCode; stem; taxonomy; *TaxonSearch*.]

Phylogenetic taxonomy, as originally conceived (Gauthier et al., 1988; de Queiroz and Gauthier, 1990, 1992) and as currently formalized in a draft code of nomenclature (draft PhyloCode, hereafter "dPC"; Cantino and de Queiroz, 2004), has not fully disengaged from two longstanding traditions of modern Linnean taxonomy: (1) recourse to a phylogenetic tree and ancestor-descendant lineages in graphical depictions and terminological definitions and (2) the continued use of morphology in addition to phylogeny in clade recognition.

As shown below, these shortcomings have generated unnecessary interpretive complexity, a flawed abbreviational scheme, and the false equation of apomorphies and taxonomic entities in phylogenetic definitions. Rather than addressing these fundamental issues regarding the logical foundations of phylogenetic definitions, advocates of the PhyloCode have focused their attention elsewhere: retrofitting "widely used" names to crown clades, devising associated naming conventions (e.g., "pan" prefix, "gens" suffix), revising/discarding the Linnean binomen, elaborating procedures for definitional priority, and establishing an official registry of phylogenetic definitions for new and converted taxa (Cantino et al., 1999; Gauthier and de Queiroz, 2001; Laurin and Anderson, 2004; Laurin and Cantino, 2004).

In this article, "phylogenetic taxonomy" refers to the logic and procedures underpinning the construction of taxonomic definitions on the basis of phylogeny (de Queiroz and Gauthier, 1992). Phylogenetic taxonomy per se does not entail endorsement of a formalized code governing taxonomic definitions (i.e., the dPC), for which the term "phylogenetic nomenclature" is reserved (de Queiroz and Gauthier, 1994). Neither of these terms should be confused or conflated with "phylogenetic systematics," which has been widely used to refer to the general practice of Hennigian cladistics in the determination of phylogenetic relationships. Phylogenetic systematics does not entail endorsement of either phylogenetic taxonomy or phylogenetic nomenclature.

THEORETICAL FOUNDATION

Phylogenetic taxonomy was founded on (1) the distinction between taxonomic diagnosis and definition (Ghiselin, 1966, 1984) and (2) a protocol for formulating taxonomic definitions based on the branching topology of phylogeny that identifies specific clades (de Queiroz and Gauthier, 1990, 1992). A brief history outlining how each of these founding propositions has fared is given below. Both arose in direct response to the use of Linnean categorical ranks and the construction of trait-based taxonomic diagnoses, as practiced in traditional (precladistic) Linnean taxonomy and phylogenetic systematics.

Other aspects of phylogenetic taxonomy are not novel, although sometimes misinterpreted as such. Restricting taxa to monophyletic groups (clades) that are presumed to have arisen from a common ancestor, for example, is certainly not a proposition new to phylogenetic taxonomy but rather central to phylogenetic systematics (Wiley, 1981; Scotland, 1992; Nixon and Carpenter, 2000, 2003). Discarding Linnean categorical ranks or redundant (monotypic) taxa, likewise, is hardly unique to phylogenetic taxonomy. Hennig (1966) and others (Nelson, 1972; Farris, 1976; Løvtrup, 1977; Wiley, 1981; Avise and Johns, 1999) have offered a range of proposals to eliminate redundant taxa and either eliminate rank altogether or calibrate it with less arbitrary temporal or topological information (for a recent review, see Ereshefsky, 2001).

Diagnosis Versus Definition

Recently, Keller et al. (2003) provided an excellent historical review of the debate regarding diagnosis and definition in taxonomy, so only a few key references are cited here. The argument is rooted in the philosophical position that taxa (including species) represent individuals

rather than classes (Ghiselin, 1966, 1974; Hull, 1976). Taxonomy, it followed, might better be viewed as an exercise in "systematization" rather than "classification" (Griffiths, 1974).

In classification, diagnoses are used to delineate taxon membership on the basis of traits. Shared traits, hence, function at first glance like Aristotelian essences, as necessary and sufficient properties for membership (Hull, 1965; de Queiroz and Gauthier, 1990; de Queiroz, 1992, 1994). Indeed, this was clearly Linneaus' original intention (Ereshefsky, 2001). In reality, however, shared traits are rarely unique and nearly always subject to transformation, loss, or dissociation. Linnean taxonomic diagnoses under an evolutionary paradigm, thus, operate more like disjunctive definitions, in which some, but not all, traits are sufficient for group membership.

If, on the other hand, taxa constitute unique historical individuals produced by a natural system (biological evolution), and if taxonomy is an attempt to capture the singular tree of life, then taxa could be defined by some other means than shared traits—say, by the topology of the tree of life itself. Although the branching pattern of phylogeny remains a hypothesis subject to revision and competing arrangements, a phylogenetic definition could aspire to point to one, and only one, clade for any given phylogeny. In this way, taxa could be defined *ostensively* simply by "pointing at them" (Ghiselin, 1974, 1995; de Queiroz, 1988a; de Queiroz and Gauthier, 1990). Later, the relationship between a phylogenetic definition and its designated taxon was interpreted as *nominalist*, such that a taxon was merely an abbreviation for its definition, which amounts to a description based on monophyly (de Queiroz, 1992, 1994). Others have countered that constructing such taxonomic definitions is as *essentialist* as trait-based diagnoses (Frost and Kluge, 1994), because "they appear to be treating the taxon as a class defined by the necessary and sufficient property of common origin" (Keller et al., 2003:99).

Thus whether a phylogenetic definition "intentionally defines a class," "ostensively points to an individual," or "nominally constructs a definition" has yet to be resolved. Fundamental operational differences, nonetheless, are easy to discern between taxonomic diagnoses and phylogenetic definitions. The traditional "differential diagnosis" amounts to a grab bag of symplesiomorphies and synapomorphies that may, or may not, be present in most group members. A proper differential diagnosis, according to Mayr et al. (1953:156), may necessitate broad comparisons: "If the nearest relatives are rare or poorly known, it is also helpful to make a comparison with a well-known, if more distant, species." Traditional diagnoses, thus, are not limited to synapomorphies in support of monophyly but rather, like taxonomic keys, are intended to facilitate identification via differentiation (e.g., see diagnoses in Romer, 1956). Some phylogeneticists simply propose limiting diagnoses to one or more synapomorphies (e.g., Nixon and Carpenter, 2000). Phylogenetic definitions, in contrast, identify clades (monophyletic groups) by specifying boundary conditions for inclusion. They do not describe "neces-

sary and sufficient properties," although this amounts to a subtle distinction in so-called apomorphy-based definitions. To discern group membership one needs a branching diagram—an independent description of phylogeny based on observed characters. Most phylogenetic definitions provide little or no information about identifying traits within a clade.

Taxonomic diagnoses and phylogenetic definitions, thus, are readily distinguished operationally and, as a result, are the subject of vigorous polemic over which will provide a better foundation for delineation of taxa. Their philosophical underpinning, in contrast, seems not to have affected proponents of either view and may well remain an ineffective means to prefer one to the other.

Protocol for Phylogenetic Definitions

Initial definitions.—The first phylogenetic definitions were coined prior to the appearance of a protocol for their formulation. They appeared (ironically) within lengthy taxonomic diagnoses in an analysis of saurischian dinosaurs (Gauthier, 1986). Aves (in this case, crown-group birds) was given a node-based definition, although definitional types had not yet been named. Six other definitions were given, all stem-based and all delimiting taxa whose basal members were extinct (Saurischia, Theropoda, Tetanurae, Coelurosauria, Maniraptora, Ornithurae). Linnean categorical ranks were eliminated.

Gauthier et al. (1988) and Estes et al. (1988) published 35 phylogenetic definitions for Lepidosauromorpha and its major subgroups, clearly distinguishing definition from diagnosis (see also de Queiroz, 1988a). Definitions now regarded as node-based were used exclusively for crown groups; stem-based definitions were used sparingly for a few higher taxa with extinct basal members (Lepidosauromorpha, Lepidosauriformes, Lepidosauria, Squamata) and for one family within Squamata (Helodermatidae). Thus, at this early stage in the development of phylogenetic taxonomy, categorical ranks were eliminated, taxonomic definitions were separated from trait-based diagnoses, and two definitional types had appeared based on statements of ancestry. One of these (later termed node-based) was used exclusively for crown clades, which were linked preferentially with widely used names (Gauthier, 1986; Gauthier et al., 1988).

Definitional "classes".—In two seminal papers on phylogenetic taxonomy, three "classes" of phylogenetic definitions were outlined—node-based, stem-based, and apomorphy-based (de Queiroz and Gauthier, 1990:39, 1992:461). Their formulation was stated in terms of ancestry and depicted graphically on a phylogenetic tree (Fig. 1c). The similarity between this graphical depiction and Hennig's (1965) tripartite temporal division of the history of an extant group (Fig. 1a) is striking although not cited as its source. Subsequently, two additional definitional patterns were erected—"stem-modified node-based" (Meng et al., 1994; Wyss and Meng, 1996) and "apomorphy-modified node-based"—for a total of five definitional "types" (Cantino and
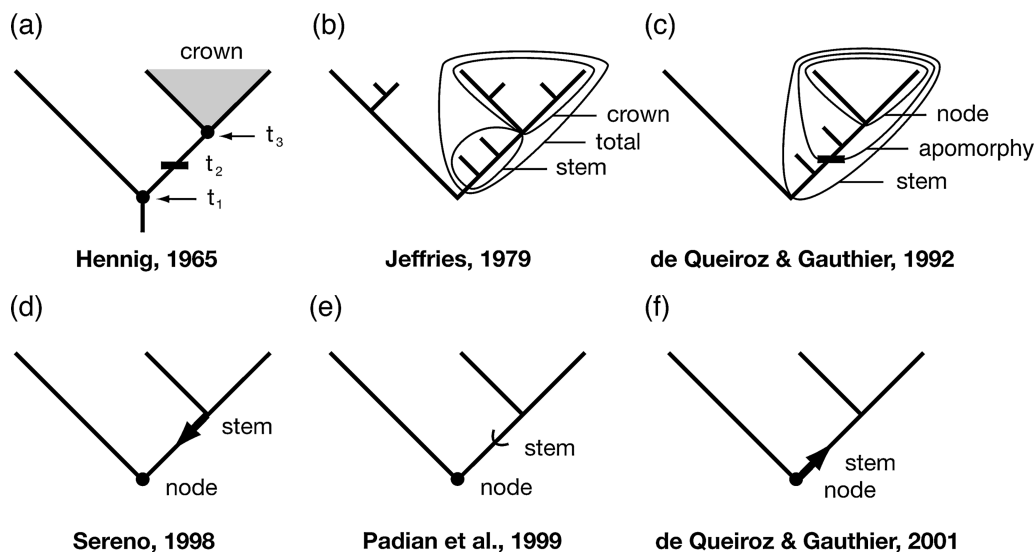
FIGURE 1. Graphical representation of node- and stem-based clades. (a) Phylogenetic tree showing the origin (t_1), evolution (t_2), and last common ancestor (t_3) of a crown group with two ancestral species shown as dots (after Hennig, 1965:fig. 4). (b) Phylogenetic tree showing crown, stem, and total groups (after Jefferies, 1979:fig. 5A). (c) Phylogenetic tree showing node-, stem-, and apomorphy-based clades (after de Queiroz and Gauthier, 1992:fig. 4). (d) Cladogram showing node- and stem-based clades (after Sereno, 1998:fig. 1; 1999:fig. 1). (e) Cladogram showing node- and stem-based clades (based on Padian et al., 1999). (f) Phylogenetic tree showing node- and stem-based groups (after Gauthier and de Queiroz, 2001:fig. 2).

de Queiroz, 2004:23–24). These types were not regarded as exhaustive. The stated purpose of the two new definitional types was to "tie names to crown clades" (Cantino and de Queiroz, 2004:24). According to the dPC, definitions for crown clades come in three forms: node-based, stem-modified node-based, and apomorphy-modified node-based.

The foregoing, not surprisingly, has engendered confusion. Following Nixon and Carpenter (2000), many critics describe phylogenetic taxonomy as the "node-pointing system." They give lip service to the three "classes" of definitions and then present the node-based pattern as representative of all definitions in phylogenetic taxonomy (e.g., Nixon and Carpenter, 2000; Dyke, 2002; Carpenter, 2003). Nixon and Carpenter (2000:299) stated that "both the node- and stem-based methods [sic] are implemented in the same fashion, with the only difference being whether a name is restricted to 'crown clades' or includes taxa from the 'stem clade'." Schuh (2003:65) stated "What is clear is that most of the literature is organized around the concept of node-based definitions; furthermore, Kojima (2003) has persuasively argued that even apomorphy-based definitions are node-based." Kojima's "argument" consisted of highlighting the fact that an apomorphy-based definition also pinpoints a particular "node" (= clade) on a cladogram. One is left to wonder what else Kojima imagined to be the object of all phylogenetic definitions?

Others have falsely implied that phylogenetic definitions—as originally conceived (de Queiroz and Gauthier, 1990, 1992) and as outlined in the dPC—do not incorporate subjective, character-state descriptions. Citing these same references, for example, Brochu

(2001:1185) stated that "definitions are based on ancestry and descent rather than the possession of subjective 'key' characters." Yet, "complex apomorphies" composed of many traits (e.g., a "flipper") that are indistinguishable from classic "key" characters are specifically cited as acceptable in the dPC (Note 9.8). de Queiroz and Gauthier (2001:17), as another example, stated that "apomorphy-based definitions are no more or less prone to such problems [referral of particular specimens to taxa] than are node- or stem-based definitions." This statement, however, clearly confuses ambiguity in the referral of particular specimens with ambiguity in the interpretation of the phylogenetic definition itself. Given perfectly complete specimens and a fully resolved phylogeny, taxonomists would still point to different nodes faced with definitions that are operationally dependent on "complex apomorphies" such as "feathers" or "feathered wings" (de Queiroz and Gauthier, 2001), as discussed in more detail below.

Definitional components.—What are the fundamental components of phylogenetic definitions, and how are they distributed among the various definitional types? Thus far, only one has been specifically identified— specifiers—the taxonomic units employed in phylogenetic definitions. They were first identified as "reference points" by Schander and Thollesson (1995) and later as "reference taxa" by Sereno (1998, 1999) and Lee (1999). The reference taxa chosen in early phylogenetic definitions tend to be maximally inclusive ingroups or outgroups (Gauthier, 1986; Gauthier et al., 1988). de Queiroz and Gauthier (1992:475, Fig. 7), for example, constructed a series of definitions for high-level craniate taxa from an indented list: "the name 'Amphibia' refers

to the clade stemming from the last common ancestor of Gymnophiona and Batrachia," and so on.

Maximally inclusive reference taxa, however, obfuscate the meaning of a taxon, "which depends on the meaning of the names listed in its definition and on the meaning of the names included in the definitions of those listed names, etc., until the meaning of the listed names are based on the names of species rather than clades" (Bryant, 1996:181; also Schander and Thollesson, 1995)—a semantic regress criticized as "recursive referencing" (Sereno, 1999:342, Fig. 10). As a solution, Bryant (1996:342–343) recommended either the use of species or citation of "some standard taxonomic reference" in definitions. He chose the latter in a revised taxonomy of Carnivora, using higher-level reference taxa, such as "Creodonta," with an attached citation—"taxa referred to Creodonta by Carroll (1988)." Joyce et al. (2004:995) recommended the same for naming crown clades with uncertain internal relationships. This protocol, however, effectively buries the precise meaning of a taxon in a citation (or in citations within that citation) and often unwittingly incorporates species of uncertain affinity.

Cantino et al. (1997) and Sereno (1998) chose the other path, citing multiple species or deeply nested genera, respectively, as reference taxa. Cantino et al. (1997) used species while acknowledging that some of the genera used in the their taxonomy may not be monophyletic. Sereno (1998) used genera to avoid species-level ambiguities, although there seems to be little reason to avoid using species or even a particular specimen tied to a species name in a phylogenetic definition. Unlike Cantino et al. (1997), Sereno (1998) and Lee (1999) used the same nested reference taxon in definitions of nested taxa, a practice referred to as "nested referencing" (Sereno, 1999:342, Fig. 10). Sereno (1998, 1999) also introduced the concept of "ingroup" versus "outgroup" reference taxa.

The term *specifier* was coined in 2000 in an earlier version of the dPC, with "internal" and "external" replacing "ingroup" and "outgroup" as previously used with "reference taxa." Unlike Schander and Thollesson's "reference points" or Sereno's "reference taxa," however, specifiers included apomorphies as well as species and specimens. As protocol for phylogenetic definitions has emerged, nested referencing using species (or specimens tied to a species nomen) has proven to constitute a major step toward clarity and simplicity in phylogenetic definitions.

Definitional rationale.—Many taxa in common use are composed of hundreds or thousands of species and thus may be defined by an almost limitless number of phylogenetic definitions. How to choose among them? So-called "apomorphy-based" definitions have been criticized as operationally inferior (Bryant, 1996; Sereno, 1998, 1999) but are still used sparingly (Cantino et al., 1997; Lee, 1998a) or enthusiastically (Gauthier and de Queiroz, 2001) and are accommodated in the dPC. Other criticisms of specific definitional types have been dispelled as unjustified (Lee, 1998a; Sereno, 1999) such as: (1) crown groups must have node-based definitions (de Queiroz and Gauthier, 1990, 1992), (2) stem-based defi-

nitions are less stable in taxonomic content than node-based definitions (Schander and Thollesson, 1995), or (3) use of more than two specifiers potentially reduces stability of taxonomic content (de Queiroz and Gauthier, 1990, 1992).

In discussing rationale, we can distinguish two levels—the formulation and relative positioning of phylogenetic definitions (Sereno, 1999). In formulation of definitions, recommendations regarding specifiers have favored (1) nested rather than basal specifiers (Sereno, 1998, 1999; Lee, 1999); (2) multiple internal or external specifiers to combat uncertain relationships (Lee, 1996a, 1998a; Cantino et al., 1997); (3) specifiers that are well known or readily available (Sereno, 1999); (4) specifiers that accommodate alternative phylogenetic arrangements (Bryant, 1997); and (5) specifiers that were originally included in traditional paraphyletic groups rather than more deeply nested members now included on the basis of monophyly (e.g., the theropod *Megalosaurus bucklandi* rather than the bird *Passer domesticus* as an internal specifier for Dinosauria; dPC: Rec. 11A).

There have been only a few recommendations regarding the relative position of phylogenetic definitions (not to be confused with the relative position of particular clade names, such as "Aves"): (1) "well supported" versus "poorly supported" clades (Schander and Thollesson, 1995); (2) "node-stem triplets" (Sereno, 1998, 1999) composed on the basis of extinction (crown/total groups; Gauthier and de Queiroz, 1992), diversity, morphology, or tradition.

Critique

Graphical Representation

Phylogenetic trees versus cladograms.—The branches of a phylogenetic tree depict ancestral lineages. Hypothetical or real common ancestors may be positioned at branch points or along internal branch segments, and terminal branches are often of different lengths to depict relative age or extinction (Eldredge, 1979). On a cladogram, in contrast, internal branches (or branch points) constitute hypotheses of relative recency of common ancestry, and ancestral or extinct taxa are located at the tips of terminal branches like other taxa. A temporal sequence of hypothetical common ancestors, branching events, and lineages may be implied, but the diagram itself remains a hypothesis of the recency of common ancestry based on an analysis of data (e.g., Schuh, 2000:8).

Four styles have been used to depict clades with phylogenetic definitions on branching diagrams. The first style to appear involves circles that circumscribe portions of a phylogenetic tree (de Queiroz and Gauthier, 1990; Fig. 1c). Node-, stem-, and apomorphy-based clades, thus, were depicted first in a style closely resembling that used previously for crown, stem, and total groups (Jefferies, 1979; Fig. 1b).

The second and third styles, in contrast, use cladograms and depict only node- and stem-based clades (Fig. 1d, e). Both use dots for node-based clades. For stem-based clades, Sereno (1998, 1999) used downward

arrows, whereas Padian et al. (1999) used arc-shaped lines.

A fourth style (Gauthier and de Queiroz, 2001), adopted in figures in the dPC, uses dots and upward arrows for node and stem-based clades, respectively (Fig. 1f). Unlike Sereno's arrows that descend from the branch point on a cladogram (Fig. 1d), these originate from a node and project upward toward the branch point of a stem-based taxon. Stem-based taxa are labeled either directly over an internal branch or near the head of the arrow. This style of diagram was identified as a "cladogram" by the authors and looks the part, with straight branch segments and terminal species of disparate age. The arrows for stem-based taxa, however, point upward, opposite the direction of the inclusive function of a stem-based definition on a cladogram. One interpretation of the arrow matches the definition of a stem-based clade given in the dPC ("ancestral lineage of specified organisms . . . after its divergence from the ancestral lineage of other organisms"; Table 1). The upward arrow, in this context, labels an ancestral lineage on a phylogenetic tree. I know of no other interpretation that could account for the upward direction of the arrow, which is opposite the direction of inclusion at the core of the definition. The diagram, thus, appears to be a hybrid—a cladogram with a stem-based definition depicted as if it were a phylogenetic tree composed of ancestral lineages.

Dots, arrows, and cladograms.—Which of these four graphical styles might best depict phylogenetic definitions? The dPC recommends that definitions be associated with a published "reference phylogeny . . . derived via an explicit, reproducible analysis" to provide "context for the definition" (dPC: Recommendation 9A, D). Presumably, this refers to quantitative analysis summarized on a cladogram or similar branching diagram, rather than a phenogram, phylogenetic tree, or some hybrid construction. For the graphical depiction of phylogenetic definitions, therefore, is there a compelling reason *not* to use an unadulterated cladogram?
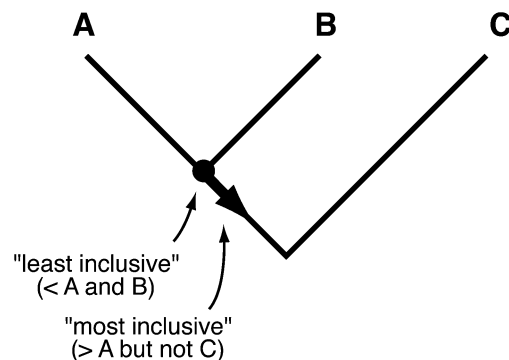

FIGURE 2. Graphical and symbolic representation for the two fundamental ways of specifying taxon membership at a branch point on a cladogram, showing a least inclusive (<), node-based (dot) taxon and a most inclusive (>), stem-based (downward arrow) taxon.

The arc-shaped line and the upward arrow are displaced from the branch point on a cladogram to which the taxon name applies (Fig. 1e, f). Placing the taxon label near the arc or adjacent to the head of an upward arrow rather than at the branch point, in addition, gives the impression that the internal branch is being labeled, as if it were an ancestral lineage on a phylogenetic tree (Fig. 1e, f). Phylogenetic definitions (node, stem) can be depicted without any ambiguity on a cladogram by a dot and downward arrow, respectively (Fig. 1d). For stem-based definitions, the arrow originates at the labeled branch point of the taxon and indicates the direction of potential inclusiveness (Fig. 2).

Symbols and Definitional Abbreviation

Current abbreviation scheme.—The dPC (Note 9.4.1) proposes a shorthand format for phylogenetic definitions, substituting capital letters for specifiers and words for phrases, such as "not" for "and the most inclusive group that contains A but not" (Table 2). Specifiers are defined

TABLE 1. Some common terms in phylogenetic taxonomy with contrasting definitional phraseology as conceptualized on a cladogram versus a phylogenetic tree. The origin of the cladogram-based phrases is given in the text. Tree-based phraseology is taken from the dPC (Note 9.4.1, Glossary).

Term	Cladogram-based	Tree-based (dPC)
Monophyletic	"a group composed of a real or hypothetical common ancestor and all of its descendants"	"a set consisting of an ancestor and all of its descendants"
Clade	"a monophyletic group"	"an ancestor and all of its descendants"
Taxon	"a named clade"	"a taxonomic group of organisms"
Phylogenetic definition	"a statement specifying the membership of a taxon"	"a statement explicitly linking a taxon name with a particular clade"
Node-based paradigm	"least inclusive clade"	"the clade stemming from the most recent common ancestor"
Node-based definition	"a statement specifying the membership of a taxon as the least inclusive clade that contains at least two internal specifiers"	"a definition that associates a name with a clade originating at a node (on a phylogenetic tree) representing the most recent common ancestor of specified descendant organisms and/or species (internal specifiers)"
Stem-based paradigm	"most inclusive clade"	"all organisms/species that share a more recent common ancestor"
Stem-based definition	"a statement specifying the membership of a taxon as the most inclusive clade that contains at least one internal specifier"	"a definition that associates a name with a clade originating on a stem (on a phylogenetic tree) representing the ancestral lineage of specified organisms and/or species (internal specifiers) after its divergence from the ancestral lineage of other specified organisms and/or species (external specifiers)"

TABLE 2.   Summary of the definitional structures, symbols, abbreviations, specifiers and qualifying clauses in the draft PhyloCode (de Queiroz and Cantino, 2004). The node-based definitional structure is shown for a crown clade.

Definitional structures
   1) Node-based: Crown Clade = (A and B (C, D, etc. as needed))
   2) Stem-based: Clade = (A not Z (X, Y, etc. as needed))
   3) Apomorphy-based: Clade (M in A)
   4) Stem-modified node-based: Clade (A and [A not Z])
   5) Apomorphy-modified node-based: Clade (A and [M in A])
Symbols and abbreviations
   A, B, . . . Z = individual specifiers
   M = apomorphy
   and = "and the least inclusive clade containing"
   not = "and the most inclusive clade containing A but not"
   in = "and the most inclusive clade exhibiting M as inherited by"
   Crown Clade = "clade in which both basal branches have living representatives"

Definitional component	Symbol	Shorthand	Longhand
Specifiers			
Species	A–Z	[binomen/author]	(same as shorthand)
Specimens	A–Z	[collection#/binomen/author]	(same as shorthand)
Apomorphy	M	[apomorphy]	(same as shorthand)
Qualifying clauses			
Excluded species/clades	(none)	(none)	"but not [species or clades with specifiers]"
Requisite "homolog"	(none)	(none)	"but with [apomorphy] as a homolog"

to include species, specimens, and apomorphies, and two kinds of "qualifying clauses" are introduced that limit clade membership (dPC Note: 11.9). The first identifies particular species or clades for exclusion; the second is a clause requiring the presence of a shared apomorphy at the base of the clade. Five definitional structures are presented, with allowance that others may be forthcoming. Finally, "crown clade" is used to recognize clades delimited by extant specifiers (one from each side of a basal dichotomy).

A shorthand abbreviation should distinguish universal versus optional components of phylogenetic definitions and accurately capture definitional structure. The shorthand recommended in the dPC, however, accomplishes neither of these goals completely, and as a result, the fundamental patterns underlying all phylogenetic definitions have not been recognized. The principal shortcomings include the following:

1. *Universal versus optional specifiers are not distinguished.* In the dPC abbreviation scheme, taxonomic specifiers (species, specimens) are given capital letters and listed as needed in ascending or descending alphabetical order. Although some general patterns were noted regarding the kinds of specifiers used in definitions (dPC: Article 11.1), these were not incorporated into the abbreviation scheme. Instead, each definitional pattern was drafted as if the specifiers were functionally equivalent (Table 2). It can be seen, however, that all definitions have one mandatory singleton, internal specifier. A second internal specifier is mandatory for node-based definitions, whereas all other specifiers (here meaning species or specimens) are optional.

2. *Apomorphies are equated with species and specimens rather than with other qualifying clauses.* In the abbreviational scheme in the dPC, apomorphies ("M") are given status equivalent to that granted specimens and species, although they play a functionally distinct role in specification of clade membership. An apomorphy is an attribute of an organism that, in the context of a phylogenetic hypothesis, can be used to qualify clade membership at the inclusive end of a stem-based definition. It constitutes a dependent clause that requires a specifier and cannot compose a complete phylogenetic definition with similar dependent clauses. It is functionally equivalent to the temporal qualifying clause, "and any extant organism/species," which includes extant species at the inclusive end of a stem-based definition (see Specifiers and Qualifiers below for further discussion).

3. *"Least inclusive" and "most inclusive" functions are not clearly indicated and uniformly applied.* In the dPC, the words "and" and "not" are used to indicate clade inclusiveness, i.e., least and most inclusive clades, respectively. "A not B," for example, is the abbreviation given for "the most inclusive clade containing A but not B." The abbreviation "M in A," however, is an abbreviation for "the most inclusive clade exhibiting character (state) M." Although this definition is also "most inclusive," the abbreviation does not contain "not." Likewise, both "and" and "not" are used in the abbreviation "(A and [A not Z])" for a "stem-modified node-based" definition but then equated with the single phrase "the most inclusive crown clade." The polarity of inclusion is the operational basis for definitional types on a cladogram, and this fundamental function must be clearly and uniformly indicated in an abbreviation scheme.

4. *Some definitional components are not represented*. In the dPC abbreviation scheme, basic patterns are given for various kinds of definitions. Some phrases that qualify clade membership are included, whereas others are not. "Crown," for example, is included as an abbreviation to indicate "and all extant organisms or species" (dPC: Note 9.4.1). Similar optional qualifying phrases involving species, time, or apomorphies are given as examples but are not represented in the abbreviation scheme.

5. *The addition of "crown" to indicate a clade with extant specifiers is potentially misleading and inefficient*. In the dPC abbreviation scheme, "crown" is used to indicate a clade defined by an extant specifier on each side of a basal dichotomy (see Revised Terminology, Special Clades). This is potentially misleading because it gives the false impression that *all* clades that could be defined by living specifiers will be established accordingly and labeled "Crown Clades" versus "Clades," when there is no mandatory rule to that effect. There is no rule forbidding the use of one or more extinct specifiers for a clade that could also be defined using extant specifiers (dPC: Note 10A.1). Further, if basal relationships within or outside the clade are ambiguous and if multiple specifiers (some extant and others extinct) are used in a node or stem-based definition, the status of the clade as a "crown" remains ambiguous, because there is no basal dichotomy and no resolution regarding the most basal specifier. Even if mandatory rules were added to overcome these difficulties, other rules would be required to give priority to a "Crown Clade" when altered phylogenetic relationships create homonymy with a previously established "Clade." If the practical concern in phylogenetics is to know if a clade includes extant representatives, a symbol can be added to the much smaller number of clades composed entirely of extinct organisms. The specifiers, in this case, would always be extinct species (or specimens tied to a species nomen).

A heuristic solution.—A modified scheme is presented here that distinguishes between *symbolic notation*, which is used to capture all of the functional components of a phylogenetic definition or set of definitions, and *shorthand abbreviation*, which replaces most symbols with the particular operating components (specifiers, apomorphies, etc.) of a given phylogenetic definition (Tables 3, 4). Here *longhand* refers to a textual rendering of a phylogenetic definition free of symbolic notation. In this manner, the fundamental patterns of phylogenetic definitions are apparent and can be mapped directly to their textual versions. A small departure from the ICZN (Ride et al., 1985; Art. 22A) is the omission of a comma between the author and date following a taxon in a longhand phylogenetic definition; the comma adds nothing but visual confusion to a line of text that may have commas between taxa. The scheme presented below is discussed and defended in the sections that follow.

There are two fundamental *definitional types*, node and stem, based on the topology of a cladogram and the polarity of inclusiveness (Fig. 2). Appropriate mathematical signs ($<$, $>$) indicate the direction of inclusiveness. Both definitional types always include one singleton, internal specifier ("A"). Node-based groups always contain a least one additional internal specifier ("B"). Stem-based groups optionally include one or more external specifiers ("C").

Both definitional types may include various *qualifiers* ("Q"), defined below as dependent phrases that qualify clade membership (Tables 3, 4). Qualifiers identify particular species, specimens, or attributes of species/specimens for inclusion/exclusion or require the presence of a particular attribute of a species or specimen in terms of form, time, or space (Table 5; Figs. 3, 4).

TABLE 3. Definitional structures, notational symbols, and specifiers and qualifiers recommended here for phylogenetic definitions.

Definitional structures
  1) Node-based: T = (<A and BQ)
  2) Stem-based: T = (>AQ but not C)

Symbols
  T = Taxon
  () = phylogenetic definition
  † = clade composed entirely of extinct organisms/species
  <= "The least inclusive clade containing"
  >= "The most inclusive clade containing"
  A = mandatory singleton internal specifier
  B = mandatory internal specifier(s)
  C = optional external specifier(s)
  Q = optional qualifier(s)

Definitional component	Symbol	Shorthand	Longhand
Specifiers			
Species	A, B, C	[binomen]	[binomen/nominal author]
Specimens	A, B, C	[binomen (collection #)]	[binomen/nominal author (collection#)]
Qualifiers			
Taxon	Q	"− [species]"	"but excluding [species]"
	Q	"+ [species]"	"and including [species]"
Time	Q	"+ extant"	"and any extant species"

TABLE 4. Hypothetical examples of symbolic notation and shorthand and longhand versions for each definitional type (node and stem-based) in the forms recommended here (i.e., with only taxon and time qualifiers). Among node-based definitions, the first is the simplest, the second exemplifies an extinct clade, and the third exemplifies the addition of a taxon qualifier. Among stem-based definitions, the first is the simplest, the second is an example with a time qualifier, and the third is an example with time and taxon qualifiers. Symbols and abbreviations are given in Table 3.

Symbolic notation	Shorthand example	Longhand
	Node-Based Definitional Structure: T = (<A and BQ)	
T = (<A and B)	Neornithes = (< *Struthio camelus* and *Tinamus tao*, *Passer domesticus*)	Neornithes Gadow 1893 = The least inclusive clade containing *Struthio camelus* Linnaeus 1758 and *Tinamus tao* Temminck 1815 and *Passer domesticus* (Linnaeus 1758)
†T = (<A and B)	†Marginocephalia = (< *Pachycephalosaurus wyomingensis* and *Triceratops horridus*)	†Marginocephalia Sereno 1986 = The least inclusive clade containing *Pachycephalosaurus wyomingensis* (Gilmore 1931) and *Triceratops horridus* Marsh 1889
†T = (<A and BQ)	†Marginocephalia = (<*Pachycephalosaurus wyomingensis* and *Triceratops horridus*— *Heterodontosaurus tucki*, *Hypsilophodon foxii*, *Ankylosaurus magniventris*)	†Marginocephalia Sereno 1986 = The least inclusive clade containing *Pachycephalosaurus wyomingensis* (Gilmore 1931) and *Triceratops horridus* Marsh 1889 but excluding *Heterodontosaurus tucki* Crompton and Charig 1962 *Hypsilophodon foxii* Huxley 1869, or *Ankylosaurus magniventris* Brown 1908
	Stem-Based Definitional Structure: T = (> AQ but not C)	
T = (>A but not C)	Passeri = (> *Passer domesticus* but not *Tyrannus tyrannus*, *Pitta sordida*, *Funarius rufus*, *Thamnophilus doliatus*)	Passeri (Passeres) Linnaeus 1758 = The most inclusive clade containing *Passer domesticus* (Linnaeus 1758) but not *Tyrannus tyrannus* (Linnaeus 1758), *Pitta sordida* (Müller 1776), *Funarius rufus* (Gmellin 1788), *Thamnophilus doliatus* (Linnaeus 1764)
T = (> AQ but not C) [Q as time qualifier]	Passeri = (>*Passer domesticus* + extant but not *Tyrannus tyrannus*, *Pitta sordida*, *Funarius rufus*, *Thamnophilus doliatus*)	Passeri (Passeres) Linnaeus 1758 = The most inclusive clade containing *Passer domesticus* (Linnaeus 1758) and any extant species but not *Tyrannus tyrannus* (Linnaeus 1758), *Pitta sordida* (Müller 1776), *Funarius rufus* (Gmellin 1788), *Thamnophilus doliatus* (Linnaeus 1764)
T = (> AQ but not C) [Q as time and taxon qualifiers]	Passeri = (> *Passer domesticus* + extant + *Corvus monedula* but not *Tyrannus tyrannus*, *Pitta sordida*, *Funarius rufus*, *Thamnophilus doliatus*)	Passeri (Passeres) Linnaeus 1758 = The most inclusive clade containing *Passer domesticus* (Linnaeus 1758) and any extant species and including *Corvus monedula* Linnaeus 1758 but not *Tyrannus tyrannus* (Linnaeus 1758), *Pitta sordida* (Müller 1776), *Funarius rufus* (Gmellin 1788), *Thamnophilus doliatus* (Linnaeus 1764)

Among the several kinds of possible qualifiers, only two are recommended for general use here (taxon qualifiers and one time qualifier; Table 3).

The symbolic representation presented here (Table 3) differs from that in the dPC (Note 9.4.1; Table 2) in several important ways. First, there are only two fundamental definitional patterns (node, stem) rather than a series of equivalent definitional types. Second, apomorphies are regarded as qualifiers rather than specifiers; apomorphies qualify clade membership at the open end of a stem-based definition that is anchored by the mandatory singleton, internal specifier A. Third, the living or extinct status of potential members of a group, likewise, is regarded as a qualifying phrase in need of recognition in a symbolic/abbreviational scheme.

Ramifications

Three definitional components.—The new symbolic notation clearly identifies three distinct functional components in phylogenetic definitions—paradigms, specifiers, and qualifiers. There are two basic ways, or *paradigms*, for circumscribing a clade using one or more terminal taxa on a cladogram (Fig. 2). The node-based paradigm, "the least inclusive clade," has an equivalent tree-based counterpart, "the clade stemming from

TABLE 5. Classification of potential qualifiers that limit, or filter, inclusion in stem-based definitions. Only taxon qualifiers ("but not") and a single time qualifier ("and any extant organisms/species") are recommended here for use in node and stem-based phylogenetic definitions, respectively.

| Type	Description	Example
Taxon	Excluded/included species	"but excluding *Youngina capensis*"
Accessory		"and including *Youngina capensis*"
Form	Apomorphy	"characterized by pennaceous feathers as a synapomorphy"
	Plesiomorphy	"characterized by feathers some of which are not plumulaceous"
Time	Datum	"and any extant organisms/species" "and any extinct organisms/species"
	Duration	"and any species that lived during the Cenozoic"
Space	Geographic range	"and any species restricted in its natural habitat to the Hawaiian Islands" "and any species with a distribution limited to what is now western North America"
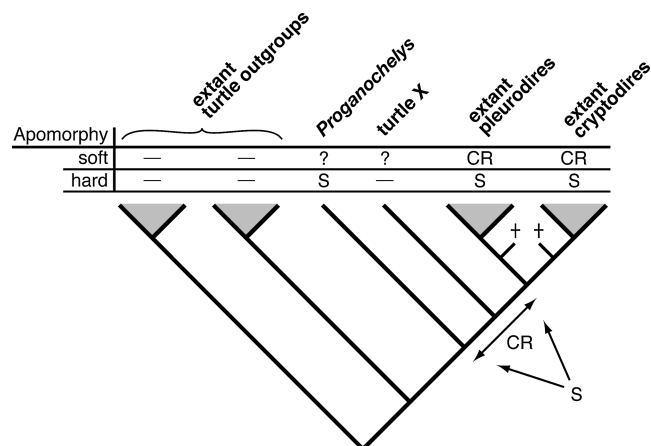
FIGURE 3. Common optimization ambiguity with apomorphies (from soft and hard morphology) as form qualifiers in phylogenetic definitions as shown among fossil and recent turtles. Shading indicates crown clades; daggers indicate extinct species. CR = carapacial ridge; S = "complete turtle shell"; — = absent; ? = unknown.

TABLE 6. Additional terms and their definitions as compared to those in the draft PhyloCode (Cantino and de Queiroz, 2004).

Term	This paper	dPC
Specification	The delimitation of clade membership by a phylogenetic definition	(no comparable definition)
Specifier	Species cited in a phylogenetic definition as an independent phylogenetic reference point	"A species, specimen, or apomorphy cited in a phylogenetic definition of a name as a reference point that serves to specify the clade to which the name applies"
Qualifier	Species or attribute of a species cited in a phylogenetic definition as a dependent clause that qualifies clade membership	(for "qualifying clause") "A part of a phylogenetic definition that specifies conditions under which the defined name cannot be applied"

the most recent common ancestor" (Table 1). Likewise, the stem-based paradigm, "the most inclusive clade," has an equivalent tree-based phraseology, "all organisms/species that share a more recent common ancestor." The polarity of "inclusiveness" (Schander and Thollesson, 1995) is the operational key to phylogenetic definitions. One of these paradigms constitutes the functional backbone of every phylogenetic definition; they must be included in an abbreviational scheme.

Other ways to circumscribe a clade, such as listing its taxonomic contents or identifying certain key subgroups for inclusion (i.e., a "taxon-based" definition), are static. They do not always specify whether new or relocated taxa ought to be included or excluded. This quality—the ability to specify clearly under alternative phylogenetic situations—is exactly why phylogenetic definitions are more precise than a simple listing of taxonomic content. Phylogenetic resolution, it should be noted, is not at issue in this connection; if the phylogenetic relationships of certain taxa are not resolved, their taxonomic assignment may not be certain under any definition. The point here is that *when relationships are fully resolved*, taxon-based definitions are not as precise regarding the inclusion or exclusion of new or relocated taxa.

Here *specifier* (with internal/external designations) is adopted as the term for the second definitional component over "reference taxon," principally because of its eponymous linkage to species and their primary role in phylogenetic definitions. The meaning of "specifier" in this article, however, refers only to species (or specimens tied to a species nomen), unlike the dPC (which also includes apomorphies) (Table 6).

The third and final definitional component is here termed a *qualifier* (Tables 5, 6). Qualifiers comprise phrases that qualify the potential taxonomic content of a phylogenetic definition. Unlike specifiers, qualifiers do *not* function as anchoring points in a phylogenetic definition but rather act as filters that set conditions on membership. Also unlike specifiers, qualifiers can be attributes of species as well as species themselves. The concept of a qualifier captures the functional unity of various things within, or appended to, phylogenetic definitions that previously have been viewed as unrelated, including (1) apomorphies, (2) phrases such as "and any extant species," (3) "designated phylogenetic contexts" (Bryant, 1997), and (4) "qualifying phrases" (dPC: Art. 11). All of these (and some others; Table 5) act by setting conditions on membership.

Only two definitional types.—The fundamental division of all definitions between those that are node-based
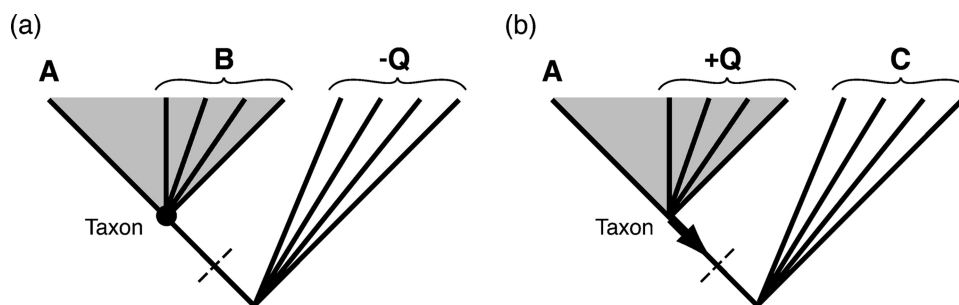

FIGURE 4. Stabilizing the taxonomic content of a taxon under conditions of uncertain ingroup and outgroup relationships. (a) Node-based definition with multiple internal specifiers (B) and a negative taxon qualifier (−Q) identifying multiple outgroups for exclusion. (b) Stem-based definition with multiple external specifiers (C) and a positive taxon qualifier (+Q) identifying multiple ingroups for inclusion.

TABLE 7.   Definitional variants previously regarded as distinctive ("apomorphy-based," apomorphy-modified node-based," "stem-modified node-based") are shown below to follow the generalized pattern for stem-based definitions: T = (> AQ not C). The first and second examples are hypothetical; the third and fourth are based on Wyss and Meng (1996) and the dPC (Note 11.9), respectively. Symbols and abbreviations are given in Table 3. Apomorphies are abbreviated "+ [apomorphy]" rather than "[apomorphy] in" as in the dPC (Note: 9.4.1). In that way, the anchoring specifer A always appears first in symbolic notation, shorthand, and longhand versions.

Symbolic notation	Shorthand example	Longhand
"Apomorphy-based" $T = (>AQ)$	Ornithurae = (>*Passer domesticus* + pygostyle)	Ornithurae Haeckel 1866 = The most inclusive clade containing *Passer domesticus* (Linnaeus 1758) and with a pygostyle as a synapomorphy
"Apomorphy-modified node-based" $T = (>AQ)$	Passeri = (>*Passer domesticus* + extant + diacromyodian syrynx)	Passeri (Passeres) Linnaeus 1758 = The most inclusive clade containing *Passer domesticus* (Linnaeus 1758) and any living species and with a diacromyodian syrynx as a synapomorphy
"Stem-modified node-based" $T = (>AQ \text{ not } C)$	Rodentia = (>*Mus musculus* + extant but not *Lepus europaeus*)	Rodentia Bowdich 1821 = The most inclusive clade containing *Mus musculus* (Linnaeus 1758) and any living species but not *Lepus europaeus* (Linnaeus 1758)
"Node-based with requisite homolog" $T = (<A \text{ and } BQ)$	Pinnipedia = (<*Otaria byronia* and *Odobenus rosmarus*, *Phoca vitulina* + flipper)	Pinnipedia Illiger 1811 = The least inclusive clade containing *Otaria byronia* Peron 1816, and *Odobenus rosmarus* Brisson 1762, *Phoca vitulina* Linnaeus 1758 and with a flipper as a homolog (synapomorphy or symplesiomorphy)

versus those that are stem-based is apparent with the proposed, more complete symbolic abbreviation. These two fundamental patterns have been obscured by the improper elevation of apomorphies as equals to taxonomic specifiers, the use of more opaque tree-based phraseology (i.e., "ancestors," "node pointing," "stemming") in definitions and terminology, and an incomplete abbreviational scheme that does not isolate or symbolize the most basic function (inclusiveness) to all phylogenetic definitions.

An "apomorphy-based" definition, thus, is regarded here as a form-qualified stem-based definition, the apomorphy serving as a qualifying clause at the open end of a stem-based definition (Table 7). The apomorphy is dependent on the mandatory singleton, internal specifier A, which anchors the definition. Clade membership requires the presence of the apomorphy and that such presence is considered synapomorphic (homologous) in the light of a phylogenetic hypothesis. The absence of the apomorphy does not automatically exclude membership, as long as that absence is understood as secondary (loss) on a cladogram. Ambiguity as a result of missing data is interpreted with delayed transformation; in other words, the absence of information in an immediate outgroup will be interpreted as absence. The apomorphy does not function as an anchor like a taxonomic specifier, which pinpoints internal and external boundaries. Apomorphies are attributes that must be evaluated seriatim in potential members to determine the true (if temporary) boundaries of a stem-based clade. If a new taxon with the apomorphy is discovered that is the sister taxon of the clade formerly sharing the apomorphy, it is absorbed into the clade. This describes a filtering function that operates away from the internal specifier (A), the only mandatory specifier in a stem-based definition (Table 3).

"Apomorphy-based" definitions also were misidentified as a unique pattern, rather than as a subclass of stem-based definitions, by authors who abandoned tree-based phraseology in definitions. Schander and Thollesson (1995:264), for example, used clade inclusiveness for the

former definitional types but retained tree-based terminology for an apomorphy-based definition: "the clade stemming from the first ancestor to possess a particular apomorphy." Likewise, Lee (1998b:26) used clade inclusiveness for the former definitions but defined an "apomorphy-based" definition as "the clade diagnosed by trait X." Presumably, "diagnosed by trait X" translates as "the most inclusive clade sharing apomorphy X." After all, it is necessary to distinguish this clade from less inclusive clades that also share apomorphy X. Later, Lee adapted Moore's (1998:566) "'type-modified' apomorphy definition" as "the most restricted clade diagnosed by character C homologous with that in taxon T" (Lee, 1999:361). This terminology is doubly confused. The "most restricted clade" is equivalent to "least inclusive clade" in a node-based definition; "diagnosed by" presumably is equivalent to "most inclusive clade" in a stem-based definition; and "character C" presumably should have been "apomorphy C," as the definition should be pinpointing the most inclusive clade sharing an apomorphy (i.e., a derived character state, not simply a character).

A "stem-modified node-based" definition, similarly, is actually a stem-based definition. It does not have equal footing as a distinct definitional type (Lee, 1998a; Sereno, 1999; Table 7). The proposed wording in the dPC for a "stem-modified node-based" definition differs from that proposed for a stem-based definition only by one word— the insertion of "crown" in front of "clade": "The most inclusive *crown* clade containing A but not Z" (dPC: Note 9.4.1; italics added). In this case, the word "crown" is operating as a time qualifier ("and any extant organisms/species"), and the definition can be rephrased "The most inclusive clade containing A *and any extant species* but not Z." The time qualifier "crown," or its equivalent "and any extant organisms/species," does not identify any additional specifiers by name. Rather, it qualifies, or filters, the set of potential members of the clade, which remains anchored by the two identified specifiers, A and Z. That this kind of definition is stem-based, rather than node-based, is particularly clear when all parts of the

definition are symbolized: T = (> AQ but not C). In this case, A and C constitute internal and external specifiers, respectively, and Q constitutes a time qualifier (Table 7).

Crown clades may be stem-based.—The erroneous notion that node-based definitions alone are applicable to crown clades has deep roots within phylogenetic taxonomy (e.g., Gauthier et al., 1988). de Queiroz and Gauthier (1992:469) stated that "names can be associated unambiguously with crown clades using node-based definitions." All crown clades were given node-based definitions in early phylogenetic taxonomies (Lepidosauromorpha: Estes et al., 1988; Gauthier et al., 1988; Craniata: de Queiroz and Gauthier, 1992). de Queiroz and Cantino (2001:823) stated "if one wants to name a 'crown' clade (terminology of Jefferies, 1979), a node-based definition must be used." The dPC simply specifies a priori that crown clades be node-based (dPC:24). When basal relations within a crown clade are poorly resolved, nevertheless, one obvious option is to use a stem-based definition with an "extant" filter that identifies the external boundary, or basal node, of the clade. As shown above, the so-called stem-modified node-based definition (e.g., Neognathae, Neoaves; Gauthier and de Queiroz, 2001), in reality, is a stem-based definition invoked precisely under these circumstances (Lee, 1998a; Sereno, 1999). The dPC, nevertheless, maintains the misleading "node-based" label. If practicing phylogenetic taxonomists cannot accurately differentiate between the two most basic definitional patterns (node, stem), then it is no wonder that critics blur the two with such ease.

Apomorphies are not specifiers.—In the earliest papers on definitional protocol (de Queiroz and Gauthier, 1990, 1992) and in the dPC (Article 11.1), apomorphies are defined a priori as specifiers. Unlike apomorphies (Table 8), however, species (1) comprise phylogenetic entities (are ontological individuals) as opposed to constituting only the attributes of phylogenetic entities; (2) act as terminal units in phylogenetic hypotheses rather than as individual character states; (3) occupy unique reference points

in phylogeny rather than ephemeral positions in character space that typically are not unique or permanent (due to homoplasy) and may not be available in taxa under consideration (missing information); (4) are composed of thousands or millions of apomorphies that, together, pinpoint, or very narrowly circumscribe, a location in organismal phylogeny as opposed to single features that frequently are subject to different interpretations (e.g., character structure, observation, and scoring); (5) are independent, meaning that specifiers, alone or in combination, can be used to construct complete phylogenetic definitions as opposed to apomorphies which must be paired with a specifier; (6) do not permit changes in clade membership when phylogenetic relationships remain unaltered as opposed to regularly allowing such changes to occur; and (7) establish clade membership by inspection of a reference phylogeny rather than also requiring a figure, description, and potentially character-state distributions to allow interpretation. Ontologically, point 1 separates species (and specimens tied to species names) as phylogenetic individuals from apomorphies or other organismal attributes. Although there is a range of species concepts and differing opinions regarding their individuality (e.g., de Queiroz, 1988b; Ereshefsky, 2001), species have never been regarded as attributes. The remaining points characterize the fundamental differences that ensue, a few of which are examined in more detail below.

Apomorphies as dependent clauses.—Apomorphies are here regarded as qualifying entities that cannot compose complete phylogenetic definitions on their own. It is questionable, for example, to offer two apomorphies as the basis of a definition, such as "the least inclusive clade including hollow-based, filamentous epidermal appendages and a tail shorter than the femur." Qualifying phrases that are temporal in nature, likewise, are meaningless by themselves or in pairs in a definition, such as "the most inclusive clade containing any extant species and any extinct species."

The first hypothetical definition cited above is constructed from two apomorphies published recently in phylogenetic definitions for clades among birdlike dinosaurs and basal birds (Gauthier and de Queiroz, 2001:25, 27) and specifies a clade that approximates Coelurosauria. Of course, Gauthier and de Queiroz (2001) did not recommend using apomorphies by themselves, although doing so would better fit their appellation "apomorphy-based." This hypothetical definition owes its ineffectiveness to the fact that apomorphies, and other singular attributes of organisms, are almost always less unique and stable in phylogeny than taxonomic specifiers. Apomorphies, thus, have never been proposed as independent entities for phylogenetic definitions free of taxonomic specifiers. They are *dependent* on taxonomic specifiers to anchor, or localize, the definition to a specific reference point in organismal phylogeny, against which they qualify clade membership.

Some pairs of taxon qualifiers (Table 5) can be combined to compose a complete phylogenetic definition, but this is only because they include species that now

TABLE 8. Comparison of specifiers (species and specimens tied to a species) and apomorphies.

	Specifier	Apomorphy
Ontological status	Phylogenetic entity	Attribute of phylogenetic entity
Phylogenetic status	Terminal unit	Character state
Uniqueness	Always unique	Rarely unique
Morphologic complexity	10^n apomorphies	Single apomorphy
Independence	Yes	No (must be used with a specifier)
Clade inclusiveness can change independent of phylogeny	No	Yes
Information required for definitional interpretation	Phylogeny	Figure, description, and character-state distribution

have become specifiers. For example, the positive taxon qualifier "and including *Homo sapiens*" and the negative taxon qualifier "but excluding *Pan troglodytes, Pan paniscus* or *Gorilla gorilla*" could be combined to compose a stem-based definition: "The most inclusive clade containing *Homo sapiens* but not *Pan troglodytes, Pan paniscus* or *Gorilla gorilla*."

If apomorphies and taxonomic specifiers are given the same status simply because both can be used to qualify (limit) clade membership, then other qualifiers must also be considered specifiers. In the following hypothetical definition, for example, a time qualifier ("and any extinct species or specimens") is used in combination with a single internal taxonomic specifier (*Homo sapiens*) to specify a stem-based taxon that has the same symbolic structure as an "apomorphy-based" definition, T = (> AQ): "Hominini = The most inclusive clade containing *Homo sapiens* and any extinct species and specimens." This is not an open-ended definition but rather includes only the most inclusive clade of extinct species that are closest to *Homo sapiens*. This hypothetical clade would include *Homo sapiens* and all *extinct* relatives closer to man than to other extant hominoids, such as *Pan paniscus* or *Gorilla gorilla*, or any other extant species.

"Complex" apomorphies as specifiers.—In the dPC "complex" apomorphies that are composed of more than a single feature are also granted roles as specifiers or as components of qualifying clauses (dPC:Arts. 9.8, 11.1). Their component parts can be parsed into those critical for the definition to apply. Alternatively, all parts of a "complex" apomorphy may be required for the definition to apply to a particular clade. The pinniped "flipper" was offered as an example (dPC:29), although in spirit only, as the component parts of a flipper were not delineated. The view taken here is that a "flipper" is a functional concept (an appendage that flips water) rather than a single "complex" character. A flipper in this view is better understood as a character complex, composed of many independent and interdependent musculoskeletal components. Such "complex" characters have the potential to introduce unnecessary ambiguity. Attempting to stabilize clade boundaries on the basis of a character complex mimics traditional diagnoses that enlist an ensemble of "key characters" or point to particular complex "key innovations" (Gallis, 2001).

Recently, Joyce et al. (2004) used a "complex" apomorphy in their definition of Testudinata to circumscribe all known turtles. Their description of a "complete turtle shell" is taken verbatim from Gaffney and Meylan (1988:161): "carapace formed from costal bones with fused ribs, neural bones with fused thoracic vertebrae, and marginal bones; plastron formed from interclavicle, clavicle, and three to five paired bones sutured together; carapace and plastron articulated at lateral margin and enclosing shoulder girdle and pelvic girdle" (Joyce et al., 2004:996). All of these features must be present to pinpoint the clade, as none is given preference. Given current knowledge of the turtle fossil record, *Proganochelys* is the basalmost stem with a "complete turtle shell" and appears to exhibit all of its features (Gaffney, 1990).

What if a complete fossil turtle skull (but nothing else) is found that is positioned with confidence as the sister taxon to *Proganochelys* and other turtles? Is it within Testudinata? Literal reading of the dPC would suggest not. However, neither is there evidence for its exclusion, as the relevant information about its skeleton is simply missing. What if, subsequently, a portion of its carapace (but no trace of the plastron) is discovered? Would it now be placed within Testudinata? To continue, what if Hay (1908) was correct in positioning the leatherback sea turtle *Dermochelys*—which lacks most of the ossifications that compose a "complete turtle shell"—outside all other extant turtles and closely related extinct species (Fig. 3, "turtle X")? In this configuration, a complete shell may be optimized in one of two locations. Optimization ambiguity, which is commonplace when considering extinct taxa, will obscure clade boundaries that are dependent on apomorphies, even when phylogenetic relationships are fully resolved.

Apomorphies and optimization.—To generalize from the problems discussed above, apomorphies owe their position on a cladogram to the *distribution and optimization of the states of a particular character*. Taxa, in contrast, owe their position on a cladogram to phylogenetic analysis, namely, *the composite interpretation of character distributions*. Given that characters, under the best circumstances, are independent of one another, the two will not always coincide. The interpretation (coding, scoring) or position (optimization) of most apomorphies can change without affecting phylogenetic relationships. On a cladogram of turtles (Fig. 3), basal homoplasy or missing information for an apomorphy used in a definition can create ambiguity in taxon boundaries even when relationships are stable and fully resolved. Operationally, thus, apomorphies and taxonomic specifiers are governed by related, but different, criteria.

Apomorphies, as a consequence of this operational difference, require more documentation and interpretation than taxonomic specifiers; one must know the structure, distribution, and scoring of a character in order to interpret clade membership. This information is usually not apparent on available published cladograms that might be used as reference phylogenies. Gauthier and de Queiroz (2001), for example, presented a cladogram depicting the relationships they regard as probable but offered no information concerning the distribution of apomorphies that are critical to the interpretation of their newly proposed "apomorphy-based" definitions for Avialae and Avifilopluma. For taxonomic specifiers, in contrast, visual examination of a reference phylogeny is sufficient.

Their definition for Avialae also demonstrates how rapidly apomorphies can relocate with no change in phylogenetic relationships. At the time of their writing, it seemed safe to presume that nonvolant theropods like *Deinonychus* and kin would never be found with "feathered wings . . . used for powered flight," their preferred apomorphy encompassing *Archaeopteryx* and more derived birds (Gauthier and de Queiroz, 2001:25). The recently described "four-winged" deinonychosaurian,

Microraptor (Xu et al., 2003), potentially expands the content of Avialae so that it overlaps with other phylogenetically defined taxa, such as Paraves (Sereno, 1998). To set clade boundaries, a taxonomist must decide what constitutes "powered flight" in living birds, how such functionality is to be interpreted in fossilized skeletons, and what the plesiomorphic condition is for Deinonychosauria.

Despite these interpretive hurdles, Avialae is well behaved compared to another of their "apomorphy-based" taxa, Avifilopluma. This taxon was erected on the presence of "hollow-based, filamentous epidermal appendages produced by follicles" (Gauthier and de Queiroz, 2001:25), despite the fact that the filaments/feathers preserved on extinct nonavian dinosaurs are not demonstrably hollow-based or produced from follicles. Without any sense of concern, the authors remarked that their newly defined taxon might overlap with a half dozen others: "*Avifilopluma* might even contain all but the basalmost theropods ... as well as taxa more distantly related to birds, such as herrerasaurs and *Eoraptor*" (Gauthier and de Queiroz, 2001:25). The "apomorphy-based" definitions proposed by Gauthier and de Queiroz (2001) underscore the need to restrict characters and their functional interpretations to diagnoses and interpretive discussion, respectively.

Crown Clades and Common Names

Accuracy in reporting.—Relocating "widely used" names to crown clades has been done "for the sake of cognitive efficiency" and to stem the tide of "unjustified phylogenetic inferences" (Joyce et al., 2004:992–993). Three widely used resources for turtles (Pritchard, 1979; Ernst and Barbour, 1989; Zug et al., 2001) were singled out as examples of the kind of transgressions that occur when taxa, such as Cryptodira, are not linked to crown clades. According to Joyce et al. (2004:993), all three promoted the mistaken belief that "all members of the *Cryptodira* [sic] retract their necks along a vertical plane" (presumably Joyce et al. meant Cryptodira, not their converted crown clade *Cryptodira*). Neontological turtle taxonomists, they suggested, are ignorant of Gaffney's taxon Casichelydia, its subdivision into Pleurodira and Cryptodira, and the fact that living pleurodires and cryptodires may have derived features absent in extinct stem taxa. A closer look at the references they chose to admonish is illuminating.

Pritchard's (1979) *Encyclopedia of Turtles* is remarkable for its detailed discussion of the then recently published cladistic classification of Gaffney (1975a, 1975b), although he maintained the traditional paraphyletic Amphichelydia in his classification. I was unable to find any version of the offending phrase "all cryptodires have vertical neck retraction." Rather, I encountered a detailed discussion of neck retraction, cervical vertebral form, and how this varies among extant turtles. Pritchard, furthermore, clearly included fossil stem taxa in Pleurodira and in all of the "widely used" families for extant turtles, in stark contrast to the usage proposed by Joyce et al. (2004).

In *Turtles of the World*, Ernst and Barbour (1989:8) actually employed Gaffney's higher-level taxonomy, which forms the basis for their reference phylogeny. There is no statement comparable to "all cryptodires have vertical neck retraction." Rather they highlighted the fact that some early cryptodires "lacked mechanisms to retract the head" but that fossils indicate that they had achieved this capability by the Early Cretaceous (Ernst and Barbour, 1989:8–10). The closest they came to the offending phrase is a table of contrasting features for pleurodires and cryptodires, in which they listed lateral and vertical neck retraction, respectively.

Turning to *Herpetology* (Zug et al., 2001), the offending phrase also could not be located. They adopted Gaffney's classificatory scheme, specifically mentioning that neck retraction arose within both clades: "The recognition of these two clades arose from their contrasting neck-retraction mechanics, but other characters support the monophyly of each" (Zug et al., 2001:437). Before discussing vertical neck retraction in cryptodires, they stated "*extant* turtles are divided into two clades based on the movement or retraction pattern of the neck" (Zug et al., 2001:435; emphasis mine); they limited their comments in this regard to extant turtles. It is clear, furthermore, that they include extinct stem species within Pleurodira and Cryptodira, as they remarked that "these two clades lived contemporaneously with the most primitive turtle, *Proganochelys*" (Zug et al., 2001:436–437). As much as one may discern, no version of the offending phrase is used in these references, and all three were aware of Gaffney's taxonomy.

It is commonplace for systematists, from Darwin to present-day paleontologists and molecular biologists, to include within higher taxa extinct stem species that date back millions of years (Sereno, 1999). The word "living" or "extant" is inserted to refer only to the crown clade. Recent molecular work on turtles, for example, spoke of "extant Pleurodira" and cited the relevant paleontological literature for stem species (Shaffer et al., 1997; Georges et al., 1998). Thus, it is not immediately apparent how the belated removal of all stem pleurodires from Pleurodira by Joyce et al. (2004) will enhance communication among these systematists or provide a seamless bridge to their work. Favored use of Pleurodira over Eupleurodira in the recent literature does not mean that most turtle taxonomists were using the former as a crown clade.

Accuracy in statements and inferences.—The claim that "unjustified inferences" require relocation of "widely used" names is a red herring for other reasons. Many phylogenetic statements and inferences, if taken verbatim, are less than precisely accurate. The subtleties of textual accuracy, it seems, have never stood as a major obstacle to progress in phylogenetics.

Statements regarding the presence or absence of some feature in a taxon fall into two broad categories, observational and transformational (Table 9). The observation that "taxon T has structure X" or that "all T has X" is not equivalent to transformational statements such as "taxon T has synapomorphy X" or "X is a synapomorphy of T." Observational statements about a taxon often

TABLE 9. Examples of observational versus transformational statements using taxon T and character (or character-state) X.

Observational	Transformational
T has X	T shares apomorphy X
All T has X	T has synapomorphy X
T is characterized by X	X is a synapomorphy of T

do not hold true for every single member for two reasons. First, most characters, be they morphological or molecular, are not essences immune to exception (loss, secondary change). Second, observational statements are often subject to missing data, either within a taxon or at its borders. Observational or transformational statements regarding soft anatomy, in addition, have never been limited to the characterization of crown clades. Below I develop these points using the example from turtles that Joyce et al. (2004) chose to highlight.

The vast majority (but not all) of extant cryptodires are capable of vertical neck retraction, a complex functional capability that involves modification of several joints in the cervical vertebrae. The statement (Joyce et al., 2004:993) that "all members of the *Cryptodira* retract their necks along a vertical plane . . . an observation based on living cryptodirans alone" thus is not completely accurate. Some extant cryptodires have lost, or severely limited, this capability (e.g., the big-headed turtle *Platysternon*). One option is to replace "all" with something less encompassing, like "most," but then it is unclear which cryptodires lack this capability. Doubt would be cast on the implication that it is a shared-derived feature of the clade, and such usage would be no clearer in this regard than that criticized by these authors.

An equivalent transformational statement that speaks more directly to the feature as a phylogenetic transformation can accommodate homoplasy. It takes the form "structure X is a synapomorphy of taxon T," or "vertical neck retraction is a synapomorphy of Polycryptodira." Inevitably statements like these also have a finite lifetime of accuracy, unless apomorphy X is tied to taxon T in a form-qualified definition. Joyce et al. (2004), however, gave a node-based definition to the relevant clade (Cryptodira, in their sense). Form-qualified definitions, nevertheless, are fraught with interpretational difficulties, as outlined above. In this case, vertical neck retraction is not an apomorphy but rather a derived function. Presumably that is the reason Joyce et al. state that it can be observed only in extant turtles. Yet, there are a number of osteological correlates indicative of this function (Witmer, 1995; Pritchard, 1997), and some fossil forms that are most closely related to Polycryptodira (or extant subclades) and exhibit all of these correlates doubtless had this functional capability in life.

Soft-tissue or developmental patterns with compelling and unique osteological correlates, likewise, are not limited for reference only to the crown clades in which they are actually observed. Many developmental biologists, for example, consider the carapacial ridge, which is present in every turtle embryo and draws the ribs into a more superficial location, to be the "key innovation" for turtles and, by inference, to have been present in *Proganochelys* (Fig. 3, CR; Gilbert et al., 2001). Is the inference of this developmental innovation among extinct species somehow less acceptable (or probable) than a statement restricting it to living species, such as "the carapacial ridge is a synapomorphy of crown turtles"? Presumably not. Using correlation to infer such "invisible" developmental morphology in stem taxa, in fact, has been promoted elsewhere in the definition of Avifilopluma, which unites birds and all of their extinct feathered kin that share "hollow-based, filamentous, epidermal appendages produced by follicles" (Gauthier and de Queiroz, 2001:25).

In sum, I know of no evidence to suggest that lexical subtleties and transgressions of the sort outlined above with regard to crown clades have stood as a significant impediment to progress or communication in systematics. At the least, it provides dubious justification for dramatically altering the taxonomic content of widely used taxa.

Revised Terminology

In light of the foregoing critique, a more precise terminology for phylogenetic taxonomy is clarified below and compared to previous usage where appropriate. The goal here is not to revise the dPC. The aim is to provide phylogenetic taxonomy with a set of terms of comparable clarity to those that have gained currency in phylogenetic systematics.

Phylogenetic Definitions

A *phylogenetic definition* is defined here as a statement specifying the membership of a *taxon*, which in turn is defined as a named *clade*, which in turn is defined as a *monophyletic group* (Table 1). In this context, phylogenetic definitions are based on "statements of ancestry" only inasmuch as the concept of a monophyletic group is defined as "a group of species that includes an ancestral species (known or hypothesized) and all of its descendants" (Farris, 1974).

A *node-based definition* is a statement specifying the membership of a taxon as the least inclusive clade that contains at least two internal specifiers. A *stem-based definition*, in turn, is a statement specifying the membership of a taxon as the most inclusive clade that contains at least one internal specifier (Table 1). A stem-based definition does not require the presence of an external specifier; one or more external specifiers are optional. The polarity of inclusiveness (i.e., the paradigm) and the invariant specifiers mentioned above unambiguously identify all phylogenetic definitions as one or the other of these two *definitional types*. Other aspects of node- and stem-based definitions are optional or variable, such as whether there are additional specifiers or qualifiers.

Terminological definitions in the dPC, in contrast, have been modeled preferentially on a phylogenetic tree. Almost all definitions in the glossary, for example, are given only in terms of a phylogenetic tree (Table 1). In the case of phylogenetic definitions, tree-based definitions necessarily refer to ancestral lineages and describe clades "originating at a node" or "stemming from a common

ancestor." A "lineage," in turn, is defined as:

> a series of entities (e.g., organisms, populations) that form a single unbroken and unbranched sequence of ancestors and descendants. That a lineage is unbranched does not deny the existence of side-branches, which are not parts of the lineage in question, or of branching at lower organizational levels (e.g., organelle lineages within a population lineage). There may even be branching at the organizational level in question as long as it is judged to be temporary (dPC: Glossary).

Why infuse critical definitions with such tree-based interpretive complexity, when the determining paradigm on a cladogram requires only a statement about inclusiveness (Härlin, 2003a)? The wordy tree-based definitions appear to owe their complexity to the interpretation of species as lineages (de Queiroz, 1988b) and phylogenetic taxonomy as the culmination of the "Darwinian Revolution" (de Queiroz and Gauthier, 1990) rather than an outgrowth of phylogenetic systematics.

Specifiers

Specifiers are species cited in a phylogenetic definition (Table 6). Specifiers may also comprise specimens, but these must be tied to a species name, a universal constituent. All definitions have one internal specifier (A). Some published definitions list a number of species without designating the mandatory internal specifier A (e.g., Cantino et al., 1997). This is merely a textual variant and can be rearranged with a designated mandatory internal specifier. In the dPC, in contrast, apomorphies are also regarded as specifiers (Table 6). *Specification* is defined here as the delimitation of clade membership by a phylogenetic definition, in which specifiers play a key role.

Qualifiers

Qualifiers are species, specimens, or attributes of species/specimens cited in a phylogenetic definition that provide conditions on clade membership. In the dPC, "qualifying clauses" are defined as "conditions under which the defined name cannot be applied" (Table 6; dPC: 48, glossary). Indeed, all but one of the qualifying phrases in the dPC are limited to a single kind of taxon qualifier, which uses a phrase beginning with "but not" to make sure that one or more species (or clades) are not part of the taxonomic content of a node-based clade. In one example, however, an apomorphy is attached to a node-based definition that reads "provided that it possessed flippers homologous with those in the aforementioned species" (Table 7, bottom). Potential qualifiers, however, are more diverse and can be divided into two types, taxon and accessory qualifiers (Table 5).

Taxon qualifiers.—Taxon qualifiers identify species for exclusion or inclusion, thereby setting conditions on clade membership. *Taxon qualifiers* are particularly useful in phylogenetic definitions when ingroup or outgroup species are unstable but have long been either included or excluded, respectively, from the taxonomic content of a particular taxon. Naming a single species from a clade for exclusion effectively excludes the entire clade, so there is little reason to list anything but species or specimens tied to species names.

In node-based definitions, stability among ingroup species is easily addressed by including additional internal specifiers. Likewise, in stem-based definitions, stability among outgroup species is easily addressed by including additional external specifiers (Fig. 4; Sereno, 1999:fig. 12; dPC: Rec. 11D, E). Additional taxon qualifiers can increase restrictions on the potential taxonomic content of a taxon, using the opposing set of species (outgroup species for node-based definitions; ingroup species for stem-based clades). The phrases "and including" and "but excluding" are recommended here rather than "and" and "but not" to avoid confusion between the species in qualifiers and those used as specifiers (Tables 3, 5).

Definitions that begin by mentioning a clade, such as "all dinosaurs closer to *Triceratops* than to Neornithes" (for Ornithischia; Sereno, 1998:61), strictly speaking, are using this clade (i.e., Dinosauria) as a negative taxon qualifier. Only members of Dinosauria are available for inclusion within Ornithischia (i.e., non-dinosaurs are excluded). This accomplishes little except adding to the definition another taxon, the definition for which is not specified. A clearer definition uses species and avoids mention of any accessory higher taxa, such as "the most inclusive clade containing *Triceratops horridus* but not *Passer domesticus*. If there is a specific reason to exclude other taxa by definition, species in the form of a taxon qualifier can be added to the definition.

Accessory qualifiers.—Accessory qualifiers use attributes, rather than taxa or specimens, to set conditions on clade membership. As a result, they are governed by criteria other than the branching pattern of phylogeny. When using accessory qualifiers, clade boundaries may change even when phylogenetic relationships remain unaltered. Accessory qualifiers are divided into *form, time,* and *space qualifiers* (Table 5; Fig. 5). Although apomorphies are the most commonly used form qualifiers, it is possible to cite a plesiomorphy. If an unordered,
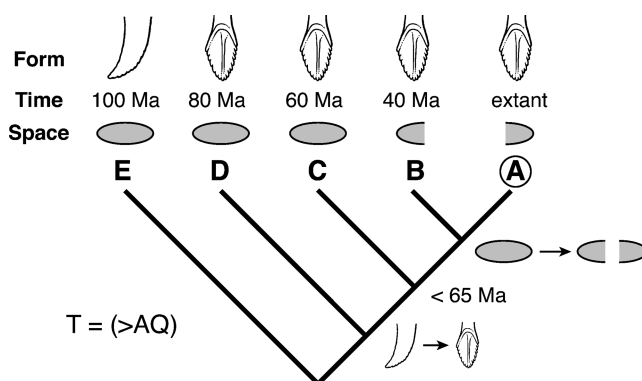

FIGURE 5. Example accessory qualifiers (form, time, space) on a cladogram of five taxa (A to E). The three clades identified on the right side of the cladogram use an apomorphy, a datum, and a particular geographic range, respectively, as accessory qualifiers in stem-based definitions. All have the symbolic structure T = (>AQ). The taxon, T, is associated with a particular phylogenetic definition. Parentheses enclose the definition, a greater than symbol (>) stands for "the most inclusive clade containing," A is a nested extant taxon, and Q is a qualifier (form, time, space).

multistate character were used as a form qualifier, for example, any character-state transformation from the primitive state would allow inclusion of that taxon within the clade (Table 5, plumulaceous feathers). Again, this is a hypothetical form qualifier, not one this author recommends. Because form qualifiers are associated with the range of problems discussed above for apomorphies, none is recommended here for use in phylogenetic definitions.

Time qualifiers use age attributes to set conditions on clade membership (Table 5). Common time qualifiers use a time horizon to assess the extant or extinct status of potential clade members. Such horizons include "the date of publication" but could easily be extended back in time (Fig. 5). Deep time qualifiers are biologically meaningful and relatively easy to assess in potential clade members. The clade of birds or mammals that radiated in the Cenozoic in response to the mass extinctions at the end of the Cretaceous, for example, has been of significant interest (Feduccia, 1995). "The most inclusive clade containing *Passer domesticus* and any species that lived during the Cenozoic" would serve to unite the largest clade of birds whose common ancestor lived at the dawn of the era. Again, this is a hypothetical time qualifier, not one this author recommends.

Space qualifiers use geographic range to set conditions on clade membership. Biological radiations often take place within a restricted geographic area, and that area can be used as a qualifier for membership within a taxon (Table 5). Hawaiian honeycreepers (Drepanidinae) appear to have diversified on the islands after a single dispersal event approximately 3.5 million years ago (Tarr and Fleischer, 1995). Drepanidinines, a celebrated insular radiation, is supported as a monophyletic clade only by limited molecular and morphological evidence. Raikow (1982:431) remarked that based on morphology, "Drepanididae is hardly definable as a monophyletic group except by a geographic argument." "The most inclusive clade containing *Drepanis funerea* and any species restricted in its natural habitat to the Hawaiian Islands" would maintain Drepanidinae as an endemic clade, excluding other closely related finch species from North America.

Space qualifiers need not be limited to recent distributions. "The most inclusive clade including *Triceratops horridus* and any species with a distribution limited to what is now western North America" would limit membership of the clade Ceratopsidae to the very characteristic group of large-bodied herbivores restricted in known range to western North America (Table 5). In the future, fossil finds in Asia may ultimately blur the morphologic and geographic distinctiveness of Ceratopsidae as it has long been known. *Turanoceratops*, a poorly known Asian species and probable sister taxon to North American ceratopsids, on these grounds would be excluded. Although one may question the need for space qualifiers in phylogenetic taxonomy, they are much less susceptible to ambiguous interpretation than published form qualifiers (i.e., apomorphies) and certainly recognize evolutionary events of equal or greater significance.

Special Clades

Crown clades.—The terms "crown" group (Jefferies, 1979) and "crown clade" have been reviewed elsewhere, the latter defined as "a living species, or a clade that can be defined by living species, whose immediate outgroup is extinct" (Sereno, 1999:336). The presence of an extinct outgroup was an integral part of Jefferies' original concept, which doubtless was based on Hennig's (1965) earlier temporal partition of the history a group into a time of origination, an intermediate duration when "typical" characters evolved, and a crown clade bounded by extant species (Fig. 1a, b). "Crown" is most often used in this manner today—to identify the most inclusive extant-bounded clade within a larger group that also includes basal members that are extinct, such as "crown-group Aves" or "crown birds."

Despite this original, and now widely used, conception of crown clade, de Queiroz and Gauthier (1992:469) substituted another definition without explanation: "clades within which both branches of the basal dichotomy are represented by extant descendants." This more recent definition, which has been repeated by others (e.g., Lee, 1996b) and adopted by the dPC, (1) *excludes* any taxon defined on the basis of extant specifiers that does not have a clear-cut basal dichotomy and (2) *includes* vast numbers of clades defined by extant specifiers whose closest known relatives are also extant. What is gained by this more expansive definition of "crown" clade? Is the intent to acknowledge clades with extant specifiers? If so, it would be simpler to recognize the much smaller number of clades in which all members are extinct (theoretically, all remaining clades could be defined by extant specifiers). This redefinition, however, undermines the relationship between, crown, stem, and total clades as outlined below.

Stem and total clades.—The term "stem clade" was proposed by Sereno (1999) to identify extinct clades positioned as sister taxa to crown clades, namely, an "extinct species or clade that has an immediate outgroup with at least one living member." Thus, like a crown clade but in reverse, a stem clade does not apply to all extinct groups but only those that have an immediate outgroup with at least one living member. A stem clade is equivalent to a "plesion" in the terminology of Patterson and Rosen (1977). Many authors including Hennig (1969) and Jefferies (1979) have used "stem group" to refer to the paraphyletic collection of stems to a crown clade (Fig. 1b). Stem clade, in contrast, refers to extinct clades outside a crown clade. A "total clade," in turn, is equivalent to the crown plus its stem clades, namely, a "clade composed of a crown taxon plus all extinct clades more closely related to it than to another crown clade" (Sereno, 1999; equals "panstem clade" of Joyce et al., 2004).

Definitional History

Almost 20 years have elapsed since the first phylogenetic definitions were published. Some taxa, such as Aves, have been defined and redefined several times; others have yet to be associated with a phylogenetic

definition. Although previously published definitions are not granted any role in the dPC, they often provide insights in the formulation of more effective definitions. Toward that end, a more nuanced approach to definitional history is presented below that (1) clearly distinguishes authors of taxonomic names from authors of phylogenetic definitions and (2) better differentiates among the ways in which definitions may be revised.

Definitional authors.—A *nominal* author is the creator of a taxon name; a *definitional* author is the creator or revisor of a phylogenetic definition. The dPC, in contrast, does not nominally differentiate authors of taxa from authors of phylogenetic definitions; all are referred to as "authors." Their differentiation is indicated solely by context or by the use of brackets for a definitional author following the nominal author of a taxon (dPC: Article 20). Although Joyce et al. (2004:994) discussed other kinds of potential authors (e.g., first to recognize the clade to which a taxon is to be applied; first to associate the taxon name with a particular clade; first to associate the taxon name with a particular apomorphy), they found it practical only to recognize what is here termed the nominal author of the taxon ("author of a name" or "actual author"; Joyce et al., 2004:994).

Textual substitution.—Comparable phrases that do not change any of the definitional components (definitional type, specifiers, qualifiers) of a phylogenetic definition do not affect taxonomic content and, therefore, do not constitute definitional revision (see also dPC: Note 13.2). Textual substitution, for example, would include the use of cladistic phraseology referring to clade inclusiveness rather than tree-based phraseology referring to ancestors and descendants, and visa versa (Table 10).

First-order revision.—Two levels of revision are recognized here that change the actual or potential taxonomic content circumscribed by a phylogenetic definition. First-order revision involves changes in specifiers or qualifiers that leave unchanged two aspects of the preceding definition: (1) definitional type and (2) anticipated clade membership. The intention of a first-order revisor, thus, is to change or edit the definition *without changing its anticipated membership*. Of course, the potential exists that such revision will alter future membership of a clade, because the original and revised definition, in fact, are different. Nonetheless, it is the *intention* of the revisor to preserve the taxonomic content of the taxon (e.g., Sereno, 1998: table 2). Changes may include any of the following:

choosing lower-level specifiers (from within the original specifiers); choosing alternative specifiers that circumscribe the same clade; or adding or removing taxon qualifiers to stabilize taxonomic content in the face of other phylogenetic arrangements. As an example, Sereno (1998) defined Ornithischia as "all dinosaurs closer to *Triceratops* than to Neornithes" (Table 10, example I). A revision reads "The most inclusive clade containing *Triceratops horridus* Marsh 1889 but not *Passer domesticus* Linnaeus 1758 or *Saltasaurus loricatus* Bonaparte and Powell 1980." This first-order revision maintains the definitional type (stem) and anticipated clade membership—i.e., the *intended clade*. At the same time, it introduces bibliographic information, textual substitution, and species-level specifiers. A second external specifier (the derived sauropod *Saltasaurus loricatus*) is added to maintain taxonomic content; given the remote, but plausible, circumstance that Sauropodomorpha is regarded as more closely related to Ornithischia than Theropoda, the additional external specifier maintains the exclusion of Sauropodomorpha from Ornithischia.

Second-order revision.—Second-order revision involves changes that result in the identification of a different clade: (1) changes in definitional type (node versus stem), (2) substitution of specifiers and/or qualifiers, or (3) the introduction/deletion of specifiers and/or qualifiers. The intention of a second-order revisor is to *change the anticipated membership of the taxon*. Gauthier (1986:14) originally defined Aves as "the most recent common ancestor of Ratitae, Tinami, and Neognathae" (Table 10, example II). A more recent revision was given as "*Archaeopteryx*, Neornithes, their most recent common ancestor and all descendants" (Sereno, 1998:65). The revision maintains the definitional type (node) but *intentionally* identifies a more inclusive clade on the cladograms of both authors, one that has traditionally been labeled Aves.

As another example, Gauthier (1986:36) defined Avialae as "Ornithurae plus all extinct maniraptorans that are closer to Ornithurae than they are to Deinonychosauria," a stem-based definition (Table 10, example III). Gauthier and de Queiroz (2001:25) redefined Avialae with the "apomorphy-based" definition "the clade stemming from the first panavian with feathered wings homologous (synapomorphic) with those of *Aves* (*Vultur gryphus* Linnaeus 1758) and used for powered flight." They implied that Gauthier (1986) also used Avialae as an "apomorphy-based" clade, because he

TABLE 10. Examples of textual substitution and first- and second-order definitional revision cited the text.

Example	Author	Revision	Shorthand	Symbolic notation
I	Sereno (1998)	Original	†Ornithischia = (>*Triceratops* but not Neornithes)	T = (>A but not B)
	Sereno (in prep.)	First-order	†Ornithischia = (>*Triceratops horridus* but not *Passer domesticus*, *Saltasaurus loricatus*)	
II	Gauthier (1986)	Original	Aves = (<Ratitae and Tinami, Neognathae)	T = (<A and B)
	Sereno (1998)	Second-order	Aves = (<*Archaeopteryx* and Neornithes)	
	Sereno (in prep.)	First-order	Aves = (<*Archaeopteryx lithographica* and *Passer domesticus*)	
III	Gauthier (1986)	Original	Avialae = (>Ornithurae but not Deinonychosauria)	T = (>A but not B)
	Gauthier and de Queiroz (2001)	Second-order	Avialae = (>Aves (*Vultur gryphus*) and with feathered wings used in powered flight as a synapomorphy)	T = (>AQ)

referred to avialans as "winged theropods." Reference to the apomorphies of a taxon, however, does not constitute specification of a definition. Replacing the original internal specifier (Ornithurae) with one intended to be more specific (Aves (*Vultur gryphus*)) is a first-order revision. Replacing the original external specifier (Deinonychosauria) with a complex form qualifier ("feathered wings . . . used for powered flight") is a second-order revision as described above. Even though the definitional type remains the same (stem), swapping a specifier for a form qualifier (in this case a poorly defined apomorphy complex involving inferred function) is considered a second-order revision, because it almost always results in flux in the content of the taxon. For example, Avialae, as redefined, may now include Deinonychosauria—if one regards the "wings" on the recently described deinonychosaurian *Microraptor* (Xu et al., 2003) as capable of "powered flight" and representative of the basal condition within Deinonychosauria.

HEURISTIC CRITERIA FOR PHYLOGENETIC DEFINITIONS

Of the many phylogenetic definitions that could apply to a given clade, some are better than others when judged on grounds of *stability* of taxonomic content, *simplicity* of definitional components, and *prior use* by phylogenetic, as well as traditional, taxonomists. Eight recommendations are summarized below and in Table 11.

Stability

Much ink has been spilt claiming that phylogenetic taxonomy will dramatically decrease stability of taxonomic content (e.g., Benton, 2000; Nixon and Carpenter, 2000, 2003; Carpenter, 2003; Fortey, 2002; Schuh, 2003). At the other extreme, stability of content has been questioned as a laudable goal in nomenclature, with alternative phylogenetic hypotheses apparently deserving alternative taxonomies (Härlin, 2003b; Kluge, 2005). Both

of the viewpoints above presuppose a narrow view of phylogenetic taxonomy, in which taxonomic content changes without any control in response to shifting phylogenetic hypotheses. Constraints on taxonomic content, nevertheless, may be imposed by judicious use of specifiers and qualifiers, so that taxa are effectively linked to an acceptable range of phylogenetic hypotheses. The phylogenetic taxonomist must evaluate what species are, or have been, most important to the meaning of a taxon— its *critical taxonomic content*—and whether there should be any constraints on the use of a name should that content change (Bryant, 1997). The dPC offers very few recommendations regarding stability of taxonomic content.

Although it is often presumed that node-based definitions are more stable than stem-based definitions, definitional type has little impact on stability (Sereno, 1999). The most important factor for stability in the face of phylogenetic uncertainty is the choice of specifiers and taxon qualifiers (Table 11). Well-known (and/or more complete), nested specifiers are critical because they are least likely to shift significantly in phylogenetic position (Sereno, 1998, 1999; Lee, 1999). It is usually the case that these same specifiers also maintain taxonomic content under alternative phylogenetic hypotheses. Stability is also enhanced in node- and stem-based definitions by the use of tandem internal or external specifiers and negative and positive taxon qualifiers, respectively (Fig. 4). When basal relations within a crown clade are uncertain and a node-based definition is preferred, for example, several (tandem) internal specifiers can be cited along with a negative taxon qualifier to exclude unwanted species (Fig. 4a).

To stabilize crown clades among turtles, for example, Joyce et al. (2004:1006) erected node-based definitions that attempt to cite all included species as internal specifiers and also cite exemplar species from all other major turtle clades as a negative taxon qualifier: "'*Testuguria*' refers to the crown clade arising from the last common ancestor of *Testudo graeca* Linnaeus, 1758, *Batagur* (orig.

TABLE 11.   Three heuristic criteria (stability, simplicity, prior use) and how they may be used in the formulation and placement of phylogenetic definitions.

Criteria	Definitional type (node/stem)	Specifiers	Qualifiers
Stability	(No preference)	Nested	Positive taxon qualifier for node-based definition
		Widely recognized, available, completely known	Negative taxon qualifier for stem-based definition
		Accommodate alternative phylogenetic relationships	Time qualifier for stem-based crown clade
		Tandem internal specifiers for node-based definition of taxon with poor basal ingroup resolution	
		Tandem external specifiers for stem-based definition of taxon with poor outgroup resolution	
Simplicity	Node-stem triplet for well-supported dichotomies or to partition a highly asymmetric cladogram	Repeat use of nested antipodal or complementary specifiers	
Prior use	Node-stem triplet to recognize traditional dichotomy	First-order revision of preexisting specifier(s)	
	First-order revision of preexisting definition(s)		

Emys) *baska* (Gray, 1831), and all other valid species listed in Appendices 8 and 9, but none of the other valid species listed in Appendix 1 or 10." Lengthy appendices with overlapping species lists and remote literature citations, however, have the potential to blur the precise meaning of a clade, given the increased likelihood of incorporating ambiguous specific or generic assignments. In this case, the clade Testuguria had already been defined (as Testudinoidae) using a batagurid as "the most recent common ancestor of *Chinemys reevesii* (a batagurid) and *Geocholone pardalis* (a testudinid), we propose the name Testudinoidae" (Shaffer et al., 1997:249). The genus and species selected, however, is not listed in the appendices in Joyce et al. Lengthy species lists, in addition, potentially jeopardize the definition of taxa in widespread use, because the definition is dependent on the correct assignment of every single cited species as residing either inside or outside the clade. This definitional form converges on a traditional list of included species and is not a good general model for phylogenetic definitions. Definitions of venerable higher taxa should accommodate the occasional variant assignment witnessed, for example, in the history of turtle systematics (Gaffney, 1984). In the case of Testudinoidae/Testuguria, a shorter, more transparent, equally stable stem-based definition for this crown clade is available. It incorporates fewer assumptions about relationships among testudinoids and includes only one or two internal specifiers, a time qualifier, and tandem external specifiers (to exclude the most closely related cryptodiran clades): "The most inclusive clade containing *Testudo graeca* Linnaeus, 1758, *Batagur baska* (Gray, 1931) and any extant species but not *Emys orbicularis* (Linnaeus, 1758) or *Platysternon megacephalum* Gray, 1831," or in shorthand notation (>*Testudo graeca*, *Batagur baska* + extant but not *Emys orbicularis, Platysternon megacephalum*).

In sum, *stability* of taxonomic content is enhanced when specifiers are (1) positioned at significant phyloge-

netic distance from the basal branch point of the taxon to be defined; (2) widely recognized, readily available, and more completely known; (3) chosen to maintain heuristic taxonomic content under alternative phylogenetic hypotheses; and (4) used in tandem or in combination with taxon qualifiers to constrain taxonomic content.

Simplicity

Repeated use of the same deeply nested specifier(s) for nested clades can also greatly reduce the number of specifiers cited in their definitions. A definitional triumvirate termed a node-stem triplet (NST), in addition, simplifies the relationship between the three taxa at a dichotomy in the face of relocation or addition of basal species or groups (Sereno, 1998, 1999; Fig. 6a). The dPC is silent on NSTs. Subdivision of Dinosauria into Ornithischia and Saurischia will always be maintained with a node-based definition for the former, stem-based definitions for the latter, and judicious selection of nested, complementary specifiers (e.g., Dinosauria = (< *Triceratops horridus* and *Passer domesticus*); Saurischia = (> *Passer domesticus* but not *Triceratops horridus*); Ornithischia = (>*Triceratops horridus* but not *Passer domesticus*)). The equivalence statement "Dinosauria = Ornithischia + Saurischia" will always apply rather than becoming more complicated over time (e.g., Dinosauria = Ornithischia + Saurischia + new basal taxon X). Anchoring well-supported, widely recognized, and/or traditional dichotomies with NSTs helps to sustain the narrative function of taxonomy (O'Hara, 1992). The split onto Ornithischia (bird-hipped) and Saurischia (lizard-hipped), after all, is probably the most widely appreciated phylogenetic dichotomy within Dinosauria.

Adding a taxon qualifier or additional internal or external specifiers to any definition within a node-stem triplet opens the possibility that the equivalence
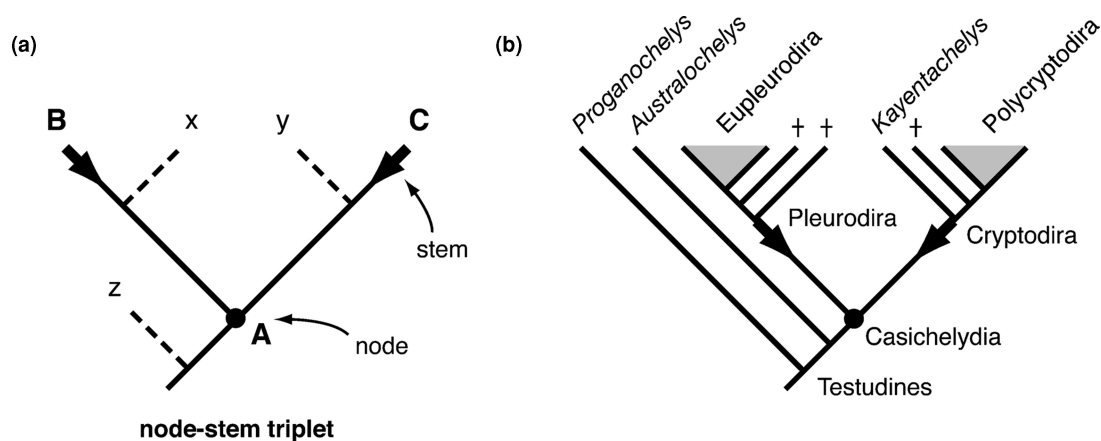

FIGURE 6. (a) A definitional configuration termed a node-stem triplet that incorporates relocated or additional basal taxa (dashed lines) without changing the relationship between the three taxa at a dichotomy (e.g., Dinosauria = Ornithischia + Saurischia). Basal taxon z is always excluded from taxon A, and taxon x and y are always absorbed by the stem-based definitions for taxon B and C. Dots and arrows indicate node- and stem-based definitions, respectively. (b) Functional node-stem triplet near the base of turtles (Testudines) involving crown turtles (Casichelydia) and respective stem clades (Pleurodira and Cryptodira). Eupleurodira and Polycryptodira comprise crown clade pleurodires and cryptodires, respectively. Daggers represent additional extinct stem taxa.

statement will not always be maintained. For example, a few taxonomists have considered Sauropodomorpha (normally within Saurischia) to be more closely related to Ornithischia. Should this prove to be the case, sauropodomorphs would be relegated to Ornithischia using the aforementioned definition. This could be prevented by including a derived sauropodomorph (e.g., *Saltasaurus loricatus*) as an additional external specifier: Ornithischia = (>*Triceratops horridus* but not *Passer domesticus* or *Saltasaurus loricatus*). Given this definition, the equivalence statement "Dinosauria = Ornithischia + Saurischia" will not hold when sauropodomorphs are more closely related to ornithischians. In that case, Dinosauria = Ornithischia + Sauropodomorpha + Theropoda. The term *conditional NST*, therefore, is applied to any NST in which one or more of its constituent definitions sets forth special conditions for membership.

In sum, *simplicity* in phylogenetic definitions is enhanced by (5) repeated use of nested specifiers for nested clades and (6) employing node-stem triplets for well-established dichotomies.

Prior Use

Consideration should be given to phylogenetic definitions that already exist. For a given taxon, their modification via textual substitution or first-order revision is preferable, because it minimizes the number and meaning of phylogenetic definitions short of arbitrarily imposing one over all possible alternatives. Importantly, prior use can apply to the work of nonphylogenetic taxonomists. How did they handle taxa in the face of new basal species, relocated species or clades, or revised apomorphies? Was the concept of a taxon linked to a particular "key" character, or have taxonomists managed the content of a taxon over time as if it were node- or stem-based? Inclusiveness (node versus stem) is the critical variable and is often best determined by taxonomic history, i.e., how taxonomists over time have included or excluded new (or relocated) basal taxa.

Some long recognized, named dichotomies owe their longevity to the management of new (or relocated) basal taxa. Nearly all taxonomists (traditional and cladistic) during the last century, for example, have maintained the equivalence statement, Dinosauria = Ornithischia + Saurischia, despite the discovery of many basal dinosaurs and dinosaurian outgroups located near the dichotomy. These taxonomists, in other words, have been maintaining a tidy dichotomy that leaves the relations between Dinosauria and its two subclades unchanged—the traditional equivalent of a node-stem triplet (Fig. 6a). Phylogenetic taxonomists would do well to recognize these dichotomies in a similar fashion (Sereno, 1998, 1999). By comparison, any other configuration of node or stem-based definitions for the three taxa mentioned above will ensure the breakdown of the equivalence statement in a matter of years, as new extinct species come to light.

Higher-level turtle taxonomy provides another example. In the course of his phylogenetic and histor-ical work, Gaffney (1975a, 1975b, 1984; Gaffney and Meylan, 1988; Gaffney, et al., 1991) employed Testudines for the reception of all known turtles and recognized a new clade, Casichelydia, for all turtles more advanced than the basal stem turtle *Proganochelys* (Gaffney, 1990) (Fig. 6b). This taxonomy, which effectively disbanded the paraphyletic ancestral grade Amphichelydia, has gained currency among morphologists and molecular biologists. Perhaps the most fundamental division was that of Casichelydia, or crown turtles, into Pleurodira and Cryptodira—a named dichotomy that Gaffney maintained without exception over three decades of systematic work. Thus, when the new stem turtle *Australochelys* was discovered, it was excluded from a node-like Casichelydia (Gaffney and Kitching, 1994); when the basal casichelydian *Kayentachelys* was discovered, it was absorbed within a stem-like Cryptodira (Gaffney et al., 1987). From its inception, Casichelydia was divided into two clades, Pleurodira and Cryptodira, which separate all extant (and nearly all extinct) turtles to either side of a basal dichotomy (Gaffney, 1975a) (Fig. 6b). Gaffney's consistent usage is readily translated into a node-stem triplet, using only two nested species as specifiers: Casichelydia = (<*Pelomedusa subrufa* and *Testudo graeca*); Pleurodira = (>*Pelomedusa subrufa* but not *Testudo graeca*); Cryptodira = (>*Testudo graeca* but not *Pelomedusa subrufa*). These definitions maintain the relationship between these three widely cited taxa no matter where extinct taxa near the base of the clade are repositioned (e.g., Joyce, 2004).

Initial phylogenetic definitions for these same clades, unfortunately, all but abandoned Gaffney's taxa and taxonomy (Lee, 1995, 1997; Joyce et al., 2004). Joyce et al. (2004:993, 998) suggested that Casichelydia and other taxa named by Gaffney were "apomorphy-based," ostensibly because of associated synapomorphy lists. Gaffney, however, never rigidly linked apomorphies with taxa. Casichelydian synapomorphies, like those at other nodes, were subject to revision (compare Gaffney and Meylan, 1998; Gaffney and Kitching, 1994). Lee (1995, 1997) used Chelonia in place of Gaffney's Testudines and restricted Testudines to crown turtles, replacing Gaffney's Casichelydia. Joyce et al. (2004) used Testudinata, rather than Chelonia or Testudines, for the clade including all known turtles and followed Lee by using Testudines for crown turtles. Both authors restricted Pleurodira and Cryptodira to their respective crown clades, replacing Gaffney's Eupleurodira and Polycryptodira with other names (Lee, 1995: Pleurodiromorpha, Cryptodiromorpha; Joyce et al., 2004: Panpleurodira and Pancryptodira).

This name shuffling was justified on grounds of "priority," the "desire to reserve widely used names for crown clades," and the implementation of a new "panstem" convention (Joyce et al., 2004:993). Here we are concerned only with the first. In the name of "priority," Joyce et al. (2004) regarded Gaffney's taxon Casichelydia as a junior synonym of several of the earliest names used to group extant turtles (Testudinata, Testudines), when fossil turtles had yet to be discovered. Following

that logic, however, the crown clade ought to be named *Testudo* (Linnaeus, 1758), as they admitted. Other subjective decisions included selecting Testudinata as the appropriate taxon for all currently known turtles with an "apomorphy-based" definition, narrowing the meaning of Testudines to apply to crown turtles, and similarly restricting Pleurodira and Cryptodira to crown clades. Over the last century, Pleurodira and Cryptodira have not always been used to neatly subdivide extant turtles, and both taxa have incorporated existing or anticipated extinct stem taxa (Gaffney, 1984:fig. 3). It is difficult to justify any of these rather profound rearrangements on grounds of "prior use."

In sum, *prior use* is reflected in phylogenetic definitions by (7) opting for textual or first-order revisions of previously published phylogenetic definitions when possible and (8) adapting definitions to maintain the relationship between taxa at long recognized dichotomies.

CONTINUITY AND CONSENSUS IN PHYLOGENETIC DEFINITIONS

Despite all of the discussion and recommendations above, there is no single procedure to construct a phylogenetic definition for a particular taxon any more than there is one way to perform a phylogenetic analysis for a particular clade. One approach has been to downplay that fact and move to establish in perpetuity some definitions over others with the aim of achieving a unitary taxonomy. Another approach outlined below holds that those phylogenetic definitions that best maintain historical continuity and current utility will gain currency among systematists, an outcome achieved by consensus rather than by the imposition of a formalized code and centralized authority.

Unitary Taxonomy

Several ongoing Web-based compilations are attempting to unify taxonomy or, at least, to make species-level taxonomy readily available (Busby, 2000; Godfray, 2002; Minelli, 2002). The stated goal of the dPC, likewise, is to create an official registry of "established" phylogenetic definitions for supraspecific taxa (and possibly species as well) in the hope that this will lead to universal adoption and a unitary taxonomy. How alternative definitions for the same taxon are to be evaluated and by whom have yet to be fully clarified.

These issues are well illustrated by a recent higher-level phylogenetic taxonomy for turtles, which presented itself as a conversion model to "replace the current rank-based nomenclature" of the International Code of Zoological Nomenclature (Joyce et al., 2004:989). Their preferred taxonomy constitutes an unfettered departure from nomenclature of the last century, despite their claim that it is "consistent with current usage ... in the last 25 years" (Joyce et al., 2001:996). Many well-known taxa were relocated, and more than half of the taxa (some 28) are new (mostly panstems). Much of the shuffling and naming is the result of realigning "widely used" taxa, such as Pleurodira, with the closest crown clade,

and effecting a panstem convention that automatically names its associated, most inclusive total clade (e.g., Panpleurodira). Although these draconian conventions have been questioned, let's say for the sake of argument that their turtle taxonomy becomes "established."

What if another turtle taxonomist has an alternative interpretation of the historical content of a taxon or a simpler, more stable phylogenetic definition? What if some taxonomists reject "complex" apomorphies in definitions and prefer to anchor Testudines using the quintessential turtle *Proganochelys quenstedti* as a specifier? What if taxonomists reject the "panstem" convention or the token phrases given as their phylogenetic definitions (e.g., "the panstem that includes crown T")? Those who might disagree are simply urged to "maintain stability by avoiding the temptation to rename them" (Joyce et al., 2004:994).

Phylogenetic Taxonomy Without the PhyloCode

An alternative approach to phylogenetic taxonomy is to acknowledge the value of definitional continuity but allow such continuity to emerge over time by consensus among taxonomists rather than by attempting to impose the preferred definitions of a handful of taxonomists. For some taxa, there exist differing opinions regarding current or historical meaning (taxonomic content), priority, or what might constitute the most appropriate phylogenetic definition. Although the PhyloCode is often described as an alternative to rank-based systems of nomenclature, an unranked taxonomy per se is neither novel in systematics nor at the heart of the draft document. Most of the PhyloCode is devoted to rules and recommendations surrounding the conversion, priority, and form of names and definitions, because its overarching aim is to establish a unitary taxonomy. But what if a unitary taxonomy is not feasible or even desirable (for a recent review, see Ereshefsky, 2001)? What if taxonomic pluralism is inevitable or even preferable? Although a full discussion is beyond the scope of this paper, it is reasonable to consider whether phylogenetic taxonomy can flourish without the PhyloCode, self-regulated by consensus, much as it operates at present.

Under such conditions, heuristic definitions ought to gain currency. Taxonomists, in this view, are free to cite, edit, or create phylogenetic definitions as they see fit, while appreciating that altering an existing phylogenetic definition without justification serves no purpose. And if two definitions coexist and persist over time from differing interpretations of the historical meaning or utility of a particular taxon, then so be it. No evidence has ever been presented that the existence of alternative phylogenetic definitions for the same taxon harms phylogenetic research or detectibly hampers communication among systematists. Few taxa have accumulated as many phylogenetic definitions as Aves (eight by my count; see *TaxonSearch*). All of these are first-order variations that identify one or the other of two clades (traditional Aves, crown Aves). Without doubt, many owe their existence to the evolution of the protocol

for phylogenetic definitions, such as the use of species as specifiers. The coexistence of multiple definitions, nonetheless, has not noticeably dampened interest in the origin of birds, complicated communication among specialists, or confused phylogenetic results. Because some phylogenetic taxonomists will not accept one or the other definition of Aves, it is certain that multiple definitions will persist in the literature with, or without, the PhyloCode.

TaxonSearch: A Web-Accessible Database for Phylogenetic Definitions

Phylogenetic taxonomists need an accessible repository for taxon names, phylogenetic definitions and relevant literature. Many taxa have fallen from use; some have been maintained but have not been given phylogenetic definitions, and others are associated with one or more phylogenetic definitions. Although there are many current Web-based compilations for the genera and species of a wide range of the diversity of life, none is available for suprageneric taxa that do more than simply present a particular indented taxonomy. For a given clade of interest, it would be very useful to have a Web-based, searchable compilation of all named higher (suprageneric) taxa, their authors and bibliographic citation, a record of proposed phylogenetic definitions, and related information. If broadly available to practicing taxonomists, such a database would function as a repository for taxonomic compilations and a tool providing access to historical and current information on taxa and their phylogenetic definitions.

TaxonSearch is a web-accessible application created for this purpose (www.taxonsearch.org) . *TaxonSearch* files are composed of records for suprageneric taxa that reside within a clade of interest. *TaxonSearch* will locate records based on any aspect, or combination of aspects, of the features that are logged for each taxon in the clade under consideration. Users can search or sort taxon records by field (e.g., nominal author, date of publication of the taxon, type of definition), locate a particular taxon, view its current phylogenetic definition, examine any previously published phylogenetic definitions, or learn about its approximate temporal range (in millions of years). Output files summarize the status of taxa and their definitions (Fig. 7a) and the historical accumulation of taxa and phylogenetic definitions (Fig. 7b). Users may also download a blank *TaxonSearch* file for compiling and, optionally, posting records for their clade of interest. The database also accommodates updates (with older versions archived) and user feedback that permits the posting of commentary on any taxon record.

An example file, Stem Archosauria, contains 770 taxon records that document all suprageneric taxa coined for clades within Archosauria that lie outside its two included crown clades, Crocodylia (extant crocodiles) and Neornithes (extant birds). The terms *active* and *inactive* describe the status of a taxon or phylogenetic definition, as interpreted by the compiler of a file (P. C. Sereno, 2005, ver. 1.0, for the file Stem Archosauria; Fig. 7a). An active taxon is one that has a complete phylogenetic definition and is in current use, or favored for such use, by the compiler of the file. An inactive taxon, in contrast, is rejected for active use by the compiler for one or more reasons, which are specified (e.g., junior synonym, no definition, etc.). The active phylogenetic definitions in Stem Archosauria follow the recommendations in this paper; the vast majority are textual variants or first-order revisions of preexisting phylogenetic definitions. Alternative definitions, if they exist, are listed in each taxon record in chronological order.
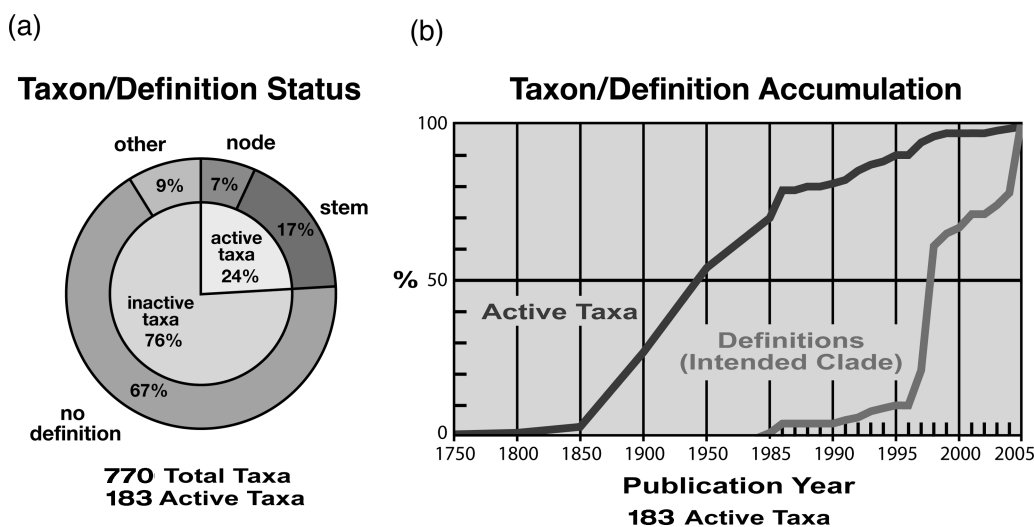

FIGURE 7. Data output from the file Stem Archosauria in the database application *TaxonSearch* (http://www.taxonsearch.org). Users can download a blank file for work within their taxon of interest. (a) Pie chart showing the status of taxa and their respective definitions within Archosauria but exclusive of crown crocodilians (Crocodylia) and crown birds (Neornithes). "Active taxa" are those in current use with phylogenetic definitions. "Inactive taxa" are those not in current use or rejected for other reasons by the compiler of the file. (b) Accumulation profile using date of publication for active taxa. Accumulation profile for intended clades using the date that the intended clade was first identified by a phylogenetic definition.

In the file Stem Archosauria, the majority of the 770 taxon records are inactive taxa (587 taxa or 76 percent), most of which have long since fallen from use and have no phylogenetic definitions. Of the 183 active taxa, a clear majority are stem-based definitions (Fig. 7a). Although the earliest active taxa date back to Linnaeus (1758), a significant number (approximately 25 percent) were coined in the last 20 years after the advent of quantitative cladistics in the mid 1980s (Fig. 7b, active taxa). In recent years, the number of new active taxa has markedly declined, suggesting that taxonomic nomenclature has caught up with the increased resolution brought by quantitative cladistics. Despite some disagreement or overlap in phylogenetic definitions, most taxa with definitions employ the same definitional type (node or stem) and identify the same intended clade as when they were first defined. The number of definitions that identify clades in current use has risen steadily since 1985 and now equals the number of active taxa (Fig. 7b, intended definitions).

Phylogenetic definitions have been applied longer (1986 to the present) and at more hierarchic levels among nonavian dinosaurs than any other clade. Gauthier (1986) published the first phylogenetic definitions. Other definitions followed: first, in entries in an encyclopedia on dinosaurs (Currie and Padian, 1997); second, in two independent efforts to organize a phylogenetic taxonomy (for nonavian dinosaurs, Sereno, 1998; for nonavian theropods, Padian et al., 1999); and third, in numerous papers with narrower taxonomic scope.

In the recent volume, *The Dinosauria* (Weishampel et al., 2004), 113 complete phylogenetic definitions are given by an assortment of authors (myself not among them), with 101 pertaining to Dinosauria and its subclades. The book provides a rare opportunity to determine whether there are preferred definitional types and how self-regulation has worked since the initial compilation of definitions for nonavian dinosaurs six years prior (Sereno, 1998). Of 101 complete phylogenetic definitions (several are incomplete), 69 percent are stem-based, 32 percent are node-based, and none employ form qualifiers (apomorphies). Thus, there is a clear preference for stem-based definitions by a factor of approximately two. This same proportion of stem-based definitions is present when considering stem archosaurs as a whole (Fig. 7a) and may be due in part to adoption of node-stem triplets, which link two stem-based taxa and one node-based taxon at recognized dichotomies. The absence of form-qualified definitions signals the abandonment of morphology as a factor in phylogenetic definitions among nonavian dinosaurs.

Using the *TaxonSearch* file Stem Archosauria, it can be determined that 74 of the 101 definitions in *The Dinosauria* were defined six years prior (Sereno, 1998). Of these 74, only 11 constitute second-order revisions. At least half of these clearly represent differing views on how a particular taxon should be defined, because the authors cited the alternative definition in Sereno (1998). This is ground for compromise and consensus in future work or, alternatively, the continuation of informed differences of opinion. Why should any one author, via the PhyloCode, preempt potential consensus or quash differences of opinion by trying to impose in perpetuity the meaning of taxa?

The high degree of agreement over definitional types and intended clades between Sereno (1998) and authors in *The Dinosauria* is significant, especially because some definitional revisions in the latter appear to have been coined unintentionally and because many lack literature citation of previously published definitions. The presence in the same volume of three definitions (all first-order variants) for both Ornithischia and Saurischia, however, underscores the need for an on-line database of phylogenetic definitions that facilitates access to definitional history. Self-regulation under these less than ideal circumstances, nevertheless, appears to be functioning reasonably well.

CONCLUSIONS

This paper argues that the logical basis of phylogenetic definitions, as captured in a new symbolic notational scheme, involves three components (definitional type, specifiers, qualifiers). There are only two definitional types (node, stem), which are based on the polarity of inclusiveness on a cladogram. Specification is (1) governed by choice of definitional type and the particular species selected as specifiers, (2) conditioned by taxonomic (species) and accessory (time, form, space) qualifiers, and (3) revised by alteration of any definitional component. In graphical presentation, terminology, and logical formulation, phylogenetic taxonomy is better grounded on the branching pattern of a cladogram rather than the ancestor-descendant verbiage associated with phylogenetic trees.

Preference for unranked phylogenetic definitions over traditional trait-based diagnoses of taxa does not stand on an anti-essentialist philosophy of taxonomy, as we have yet to agree on how best to frame that perspective. Nor does it stand on stability of taxonomic content, given that both traditional diagnoses and phylogenetic definitions have mechanisms to constrain taxonomic content and both are, and should continue to be, subject to revision. Phylogenetic taxonomy is about precision in the identification of clade boundaries during a time of explosive growth in our knowledge of, and reference to, phylogeny.

REFERENCES

Avise, J. C., and G. C. Johns. 1999. Proposal for a standardized temporal scheme of biological classification for extant species. Proc. Natl. Acad. Sci. USA 96:7358–7363.

Benton, M. J. 2000. Stems, nodes, crown clades, and rank-free lists: Is Linnaeus dead? Biol. Rev. 75:633–648.

Brochu, C. A. 2001. Progress and future directions in archosaur phylogenetics. J. Paleont. 75:1185–1201.

Bryant, H. N. 1996. Explicitness, stability, and universality in the phylogenetic definition and usage of taxon names: A case study of the phylogenetic taxonomy of the Carnivora (Mammalia). Syst. Biol. 45:174–189.

Bryant, H. N. 1997. Cladistic information in phylogenetic definitions and designated phylogenetic contexts for the use of taxon names. Biol. J. Linn. Soc. 62:495–503.

Busbey, F. A. 2000. The quiet revolution: Biodiversity informatics and the internet. Science 289:2309–2312.

Cantino, P. D., H. N. Bryant, K. de Queiroz, M. J. Donoghue, T. Eriksson, D. M. Hillis, and M. S. Y. Lee. 1999. Species names in phylogenetic nomenclature. Syst. Biol. 48:790–807.

Cantino, P. D., and K. de Queiroz. 2004. PhyloCode: A phylogenetic code of biological nomenclature, Version 2b (June 17, 2004). http://www.ohio.edu/phylocode/.

Cantino, P. D., R. G. Olmstead, and S. J. Wagstaff. 1997. A comparison of phylogenetic nomenclature with the current system: A botanical case study. Syst. Biol. 46:313–331.

Carpenter, J. M. 2003. Critique of pure folly. Bot. Rev. 69:79–92.

Currie, P. J., and K. Padian. 1997. The encyclopedia of dinosaurs. Academic Press, San Diego.

de Queiroz, K. 1988a. Systematics and the Darwinian revolution. Philos. Sci. 55:238–259.

de Queiroz, K. 1988b. The general lineage concept of species, species criteria, and the process of speciation. Pages 57–75 in Endless forms: Species and speciation (D. J. Howard and S. J. Berlocher, eds.). Oxford University Press, Oxford, UK.

de Queiroz, K. 1992. Phylogenetic definitions and taxonomic philosophy. Biol. Philos. 7:295–313.

de Queiroz, K. 1994. Replacement of an essentialist perspective on taxonomic definitions as exemplified by the definition of "Mammalia." Syst. Biol. 43:497–510.

de Queiroz, K., and P. D. Cantino. 2001. Taxon names, not taxa, are defined. Taxon 50:821–826.

de Queiroz, K., and J. Gauthier. 1990. Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. Syst. Zool. 39:307–322.

de Queiroz, K., and J. Gauthier. 1992. Phylogenetic taxonomy. Annu. Rev. Ecol. Syst. 23:449–480.

de Queiroz, K., and J. Gauthier. 1994. Toward a phylogenetic system of biological nomenclature. TREE 9:27–31.

Dyke, G. J. 2002. Should paleontologists use "Phylogenetic" nomenclature? J. Paleontol. 76:793–796.

Eldredge, N. 1979. Cladism and common sense. Pages 165–198 in Phylogenetic analysis and paleontology (J. Cracraft, and N. Eldredge, eds.). Columbia University Press, New York.

Estes, R., K. de Queiroz, and J. Gauthier. 1988. Phylogenetic relationships within Squamata. Pages 119–281 in Phylogenetic relationships of the Lizard families: Essays Commemorating Charles L. Camp (R. Estes, and G. K. Pregill, eds.). Stanford University Press, Stanford, California.

Ereshefsky, M. 2001. The poverty of the Linnean hierarchy. Cambridge University Press, Cambridge, UK.

Ernst, C. H., and R. W. Barbour. 1989. Turtles of the world. Smithsonian Institution Press, Washington, DC.

Farris, J. S. 1974. Formal definitions of paraphyly and polyphyly. Syst. Zool. 23:548–554.

Farris, J. S. 1976. Phylogenetic classification of fossils with recent species. Syst. Zool. 25:271–282.

Feduccia, A. 1995. Explosive evolution in Tertiary birds and mammals. Science 267:637–638.

Fortey, P. L. 2002. PhyloCode—pain, no gain. Taxon 51:43–54.

Frost, D. R., and A. G. Kluge. 1994. A consideration of epistemology in systematic biology, with special reference to species. Cladistics 10:259–294.

Gaffney, E. S. 1975a. A phylogeny and classification of the higher categories of turtles. Bull. Am. Mus. Nat. Hist. 155:389–436.

Gaffney, E. S. 1975b. A taxonomic revision of the Jurassic turtles Portlandemys an Plesiochelys. Am. Mus. Novitates 2574:1–19.

Gaffney, E. S. 1984. Historical analysis of theories of chelonian relationship. Syst. Zool. 33:283–301.

Gaffney, E. S. 1990. The comparative osteology of the Triassic turtle Proganochelys. Bull. Am. Mus. Nat. Hist. 194:1–263.

Gaffney, E. S., and J. H. Hutchinson, F. A. Jenkins Jr., and L. J. Meeker. 1987. Modern turtle origins: The oldest known cryptodire. Nature 237:289–291.

Gaffney, E. S., and J. W. Kitching. 1995. The most ancient African turtle. Nature 369:55–58.

Gaffney, E. S., and P. A. Meylan. 1988. A phylogeny of turtles. Pages 157–219 in The phylogeny and classification of the Tetrapods. Vol. 1. Amphibians, reptiles, birds (M. J. Benton, ed.). Clarendon Press, Oxford, UK.

Gaffney , E. S., P. A. Meylan, and A. R. Wyss. 1991. A computer assisted analysis of the relationships of the higher categories of turtles. Cladistics 7:313–335.

Gallis, F. 2001. Key innovations and radiations. Pages 581-605 in The character concept in evolutionary biology (G. P. Wagner, ed.). Academic Press, San Diego, California.

Gauthier, J. A. 1986. Saurischian monophyly and the origin of birds. Pages 1–55 in The origin of birds and the evolution of flight (K. Padian, ed.). Mem. Calif. Acad. Sci. 8.

Gauthier, J., and K. de Queiroz. 2001. Feathered dinosaurs, flying dinosaurs, crown dinosaurs, and the name "Aves." Pages 7–41 in New perspectives on the origin and early evolution of birds: Proceedings of the International Symposium in Honor of John H. Ostrom (L. F. Gall and J. Gauthier, eds.). Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

Gauthier, J., R. Estes, and K. de Queiroz. 1988. A phylogenetic analysis of Lepidosauromorpha. Pages 15–98 in Phylogenetic relationships of the Lizard families: Essays commemorating Charles L. Camp (R. Estes and G. K. Pregill, eds.). Stanford University Press, Stanford, California.

Georges, A., J. Birrell, K. M. Saint, W. McCord, and S. C. Donnellan. 1998. A phylogeny for side-necked turtles (Chelonia:Pleurodira) based on mitochondrial and nuclear gene sequence variation. Biol. J. Linn. Soc. 67:213–246.

Ghiselin, M. T. 1966. Application of the theory of definitions to taxonomic principles. Syst. Zool. 15:127–130.

Ghiselin, M. T. 1974. A radical solution to the species problem. Syst. Zool. 23:536–544.

Ghiselin, M. T. 1984. "Definition," "character," and other equivocal terms. Syst. Zool. 33:104–110.

Ghiselin, M. T. 1995. Ostensive definitions of the names of species and clades. Biol. Philos. 10:219–222.

Gilbert, S. F., G. A. Loredo, A. Brukman, and A. C. Burke. 2001. Morphogenesis of the turtle shell: The development of a novel structure in tetrapod evolution. Evol. Dev. 3:47–58.

Godfray, H. C. J. 2002. Challenges for taxonomy. Nature 417:17–19.

Griffiths, G. C. D. 1974. On the foundations of biological systematics. Acta Biotheor. 23:85–131.

Härlin, M. 2003a. On the relationship between content, ancestor, and ancestry in phylogenetic nomenclature. Cladistics 19:144–147.

Härlin, M. 2003b. Taxon names as paradigms: The structure of nomenclatural revolutions. Cladistics 19:138–143.

Hay, O. P. 1908. The fossil turtles of North America. Carnegie Inst. Washington Publ. 75:1–568.

Hennig, W. 1965. Phylogenetic systematics. Annu. Rev. Entomol. 10:97–116.

Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana.

Hennig, W. 1969. Die Stammesgeschichte der Inseckten. Waldemar Kramer, Frankfurt-am-Main.

Hull, D. L. 1965. The effect of essentialism on taxonomy—two thousand years of stasis (I). Brit. J. Philos. Sci. 15:314–326.

Hull, D. L. 1976. Are species really individuals? Syst. Zool. 25:174–191.

Jefferies, R. P. S. 1979. The origin of chordates—a methodological essay. Pages 443–477 in The origin of major invertebrate groups (M. R. House, ed.), Academic Press, London.

Joyce, W. G. 2004. A phylogeny of turtles and the age of the turtle crown. J. Vert. Paleontol. Suppl. 24:77A.

Joyce, W. G., J. F. Parham, and J. A. Gauthier. 2004. Developing a protocol for the conversion of rank-based taxon named to phylogenetically defined clade names, as exemplified by turtles. J. Paleontol. 78:989–1013.

Keller, R. A., R. N. Boyd, and Q. D. Wheeler. 2003. The illogical basis of phylogenetic nomenclature. Bot. Rev. 69:93–110.

Kluge, A. G. 2005. Taxonomy in theory and practice, with arguments for a new phylogenetic system of taxonomy. Pages 7–52 in Ecology and evolution in the tropics: A herpetological perspective (M. A. Donnelly, B. I. Crother, C. Guyer, M. H. Wake, and M. E. White, eds.). University of Chicago Press, Chicago, Illinois.

Kojima, J.-I. 2003. Apomorphy-based definition also pinpoints a node, and PhyloCode names prevent effective communication. Bot. Rev. 69:44–58.

Laurin, M., and J. S. Anderson. 2004. Meaning of the name Tetrapoda in the scientific literature: An exchange. Syst. Biol. 53:68–80.

Laurin, M., and P. D. Cantino. 2004. First International Society of Phylogenetic Nomenclature Meeting: A report. Zool. Scr. 33:475–479.

Lee, M. S. Y. 1995. historical burden in systematics and the interrelationships of 'parareptiles.' Biol. Rev. 70:459–547.

Lee, M. S. Y. 1996a. The phylogenetic approach to biological taxonomy: Practical aspects. Zool. Scr. 25:187–190.

Lee, M. S. Y. 1996b. Stability in meaning and content of taxon names: An evaluation of crown-clade definitions. Proc. R. Soc. Lond. B 263:1103–1109.

Lee, M. S. Y. 1997. Pariesaur phylogeny and the origin of turtles. Zool. J. Linn. Soc. 120:197–280.

Lee, M. S. Y. 1998a. Phylogenetic uncertainty, molecular sequences, and the definition of taxon names. Syst. Biol. 47:719–726.

Lee, M. S. Y. 1998b. Ancestors and taxonomy. Trends Ecol. Evol. 13:26.

Lee, M. S. Y. 1999. Reference taxa and phylogenetic nomenclature. Taxon 48:31–34.

Linnaeus, C. 1758. Systema Naturae, vol. 1 (10th ed.). Laurentius Salvius, Holmia.

Løtrup, S. 1977. The phylogeny of the Vertebrata. John Wiley & Sons, London.

Mayr, E., E. G. Linsley, and R. L. Usinger. 1953. Methods and principles of systematic zoology. McGraw-Hill, New York.

Meng, J., A. R. Wyss, M. R. Dawson, and R. J. Zhal. 1994. Primitive fossil rodent from Inner Mongolia and its implications for mammalian phylogeny. Nature 370:134–136.

Minelli, A. 2002. The staus of taxonomic literature. TRENDS Eco. Evol. 18:75–76.

Moore, G. 2003. Should taxon names be explicitly defined? Bot. Rev. 69:2–21.

Nelson, G. J. 1972. Phylogenetic relationships and classification. Syst. Zool. 21:227–230.

Nixon, K. C., and J. M. Carpenter. 2000. On the other "phylogenetic systematics." Cladistics 16:298–318.

Nixon, K. C., and J. M. Carpenter. 2003. The PhyloCode is fatally flawed, and the "Linnaean" system can easily be fixed. Bot. Rev. 69:111–120.

O'Hara, R. J. 1992. Telling the tree: Narrative representation and the study of evolutionary history. Biol. Philos. 7:135–160.

Padian, K., J. R. Hutchinson, and T. R. Holtz Jr. 1999. Phylogenetic definitions and nomenclature of the major taxonomic categories of the carnivorous Dinosauria (Theropoda). J. Vert. Paleontol. 19:69–80.

Patterson, C., and D. E. Rosen. 1977. Review of the ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. Bull. Am. Mus. Nat. Hist. 158:85–172.

Pritchard, P. C. H. 1979. Encyclopedia of turtles. TFH Publications, Jersey City, New Jersey.

Raikow, R. J. 1982. Monophyly of the Passeriformes: Test of a phylogenetic hypothesis. Auk 99:431–445.

Ride, W. D. L. et al. (eds.) 1985. International Code of Zoological Nomenclature, 3rd ed. University of California Press, Berkeley.

Romer, A. S. 1956. Osteology of the Reptilia. University of Chicago Press, Chicago, Illinois.

Schander, C., and M. Thollesson. 1995. Phylogenetic taxonomy—some comments. Zool. Scr. 24:263–268.

Schuh, R. T. 2000. Biological systematics: Principles and applications. Cornell University Press, Ithaca, New York.

Schuh, R. T. 2003. The Linnaean system and its 250-year persistence. Bot. Rev. 69:59–78.

Scotland, R. W. 1992. Cladistic theory. Pages 3–13 in Cladistics (P. L. Forey, C. J. Humphries, I. J. Kitching, R. W. Scotland, D. J. Siebert, and D. M. Williams, eds.). Clarendon Press, Oxford, UK.

Sereno, P. C. 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. N. Jb. Geol. Paläont. Abh. 210:41–83.

Sereno, P. C. 1999. Definitions in phylogenetic taxonomy: Critique and rationale. Syst. Biol. 48:329–351.

Shaffer, H. B., P. Meylan, and M. L. McNight. 1997. Tests of turtle phylogeny: Molecular, morphological, and paleontological approaches. Syst. Biol. 46:235–268.

Tarr, C. L., and R. C. Fleischer. 1995. Evolutionary relationships of the Hawaiian honeycreepers (Aves, Drepanidinae). Pages 147–159 in Hawaiian biogeography: Evolution on a hot spot Archipelago (W. L. Wagner and V. A. Funk, eds.). Smithsonian Institution Press, Washington, DC.

Weishampel, D., B. P. Dodson, and H. Osmólska. 2004. The Dinosauria, 2nd ed. University of California Press, Berkeley.

Wiley, E. O. 1981. Phylogenetics: The theory and practice of phylogenetic systematics. John Wiley & Sons, New York.

Witmer, L. M. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. Pages 19–33 in Functional morphology in vertebrate paleontology (J. J. Thomason, ed.). Cambridge University Press, Cambridge, UK.

Wyss, A., and J. Meng. 1996. Application of phylogenetic taxonomy to poorly resolved crown clades: A stem-modified node-based definition of Rodentia. Syst. Biol. 45:559–568.

Xu, X., Z.-H. Zhou, X.-L. Wang, X.-W. Kuang, F.-C. Zhang, and X.-K. Du. 2003. Four-winged dinosaurs from China. Nature 421:335–340.

Zug, G. R., L. J. Vitt, and J. P. Caldwell. 2001. Herpetology, 2nd ed. Academic Press, San Diego, California.