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NOTE

A RATIONALE FOR DINOSAURIAN TAXONOMY

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Although the principal aims of phylogenetic taxonomy have been articulated (de Queiroz and Gauthier, 1990, 1992), a general rationale for construction and maintenance of taxonomic definitions has yet to emerge. What constitutes a phylogenetic definition? Which definitional types or reference taxa should be employed, and are these available for revision? Is priority of publication the only arbiter of redundancy?

These unresolved issues are evident in two recent taxonomies for Theropoda. The scheme by Padian et al. (1999), an outgrowth of entries in the Encyclopedia of Dinosaurs (Currie and Padian, 1997a), differs from that by Sereno (1997, 1998; Fig. 1) in the following major ways.

Rationale—Of the three definitional constructs in phylogenetic taxonomy (node, stem, apomorphy), two (node, stem) have been widely applied (de Quieroz and Gauthier, 1990, 1992). Recently, I advocated the use of definitional triumvirates termed node-stem triplets (NST) and well known nested reference taxa to stabilize current taxonomy and taxonomic content. I have applied this rationale to dinosaurian taxonomy (Sereno, 1996, 1997, 1998, 1999a, b). Based on a consideration of diversity, morphologic change, and tradition, a backbone of NSTs was constructed to link together available higher taxa (Fig. 1). A basal NST was positioned at Dinosauria (also Padian and May, 1993); there are 10 NSTs within Ornithischia (Fig. 1A) and 17 within Saurischia (Fig. 1B). No taxa have identical current taxonomic content (i.e., node- and stem-based taxa that include the same currently known taxa) and new taxa (two) were introduced only to complete NST's outside Aves.

Padian et al. (1999), in contrast, do not detail their rationale for choice of reference taxa or placement of node- versus stem-based definitions, except to state their preference for eponymous reference taxa and their desire to "provide two sister-taxa that are stem-based for each major node named." They defined four taxa, Eusaurischia, Carnosauria, Eumaniraptora, and Aviale, which differ only in definitional type (node versus stem) from Saurischia, Allosauroidea, Paraves, and Aves, respectively. Thus, although each pair of companion taxa (e.g., Saurischia, Eusaurischia) refer to different common ancestors by definition (Brochu, 1997), at present they differ only in potential taxonomic content.

Priority—Priority is a heuristic principle with long-standing usage in Linnaean taxonomy at low taxonomic levels. Its application to higher-level taxa by Padian et al. (1999), however, is less than straightforward.

Padian et al. (1999:72), for example, claim that Avetheropoda has priority over Neotetanurae because Neotetanurae "was published shortly after the name Avetheropoda." The taxon Avetheropoda, however, was coined by Paul (1988) many years before Neotetanurae (Sereno et al., 1994). Paul erected Avetheropoda for a group that included nearly all of the taxa that Gauthier (1986) had previously included in Tetanurae. Paul's Avetheropoda, on the other hand, might be equally well matched with Coelurosauria or Maniraptora sensu Gauthier (1986), because *Compsognathus, Coelurus,* and *Archaeopteryx* were positioned as basal avetheropods on his phylogenetic tree (Paul, 1988:fig. 10-1). These comparisons will remain speculative because Paul (1988) objected to continued use of Carnosauria and Coelurosauria and did not discuss how Avetheropoda might compare to any of the theropod clades described by Gauthier (1986).

Given this ambiguous relationship, Sereno et al. (1994:270, fig. 3) erected the taxon Neotetanurae to recognize an additional hierarchical level within Gauthier's scheme that would unite Allosauroidea and Coelurosauria to the exclusion of several basal tetanurans. Approximately one month earlier, Holtz (1994:1106) independently adapted Avetheropoda to unite a similar clade composed of Allosauridae and Coelurosauria. Neither author provided a phylogenetic definition for their respective taxa. Sereno (1997:table 1) first indicated definitional status by listing Neotetanurae as a node-based group composed of stem-based Allosauroidea and Coelurosauria. Shortly thereafter, Currie and Padian (1997b:39) described Avetheropoda "as the node within Tetanurae comprising the stem groups Coelurosauria and Carnosauria." Sereno (1998: table 4) provided the first phylogenetic definition, listing Neotetanurae as "*Allosaurus,* Neornithes, their most recent common ancestor and all descendants." Padian et al. (1999:72) adopted an identical definition for Avetheropoda, "the most recent common ancestor of Neornithes and *Allosaurus* and all descendants of that ancestor."

Utility, in my opinion, should carry more weight than priority in phylogenetic definitions. Nonetheless, if priority is invoked, it must reside with the taxon whose common ancestor was first identified unambiguously. This is achieved in phylogenetic definitions by an explicit relational statement about ancestry that links two or more reference taxa. That a particular taxon is node- or stem-based and is composed of other node- or stem-based groups is not sufficient information (Bryant, 1996; Sereno, 1999a). In this regard, Neotetanurae has priority over Avetheropoda.

Priority regarding usage of the much older taxon Ornithurae was also discussed. Although Gauthier (1986:13) provided a clear stem-based definition for Ornithurae—"extant birds . . . and all other taxa that are closer to extant birds than *Archaeopteryx.*"—Padian et al. (1999:75) preferred Martin's (1983) previous use of the taxon, which they described as "taxon-based" and including Hesperonithiformes, Ichthyornithiformes, and Neornithes.

Martin (1983), however, did not formally define Ornithurae and did not describe the taxon as limited to a particular set of known subgroups. Rather, Martin believed there to be a deep dichotomy in avian phylogeny between avians more closely related to *Archaeopteryx* and those more closely related to living birds. He referred to the former as "Sauriurae" and the latter as Ornithurae. Ornithurines, he posited, "must have existed as a separate lineage at least as far back as the earliest known sauriurine bird, *Archaeopteryx*" (Martin, 1983:310–311). Clearly Martin would have included additional basal taxa within Ornithurae, as long as they were more closely related to living birds than to *Archaeopteryx.* If a phylogenetic definition must be read into Martin's statements about Ornithurae, it would be similar to that given by Gauthier (1986). That Martin's "Sauriurae" is surely a paraphyletic group that includes avians more closely related to Neornithes is irrelevant.

Historical Interpretation—In many instances, Padian et al. (1999) have attributed node- or stem-based definitions to authors who did not present phylogenetic definitions, specify definitional types, or mention reference taxa. In other instances, taxonomic definitions are cited incorrectly.

Padian et al. (1999:fig. 1B), for example, presented a cladogram of Ceratosauria marked with eight node- and stem-based taxa that was attributed to "Rowe et al. (1997), Holtz (1994), and other sources." Of these eight taxa, Rowe et al. (1997:109) only defined Abelisauridae. Rowe et al.'s (1997) definition of Abelisauridae, furthermore, was stem-based, rather than node-based, as shown on the cladogram in Padian et al. (1999). Of the same eight taxa, Holtz (1994) only defined Neoceratosauria and Abelisauroidea. Holtz's (1994:1104) definition of Neoceratosauria, furthermore, was node-based, rather than stem-based, as shown on the cladogram in Padian et al.

Padian et al.'s (1999:fig. 1C) cladogram of "Carnosauria" displayed nine additional node- and stem-based taxa that were presented as "mostly after Holtz (1994) and Sereno et al. (1996)." Holtz (1994:1105)

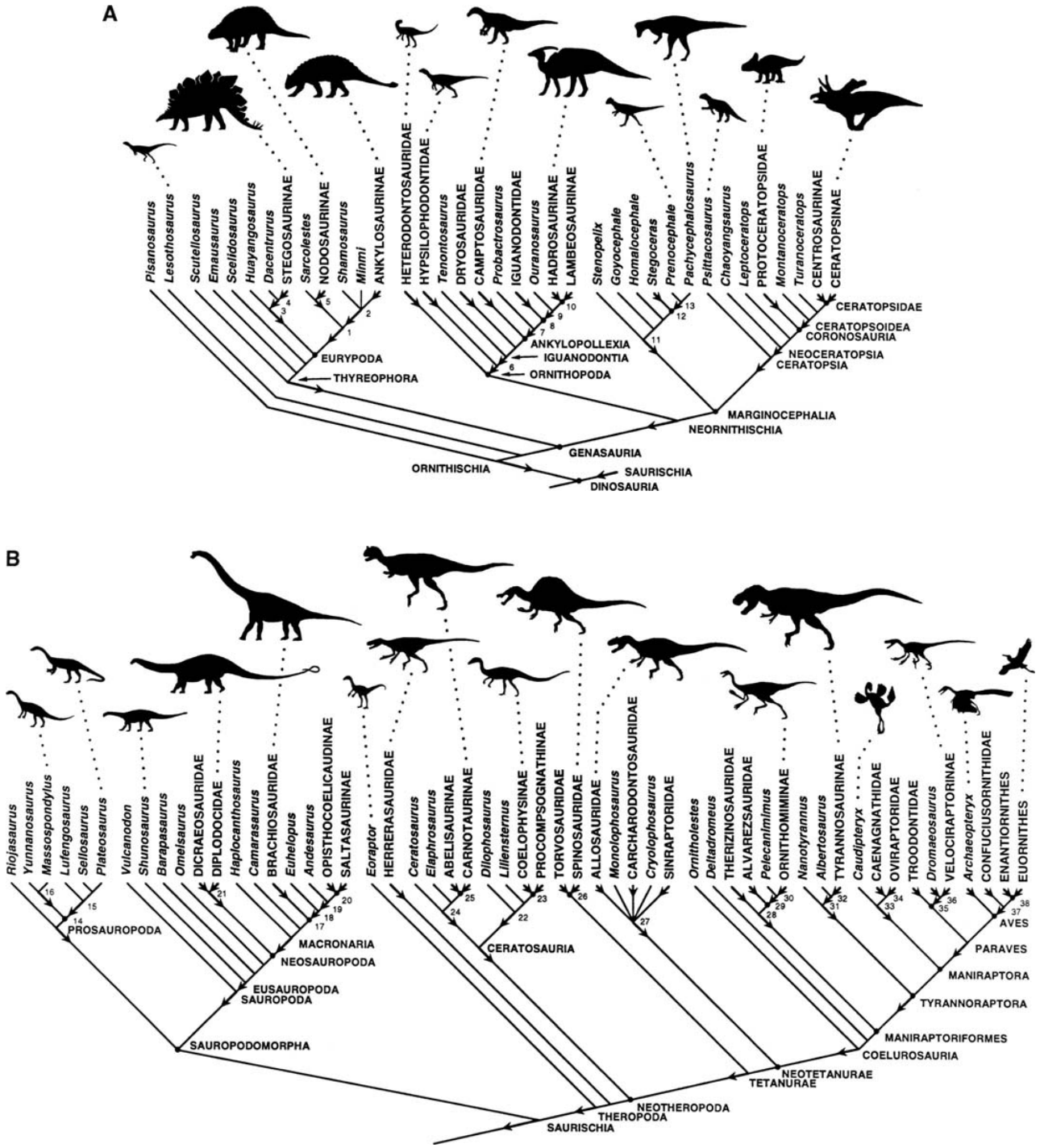

FIGURE 1. Phylogenetic diagram for Ornithischia (**A**) and Saurischia (**B**) showing the locations of node-based (dot) and stem-based (arrow) taxa. **Abbreviations**: **1**, Ankylosauria; **2**, Ankylosauridae; **3**, Stegosauria; **4**, Stegosauridae; **5**, Nodosauridae; **6**, Euornithopoda; **7**, Styracosterna; **8**, Hadrosauriformes; **9**, Hadrosauroidea; **10**, Hadrosauridae; **11**, Pachycephalosauria; **12**, Pachycephalosauridae; **13**, Pachycephalosaurinae; **14**, Plateosauria; **15,** Massospondylosauridae; **16**, Plateosauridae; **17**, Titanosauriformes; **18**, Somphospondyli; **19**, Titanosauria; **20**, Saltasauridae; **21**, Diplodocoidea; **22**, Coelophysoidea; **23**, Coelophysidae; **24**, Ceratosauroidea; **25**, Abelisauridae; **26**, Spinosauroidea; **27**, Allosauroidea; **28**, Ornithomimosauria; **29**, Ornithomimoidea; **30**, Ornithomimidae; **31**, Tyrannosauroidea; **32**, Tyrannosauridae; **33**, Oviraptorosauria; **34**, Caenagnathoidea; **35**, Deinonychosauria; **36**, Dromaeosauridae; **37**, Ornithurae; **38**, Ornithothoraces. For node- and stem-based definitions, see Sereno (1998, in press).

defined only one (Tetanurae) of these nine taxa, and Sereno et al. (1996) did not present any phylogenetic definitions.

Padian et al. (1999:77) suggested that Gauthier's (1986) usage of Sauropodomorpha "as a stem" has priority over Sereno's (1997, 1998; Fig. 1B) node-based definition. Gauthier (1984, 1986), however, only listed included taxa; he did not provide a phylogenetic definition for Sauropodomorpha or discuss in any manner its potential taxonomic content.

References to other taxonomic definitions in the *Encyclopedia of Dinosaurs* are flawed by similar inaccuracies. Padian (1997:546-549), for example, assigned node-based status to many higher-level taxa within Ornithischia, citing Sereno (1986). Sereno (1986), however, did not specify or imply anything concerning the potential taxonomic content of taxa, and the paper was published before the concept of a node-based definition was clearly articulated (de Queiroz and Gauthier, 1990).

Because taxa are the currency of much of evolutionary biology, consensus in taxonomy is a laudable goal. Phylogenetic systematics has arisen, in part, to clarify the meaning of taxa. This goal is best achieved by careful historical interpretation, judicious selection of reference taxa, and an effective configuration of taxonomic definitions.

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