

PHYLOGENETIC DEFINITIONS AND NOMENCLATURE OF THE MAJOR TAXONOMIC CATEGORIES OF THE CARNIVOROUS DINOSAURIA (THEROPODA)

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ABSTRACT—Standardized stem-based and node-based terms are proposed for the major groups of theropod dinosaurs recognized as relatively stable by recent phylogenetic analyses. The proposed terminology is intended to resolve conflict among names applied to the same clade, or sometimes applied without indication of whether the taxon is node-based or stem-based. In all cases but one, these names are already in the literature. We propose the new node-based name *Eumaniraptora* to refer to the most recent common ancestor of *Deinonychus* and *Neornithes* and all descendants of that ancestor. We also suggest the following points: (1) node- and stem-based taxa are preferable to apomorphy-based taxa because they are generally more stable; (2) names already used in the literature should be conserved as far as possible, though sometimes their basis requires adjustment (changing nodes to stems and vice versa and converting apomorphy-based taxa to stems and nodes); (3) the uses of some terms by some authors can be adjusted to reflect priority or common use; (4) in general, names should be based on well-resolved phylogenies; and (5) as a corollary, we recommend a moratorium on new names for theropodan nodes and stems until the phylogenetic relationships of theropodan sub-clades are better resolved.

INTRODUCTION

The advent of the Phylogenetic System (de Queiroz and Gauthier, 1990, 1992, 1994) has destabilized much of traditional classification in both theory and practice. It has emphasized monophyletic groups and de-emphasized the often paraphyletic Linnean groupings and rankings, as an extension of Hennig's principles of Phylogenetic Systematics. Although many of the rules of the International Code of Zoological Nomenclature are not violated by the philosophy of the Phylogenetic System, it is also true that the Code does not provide guidance on many nomenclatural problems of the new system; nor have comprehensive new rules been set in place for the Phylogenetic System. (For some recent discussions see Bryant [1994, 1996], Cantino et al. [1997], Dominguez and Wheeler [1997], Lee [1996], and Schander and Tholleson [1995]).

The need for stability in nomenclature and in the rules of classification (not only of phylogenetic analysis) prompts a proposal to standardize the taxonomic definitions and names of major groups within the theropod dinosaurs (Padian et al., 1997; Currie and Padian, 1997; see also Padian and May, 1993; Holtz, 1994, 1996a, b). Since Gauthier (1984, 1986) first published his revised phylogeny of saurischian dinosaurs, new discoveries and new phylogenies have appeared at a rapid pace, often creating duplicative or conflicting terminology. Whereas priority of name, as in the Linnean system, is a desideratum at lower taxonomic levels as well as generally, in practice many authors have overlooked the fact that simply because one or more members of a group may prove closer to other taxa, that is not a reason to abandon the name of the original group. Furthermore, in these still early days of cladistic analysis and classification, authors often have not recognized differences among node-based, stem-based, taxon-based, and apomorphy-based definitions, which has in turn caused instability and led to more duplication and conflict of nomenclature. (See de Queiroz and Gauthier [1990, 1992, 1994], Padian and May [1993], Padian [1997a], and Sereno [1997] for basic definitions and discussions in the context of Dinosauria.) This is to be expected; in the evolution of cladistics, the development of theory has far outstripped that of practice, and many procedures and protocols have yet to be standardized.

The purpose of this paper is to attempt to standardize a nomenclature for the higher systematic categories of Theropoda. Extinct theropods comprise about 40% of currently valid genera of Mesozoic dinosaurs, even if Mesozoic avians are not included; however, many names of genera and higher categories are based on poorly known material. One of our purposes in standardizing names is to offer node- and stem-based definitions for taxa based on well-known forms, to increase potential stability and make further comparisons easier.

It might be argued that classification is merely a by-product of phylogeny; therefore, all names are potentially unstable because the phylogeny on which they are based may change. But definitions are not based on the stability of taxonomic content; they are based on ancestry. Any two organisms in the world, past or present, have a common ancestry and their unity as an evolutionary taxon is described by that definition. Some definition names, such as the unity of humans with dandelions or of wombats with skunk cabbages, have little phylogenetic utility in discussions of evolutionary questions. Nonetheless, this does not deny their common ancestry at some point in the history of life, a fact that cannot change, and this is the basis of the definition. With new discoveries and analyses, diagnoses will change, and phylogenetic positions of individual taxa can shift, but definitions will not, and this is why it is important to standardize them. As we will see, it is far easier to construct unambiguous definitions and nomenclature when the phylogeny approaches a simple Hennigian comb; as branching patterns become more complex, the use of names depends even more on well-corroborated phylogenies.

MATERIALS AND METHODS

The following discussion of the suggested classification of Theropoda is based on the methods of phylogenetic systematics, as revised from Hennig's original formulation by a variety of authors (e.g., Eldredge and Cracraft, 1980; Wiley, 1981) and practiced in any current issue of journals in comparative biology, notably *Systematic Biology* and *Cladistics*. The use of terminology has been gleaned from a variety of sources. Its particulars cannot satisfy every worker's phylogeny, nor can the original intent of every author be honored faithfully, for reasons

just mentioned. However, it is offered in constructive spirit as a starting point. Several precepts are considered as given:

1. Definitions are more stable than diagnoses. The distributions of synapomorphies (diagnoses) can be found to change with new discoveries; definitions of taxa never can, because any two organisms must have a common ancestry and the name denoting that relationship cannot change.
2. Node-based and stem-based definitions are relatively stable; apomorphy-based and taxon-based definitions are less stable (Padian and May, 1993). Hence, only the former two are used here. Apomorphy-based definitions are unstable because their hierarchical distributions are subject to shifting as new specimens are discovered and existing ones are re-analyzed. Besides, an apomorphy may arise independently in another taxon. Taxon-based definitions are unstable because any single member of a list of taxa may eventually be found to belong to another group (e.g., as *Tyrannosaurus* was re-assigned from the Carnosauria to the Coelurosauria).
3. Node-based taxa require diagnoses; stem-based taxa do not have diagnoses because they represent branches that proceed from a node. A stem-group is simply identified as all members of a node-taxon that are closer to one specified member of the clade than to a second specified member. The first branching point (node) within a stem-based taxon receives a diagnosis (list of synapomorphies), like any other node.
4. It is unnecessary to name every stem and node. Groups that contain only one or two taxa may not require names, like those that are particularly unstable because they are based on a weak list of synapomorphies. However, when new suprageneric taxa are named, they should preferably be specified as stem-based or node-based taxa, for reasons suggested above.
5. Names should be based on explicit, well corroborated phylogenetic hypotheses. In part, this is a corollary of the previous point; we will return to its consequences.

Definitions proposed here are based principally on Gauthier (1984, 1986) and previous literature that he discusses; on Padian and May (1993), Holtz (1994, 1995, 1996a), Holtz and Padian (1995), Novas (1994, 1996), Sereno and Novas (1992, 1994), Sereno et al. (1993, 1994, 1996), Currie and Padian (1997), and Sereno (1997), as well as on other sources cited. In the figures, node-based taxa are designated by the customary junctions of branches; stem-based taxa are designated by arc segments bisecting branches on both sides of a node (as used in Currie and Padian, 1997).

We have not found it possible or practicable to use a single rule or criterion inflexibly in attempting to suggest a standardized nomenclature. Some arbitrary decisions have had to be made because some existing names are clearly redundant, and others were not specified as nodes or stems. For this reason, we made an effort to circulate early versions of our proposed nomenclature among a wide group of concerned systematists. But it was not possible to be entirely consistent with criteria for making decisions, because of the histories and uses of various names. In the Linnean System, priority of names does not extend to higher categories. The Phylogenetic System has not received extensive enough treatment or acceptance to provide ease of communication; where we recommend against names with obvious priority, we try to explain our decisions.

SYSTEMATIC PALEONTOLOGY

Basal Theropoda

Theropoda is stem-defined as all Saurischia closer to Neornithes than to *Cetiosaurus*, which was one of the first named members of the Sauropodomorpha, the sister-group to Theropoda within Saurischia (Padian and May, 1993); though any

well-accepted sauropod genus would fit. There is ambiguity about many proposed synapomorphies (Gauthier, 1986; Sereno and Novas, 1992, 1994; Novas, 1994; Sereno et al., 1993, 1994, 1996; etc.), but the monophyly of Saurischia is still well supported (Novas, 1996).

There is controversy about taxa at the base of the theropod tree that, regardless of the outcome of future systematic analyses, still can have contingent resolution in nomenclature (Fig. 1A). Herrerasauridae and *Eoraptor* are placed as basal theropods by some authors (e.g., Sereno and Novas, 1994; Novas, 1996; Sereno 1997), but others reserve judgment because these taxa appear to lack many synapomorphies of both theropods and saurischians, such as the long neck, the elongated second digit, and the failure of the first metatarsal to contact the ankle (e.g., Gauthier, 1986; Holtz and Padian, 1995). Until recently, analyses of herrerasaurids (e.g., Reig, 1963; Colbert, 1970; Galton, 1977; Gauthier, 1986; Brinkman and Sues, 1987) have regarded them either as basal saurischians or as outside Dinosauria. The definition of Theropoda in either event does not change. According to Gauthier (1986) and Rowe and Gauthier (1990), the stem Theropoda can be divided into two basal stem-groups: Ceratosauria and Tetanurae (Fig. 1). Whether or not *Eoraptor* and Herrerasauridae are eventually accepted as basal theropods, the name Neotheropoda (Bakker, 1986) is still the node uniting Ceratosauria and Tetanurae, and is definable as the most recent common ancestor uniting Neornithes and *Ceratosaurus*, and all descendants of that common ancestor.

Ceratosauria

Ceratosauria (Gauthier, 1984, 1986; Rowe and Gauthier, 1990; Rowe et al., 1997) includes all neotheropods closer to *Ceratosaurus* than to Neornithes (Fig. 1B). Ceratosaurids are known from the Late Triassic (*Coelophysis*, *Liliensternus*) through the Early Jurassic (*Dilophosaurus*, *Segisaurus*, *Sarcosaurus*, *Syntarsus*), the Late Jurassic (*Ceratosaurus*), and the Cretaceous (*Abelisaurus*, *Carnotaurus*, etc.) (Bonaparte, 1991; Novas, 1991, 1992; Holtz, 1994; Rowe et al., 1997). Ceratosauria has been divided into the stems Coelophysoidea (*Dilophosaurus* and Coelophysidae) and Neoceratosauria (*Ceratosaurus*, Abelisauridae, and possibly *Elaphrosaurus*). However, these definitions are taxon-based and require revision: Coelophysoidea comprises all ceratosaurids closer to *Coelophysis* than to *Ceratosaurus*, Neoceratosauria comprises all ceratosaurids closer to *Ceratosaurus* than to *Coelophysis*, and Abelisauridae is a stem that comprises all neoceratosaurids closer to *Carnotaurus* than to *Ceratosaurus*. Abelisauridae (following Bonaparte and Novas, 1985) is a node that includes *Carnotaurus* and *Abelisaurus*, and all descendants of their most recent common ancestor. *Elaphrosaurus* has been suggested as the sister-taxon of Abelisauridae (Holtz, 1994), but its placement may change with future analyses. Other subgroups, such as the node uniting Coelophysoidea and Neoceratosauria, have not yet been named pending conclusive cladistic analysis of the Ceratosauria and basal theropods. *Ceratosaurus* is used as the primary reference taxon for Ceratosauria rather than more well understood theropods such as *Coelophysis*. This approach to anchoring clades with their eponymous genera prevents confusion—e.g., if *Ceratosaurus* is later determined to be closer to birds than *Coelophysis* is, then *Ceratosaurus* will remain a ceratosaur while *Coelophysis* will be a non-ceratosaurian (and thus non-neotheropodan) theropod. The definitions of ceratosaurian subclades that we propose also prevents other confusing situations such as the inclusion of birds within neoceratosaurids or abelisauroids, because the validity of Neoceratosauria and Abelisauridae are contingent on the status of *Ceratosaurus* and *Coelophysis* as ceratosaurids.

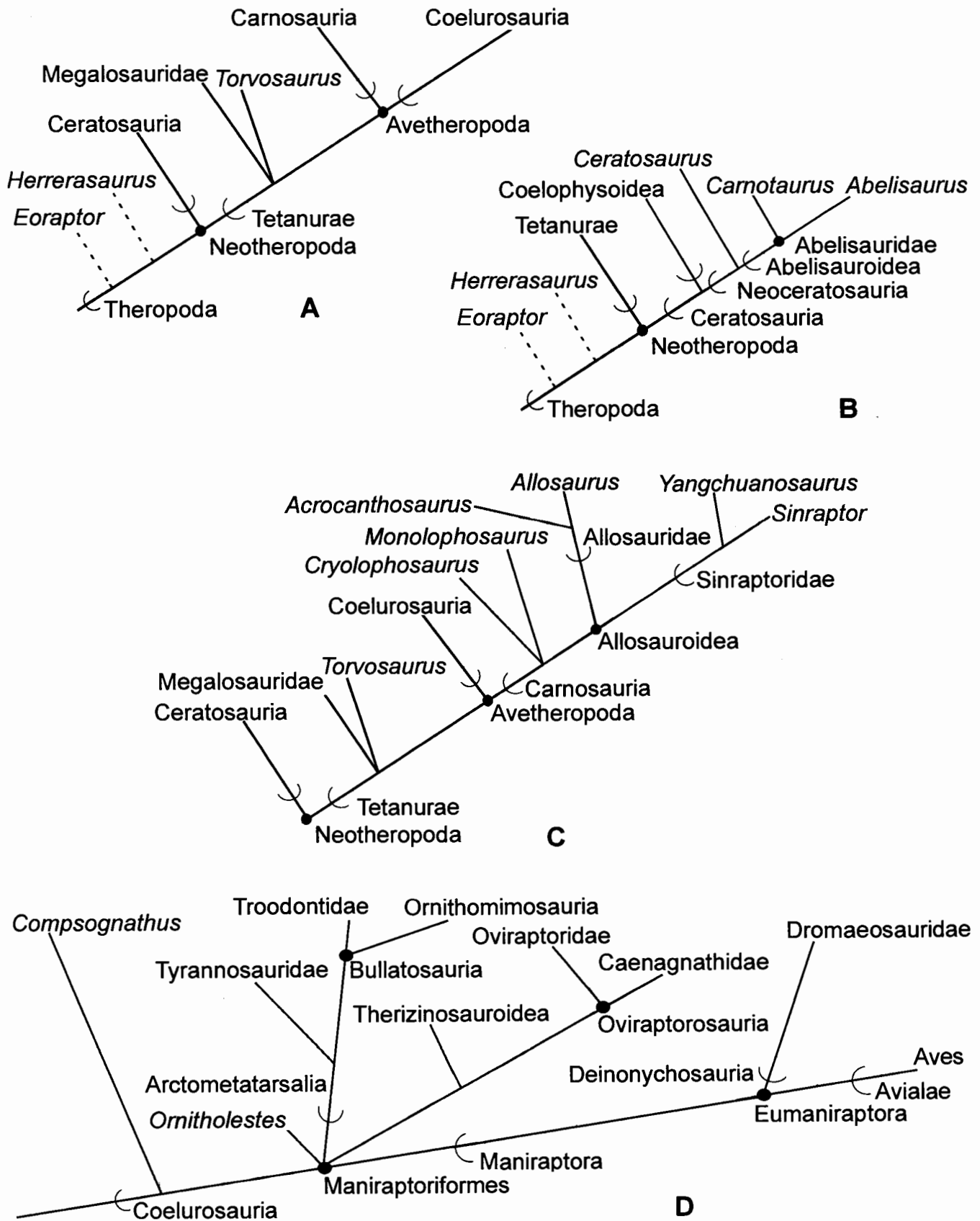


FIGURE 1. A, nomenclature of basal theropod groups, mostly after Gauthier (1986) and Holtz (1994); see Currie and Padian (1997). B, nomenclature of Ceratosauria, after Rowe et al. (1997), Holtz (1994), and other sources. C, nomenclature of Carnosauria, mostly after Holtz (1994) and Sereno et al. (1996). D, nomenclature of Coelurosauria, mostly after Holtz (1994, 1996b).

Tetanurae

The stem-taxon Tetanurae, according to Gauthier (1986), comprises two principal stems, Carnosauria and Coelurosauria (Fig. 1), which Holtz (1994) united at the node Avetheropoda (following use of the name by Paul, 1988). Avetheropods ranged from at least the Middle Jurassic through the latest Cretaceous and, in the case of Neornithes, to the present day. This node is the same as Neotetanurae (Sereno et al., 1994), which was published shortly after the name Avetheropoda. Tetanurae is defined as all neotheropods more closely related to Neornithes than to *Ceratosaurus*. Avetheropoda is defined as the most recent common ancestor of Neornithes and *Allosaurus* and all descendants of that ancestor.

Some taxa, including *Torvosaurus*, *Spinosaurus*, *Baryonyx*, *Afrovenator*, and poorly understood "megaloosaurs" such as *Piatnitzkysaurus*, *Eustreptospondylus*, *Poikilopleuron*, and *Megalosaurus*, may fall outside the Avetheropoda but are still usually considered basal members of the Tetanurae (Holtz, 1994, 1995; Charig and Milner, 1997; fig. 1A, C). The term "megaloosaur," which dates back to William Buckland's 1824 description of *Megalosaurus*, is widely considered an unnatural assemblage of incompletely known or poorly preserved medium-sized to large theropods of the Early to Late Jurassic and Early Cretaceous (Padian, 1997b). Work is still needed on the removal of indeterminate remains and taxa that clearly belong to other clades, and on the definition and diagnosis of a monophyletic Megalosauridae, if this is in fact possible. We refrain from offering definitions for problematic taxa such as "Torvosauroida" and "Spinosauroida" until more comprehensive phylogenetic analyses clarify this area of theropod phylogeny further.

Novas (1992) used Tetanurae as a node-based taxon (all descendants of the most recent common ancestor of *Allosaurus* and birds; Avetheropoda in the present paper), and he coined the name Avipoda as a more inclusive taxon. However, as noted above, Tetanurae is explicitly a stem-taxon. Avipoda was not explicitly defined as stem-based (in which case it would be a synonym of Tetanurae), node-based, or otherwise. This name is potentially available for some clade within Tetanurae, pending increased resolution of the relationships of basal tetanurans.

Carnosauria

Carnosauria comprises all avetheropods closer to *Allosaurus* than to Neornithes. Coelurosauria comprises all avetheropods closer to Neornithes than to *Allosaurus*. (Sereno [1997] uses the term Allosauroida as the sister stem-taxon to Coelurosauria, but by priority of definition [Gauthier, 1986] the sister taxon of Coelurosauria must be Carnosauria. We suggest below using Allosauroida as a node connecting the stems Allosauridae and Sinraptoridae (as used by Currie and Zhao [1994] to unite these two taxa to the exclusion of other carnosaurs), which is currently unnamed; see also Holtz and Brett-Surman, 1997.)

Gauthier (1986) did not formally define Carnosauria apart from listing included taxa: the genera *Allosaurus*, *Acrocanthosaurus*, *Indosaurus*, *Alectrosaurus*, *Dryptosaurus*, *Albertosaurus*, *Alioramus*, *Daspletosaurus*, *Indosuchus*, *Tarbosaurus*, and *Tyrannosaurus*. By implication, Carnosauria would be defined as these taxa and all others closer to them than to birds within Tetanurae (as Gauthier's cladogram in his fig. 9 indicates). Gauthier formally defined Carnosauria with some misgivings, acknowledging that many characters that appeared to distinguish the group were probably size-related convergences, as they were with large ceratosaurs and "megaloosaurs." These reservations soon turned out to be justified.

Some background on the historical placement of tyrannosaurs is important. Novas (1992) and Holtz (1994) realized that tyrannosaurs, despite their great size, are not carnosaurs, but coelurosaurs, as von Huene (1923, 1926), who coined the terms

Carnosauria and Coelurosauria, first recognized. It was W. D. Matthew who suggested to von Huene in correspondence that tyrannosaurs and ornithomimids might be closely related, on the basis of their foot structure (a conclusion independently reached by Holtz, 1994). Accordingly, von Huene (1923) placed tyrannosaurs within coelurosaurs; however, his conception of coelurosaurs and carnosaurs was very different than it became to later workers. He also included ceratosaurs in Coelurosauria, which he thought included Hallopoda (now generally regarded as crocodylomorphs) as its basal taxon; coelurosaurs were contrasted with megalosaurs, which von Huene (1923, 1926) thought were the forerunners of allosaurids. In 1932 he returned tyrannosaurs to the Carnosauria (von Huene 1932:243–245) for a variety of reasons. Hence his conception of tyrannosaurid relationships among coelurosaurs was not really very similar in detail to those of later workers.

The recent reassignment of tyrannosaurids to the Coelurosauria (Novas 1992; Holtz 1994) removes *Albertosaurus*, *Alectrosaurus*, *Alioramus*, *Daspletosaurus*, *Tarbosaurus*, and *Tyrannosaurus* from Carnosauria. The removal of some taxa that turned out to belong to Abelisauridae (*Indosuchus* and *Indosaurus*; Molnar, 1990; Bonaparte, 1991; see above) leaves *Allosaurus*, *Acrocanthosaurus*, and *Dryptosaurus* among Gauthier's original constitution of Carnosauria. According to some recent analyses, *Dryptosaurus* is more likely a coelurosaur than a carnosaur (Denton, 1990; Holtz, 1995; but see Carpenter et al., 1997), so Carnosauria is reduced to two genera, *Allosaurus* and *Acrocanthosaurus*, which were already regarded as closely related by Stovall and Langston (1950). Holtz (1994) included both in the Allosauridae, distinguished by the form of the pubic foot (longer anteriorly than posteriorly, triangular in ventral view). This rather weak unity is by default of incomplete or incompletely described material in other taxa, including *Acrocanthosaurus*, *Chilantaisaurus*, *Piatnitzkysaurus*, and *Szechuanosaurus* (Molnar et al., 1990). Holtz (1995) regarded the last two genera as possible members of this branch, but outside Allosauridae.

Current versions of the Carnosauria (Fig. 1C) eloquently demonstrate the changing views of theropod phylogeny. Holtz (1995) included many recently described taxa in his analysis, and found that many of them could be grouped into a monophyletic, globally distributed Carnosauria, including taxa from Antarctica (*Cryolophosaurus*), China (*Monolophosaurus* and the Sinraptoridae: *Sinraptor* and *Yangchuanosaurus*), Africa (*Carcharodontosaurus* and the poorly known *Bahariasaurus* [if a valid taxon]), possibly forming a monophyletic "Carcharodontosauridae"—see below for comments), South America (*Giganotosaurus*, also possibly a "carcharodontosaurid"), and North America (the Allosauridae: *Allosaurus* and related taxa; and the problematic *Acrocanthosaurus*, which was regarded as a "carcharodontosaurid" by Sereno et al., 1996).

Given the current instability in diagnosing the content and hence the synapomorphies of the allosauroid groups, Allosauridae and Sinraptoridae can be defined only with reference to their eponymous genera. Hence, Allosauridae comprises *Allosaurus* and all allosaurids closer to it than to *Sinraptor*; Sinraptoridae comprises *Sinraptor* and all allosaurids closer to it than to *Allosaurus*. Allosauroida is a node-based taxon that includes *Allosaurus* and *Sinraptor* and all descendants of their most recent common ancestor. Allosauridae and Sinraptoridae are here-in defined as stem-based taxa; neither Sereno et al. (1994) nor Holtz (1994) indicated node- or stem-based definitions, but rather used characters and included taxa. Stem-based definitions are included here because at present the taxa are minimally monotypic: despite the somewhat optimistic scheme presented in Figure 1C, no consensus exists on the membership of more than one genus per taxon.

Resolution of allosauroid phylogeny is a difficult matter, part-

ly because many taxa that are clearly allied to the group are incompletely known or have had their systematic characters interpreted differently by different workers. Consequently, the memberships of Allosauridae and Sinraptoridae are at present not agreed upon, apart from their nominal genera. Sereno et al. (1994), for example, placed *Sinraptor* and *Yangchuanosaurus* in Sinraptoridae, and *Acrocanthosaurus*, *Allosaurus*, *Cryolophosaurus*, and *Monolophosaurus* in Allosauridae. Holtz (1994) placed only *Allosaurus* and *Acrocanthosaurus* in Allosauridae. Holtz (1995) regarded *Monolophosaurus* as a tetanurine outside Avetheropoda, but later (1996a) found it to be the sister taxon to Allosauroidae, with *Cryolophosaurus* as a more basal carnosaur. Holtz (1996a) also found *Giganotosaurus* and *Carcharodontosaurus* (and other putative "carcharodontosaurids") to be allosauroids closer to Allosauridae than to Sinraptoridae. However, Novas (1997) suggested that carcharodontosaurids (e.g., *Giganotosaurus* and *Carcharodontosaurus*) could be closely related to Abelisauridae. Meanwhile, Sereno et al. (1996) also found *Carcharodontosaurus* to be in Allosauroidae, but suggested that *Acrocanthosaurus* and *Giganotosaurus* might be members of the clade "Carcharodontosauridae" instead of Allosauridae. *Acrocanthosaurus* was known until recently only from incomplete specimens, but more material has been discovered in the past few years (Harris, 1998). We refrain from defining "Carcharodontosauridae" until its membership and relationships are better resolved. The latest discoveries, such as *Neovenator* (Hutt et al., 1996) and undescribed carnosaur material from Dinosaur National Monument, demonstrate our increasing knowledge of carnosaurian diversity. Other poorly known or as yet incompletely described taxa such as *Piatnitzkysaurus*, *Chilantaisaurus*, *Becklespinax*, and *Metriacanthosaurus* (see Molnar, 1990; Molnar et al., 1990) may be allosauroids as well, but their evolutionary relationships have not yet been conclusively established.

Coelurosauria

Gauthier (1986) redefined Coelurosauria in cladistic terms as a stem-based taxon comprising Neornithes and all tetanurans closer to Neornithes than to Carnosauria. He listed Ornithomimidae, *Compsognathus*, *Ornitholestes*, *Coelurus*, *Microvenator*, *Sauromitholestes*, *Hulsanpes*, *Elmisauridae*, *Caenagnathidae*, *Deinonychosauria*, and *Avialae* (*Archaeopteryx* plus other birds) as component taxa of Coelurosauria. To these can be added Therizinosauroidae, now generally considered close to Oviraptoridae (Russell and Dong, 1994; Holtz, 1994, 1996a, b; Sues, 1994, 1997). Gauthier's (1986) analysis did not recognize specific subgroups within Coelurosauria, except to link Deinonychosauria with Avialae (*Archaeopteryx* + other birds in his formulation; Aves of most other workers; see below). Gauthier's definition of Deinonychosauria (Colbert and Russell 1969) included Troodontidae and Dromaeosauridae, a view corroborated in some recent phylogenies (Sues, 1997; Sereno, 1997), although troodontids have been regarded as the sister taxon to ornithomimids (e.g., Holtz, 1994). Deinonychosauria could be retained as the node corresponding to Holtz's (1994) unnamed "node 11"; however, Holtz (1996b), in reanalyzing the nomenclature, called this node Maniraptoriformes (Fig. 1D).

Gauthier's definition of Deinonychosauria was taxon-based, and requires revision. It has been redefined as a stem-based taxon comprising all maniraptorans closer to *Deinonychus* than to Neornithes (Padian et al., 1997); its sister taxon is Avialae, comprising all maniraptorans closer to Neornithes than to *Deinonychus*. Sereno (1997) uses Deinonychosauria as a node comprising Dromaeosauridae and Troodontidae, which is consistent with Gauthier's original intent; however, some more recent analyses have placed Troodontidae closer to Neornithes than to Dromaeosauridae (e.g., Forster et al., 1998), so there

may be some evidence why not to conserve Gauthier's original taxonomic content. Regardless of which phylogeny is correct, Deinonychosauria is still stable as a stem taxon. Sereno (1997: 444) listed the term Paraves as a stem-taxon containing Deinonychosauria and Neornithes (all maniraptorans closer to Neornithes than to *Oviraptor*), with Oviraptorosauria as its sister stem within the node Maniraptora (a problem we discuss below). We proposed the name Eumaniraptora for the node uniting the stems Deinonychosauria and Avialae (Padian et al., 1997). We suggested the name Eumaniraptora because this node represents an important juncture in theropod evolution (the most recent common ancestor of avialians and their deinonychosaurian relatives), and deserves a term facilitating reference to it. The difference between the use of the terms Paraves and Eumaniraptora is important because the former is a stem-name and the latter is a node-name, and the two schemes use terms such as Deinonychosauria rather differently. If oviraptorosaurs are accepted as maniraptorans, which seems true in most current formulations, then Paraves can be a valid stem within Maniraptora, with oviraptorosaurs as its sister taxon.

Holtz's (1994, emended 1996b) analysis of the phylogenetic relationships among the subclades of Theropoda found a major node within Coelurosauria, diagnosed by the possession of the semilunate carpal of the wrist and several other features. Holtz (1994) applied Gauthier's (1986) name Maniraptora to this node, but revised it to Maniraptoriformes (1996b) upon recognizing that the name Maniraptora already had a definition (Gauthier, 1986) that explicitly excluded ornithomimids, which Holtz had included in his Maniraptora. Accordingly, Holtz (1996b) defined Maniraptoriformes as *Ornithomimus* and birds (Aves), and all the descendants of their most recent common ancestor. According to Gauthier's (1986:30, 35, fig. 9) formulation, Maniraptora represents the stem group composed of all coelurosaurs (Maniraptoriformes) more closely related to Aves than to *Ornithomimus*.

Within Maniraptoriformes, Deinonychosauria and Avialae form the two stems of the monophyletic group Eumaniraptora (the node-based name that we suggest) within the stem-based Maniraptora (following Gauthier's [1986] usage; Holtz, 1996b non 1994; Fig. 1D). A second monophyletic group (Arctometatarsalia), suggested by Holtz (1994), is formed by Ornithomimosauria + Troodontidae (Bullatosauria), plus Tyrannosauridae; and Oviraptoridae, Caenagnathidae (=Elmisauridae), and Therizinosauroidae may form a third monophyletic group (designated Oviraptorosauria by Russell and Dong [1994]). Sues (1994, 1997) determined that *Chiostenes* is the senior subjective synonym of *Caenagnathus*, but that Caenagnathidae is the correct name for the clade to which it belongs, and therefore is a senior synonym of Elmisauridae. *Ornitholestes*, *Dryptosaurus*, and *Compsognathus* appear to be outgroups to all these taxa within Coelurosauria; however, Holtz (1996b) pictured *Ornitholestes* in a polytomy with Arctometatarsalia, Maniraptora, and Oviraptorosauria within Maniraptoriformes. The relationship of *Ornitholestes* to other coelurosaurs is currently unresolved.

Arctometatarsalia was established by Holtz (1994) to encompass all coelurosaurian theropods that shared the "arctometatarsalian" condition, a name given to the proximally pinched third metatarsal by Holtz (1994; from the Latin *arctus*, meaning compressed). He defined Arctometatarsalia as the first theropod with this condition and all of its descendants, which included by his formulation Ornithomimosauria, Troodontidae, Tyrannosauridae, Caenagnathidae (Elmisauridae), and *Avimimus*. However, Holtz (1996b) revised this definition because he recognized that an apomorphy-based definition was potentially unstable, and the condition had also been found in *Mononykus* (Perle et al., 1994), an early avialian. Moreover, new evidence indicates that Caenagnathidae (Elmisauridae) is closer to Ovi-

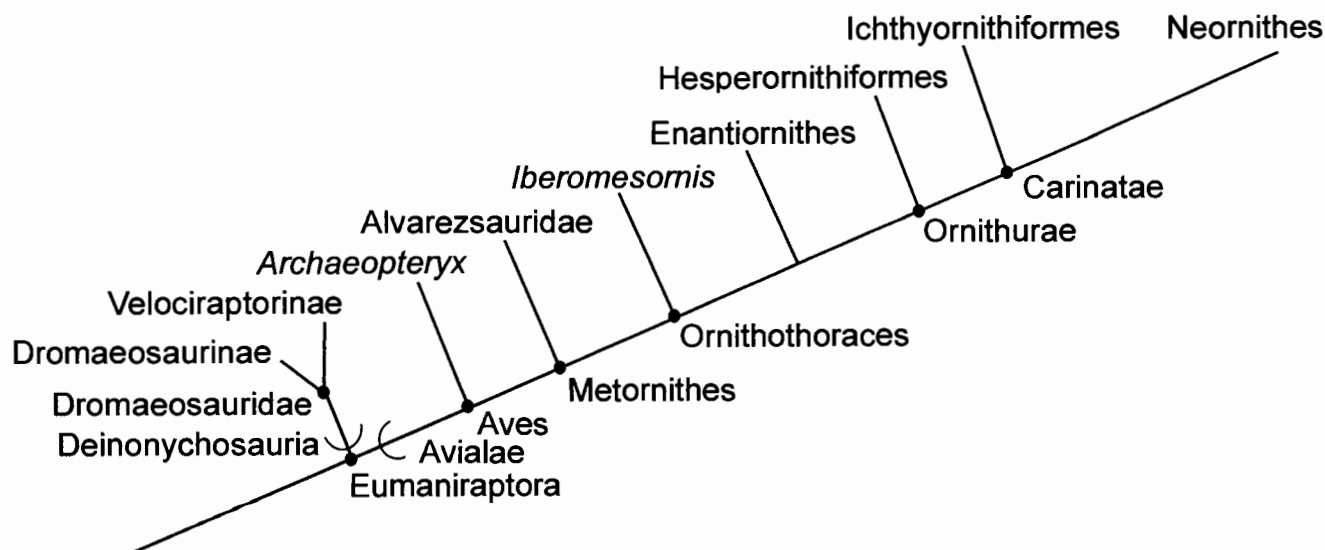


FIGURE 2. Nomenclature of the major groups of Eumaniraptora, mostly after Currie (1995), Chiappe (1997), and Currie and Padian (1997).

raptoridae than to the other Arctometatarsalia (Sues, 1997), and *Avimimus*, as originally described, may be a chimera (Holtz, 1996a, b). Consequently, Holtz (1996b) amended the definition of Arctometatarsalia from an apomorphy-based to a stem-based taxon: the clade comprising *Ornithomimus* and all coelurosaurs closer to *Ornithomimus* than to Aves. In his formulation, Arctometatarsalia principally comprises Ornithomimosauria and Troodontidae (which together form Bullatosauria), plus Tyrannosauridae. The node Bullatosauria collapses to a more inclusive node (Maniraptoriformes) if this phylogeny is eventually rejected (Sues, 1997; Sereno, 1997; Forster et al., 1997), but it is valid in cases that unite Ornithomimosauria and Troodontidae within a more inclusive maniraptoriform group.

Ornithomimosauria has a more problematic history. Following Holtz's phylogeny, it would include all bullatosaurids closer to *Ornithomimus* than to *Troodon*; Troodontidae reciprocally would include all bullatosaurids closer to *Troodon* than to *Ornithomimus*. If the monophyly of the groups included in Arctometatarsalia (Bullatosauria and [Bullatosauria + Tyrannosauridae]) is rejected, the name Arctometatarsalia still serves as the stem defining *Ornithomimus* and all coelurosaurs closer to it than to Neornithes. Ornithomimosauria could take a more conventional node-based definition that includes recognized genera in that taxon: for example, *Pelecanimimus* and *Ornithomimus* and all the descendants of their most recent common ancestor. Bullatosauria would be a redundant taxon; Troodontidae and Tyrannosauridae would require definitions including their eponymous taxa, but it would be best to avoid definitions until their phylogenetic positions are more generally agreed upon (See Discussion, below).

Oviraptorosauria is also problematic. It was established by Barsbold (1976b) to emphasize the distinctness of the taxon he named Oviraptoridae (1976a). Osmólska (1976) included *Oviraptor* in the poorly known Caenagnathidae (now replacing Elmisauridae [Sues 1997] by seniority; *Caenagnathus* itself has been recognized as a junior synonym of *Chirostenotes*), but the taxonomic content of Oviraptorosauria and Oviraptoridae still did not differ. Barsbold (1983) first used Oviraptorosauria to include Oviraptoridae and Caenagnathidae, but did not define it phylogenetically. Russell and Dong (1994:2121) used Oviraptorosauria to include "ornithomimids, therizinosauroids, troodonts, and oviraptorosaurs," but in their phylogeny (1994:2125) troodontids, therizinosauroids, and ornithomimids were

listed as successive outgroups to "oviraptorosaurs." Here, we presume that they meant "oviraptorosaurs" to include the traditional content of oviraptorids and caenagnathids; but it is difficult to understand whether their intention was to include the troodontid-therizinosauroid-ornithomimid grouping, which they regarded as provisional, within Oviraptorosauria proper. Sues (1997) conservatively and sensibly uses Oviraptorosauria as a node in Barsbold's (1983) sense of Oviraptoridae plus Caenagnathidae (=Elmisauridae), but not including Therizinosauroidea (the sister taxon of Oviraptoridae plus Caenagnathidae) as Russell and Dong (1994) had done. These are all valid and potentially usable definitions, but they differ substantially. Partly to circumvent this confusion, Currie and Padian (1997:508) suggested a definition of Oviraptorosauria as all coelurosaurs closer to *Oviraptor* than to Aves, which also agrees with Sereno's (1997) formulation. However, Sues (1997) accepts Barsbold's (1983) taxonomy as node-based, which is more consistent with common usage. We endorse the latter definition for Oviraptorosauria, i.e., *Oviraptor* and *Chirostenotes* (=Caenagnathus) and all descendants of their most recent common ancestor. Within Oviraptorosauria, Oviraptoridae may be stem-defined as all taxa closer to *Oviraptor* than to *Chirostenotes* (=Caenagnathus); Caenagnathidae (Elmisauridae) is reciprocally all taxa closer to *Chirostenotes* (=Caenagnathus) than to *Oviraptor*, as nearly everyone agrees. The node uniting Oviraptorosauria and Therizinosauroidea, or the stem containing Oviraptorosauria, are left unnamed at this time. The phylogenetic position of Therizinosauroidea (and Therizinosauridae) is problematic and we defer a formal phylogenetic definition of this taxon as well.

Other poorly known taxa, such as the recently discovered *Bagaraatan* (Osmólska, 1996) and *Deltadromeus* (Sereno et al., 1996), and the long known but poorly understood *Coelurus*, may be other basal (i.e., non-maniraptoriform) coelurosaurs, members of other less inclusive clades within Coelurosauria, or non-coelurosaurian tetanurines (see also Norman, 1990).

Avialae and Aves

Gauthier (1986) established the term Avialae ("bird-wings") to encompass *Archaeopteryx* plus ornithurine birds. Gauthier used the term "ornithurine" birds in a somewhat different sense than other workers, defining it as living birds and all avialians

closer to them than to *Archaeopteryx*. In that work, Gauthier also proposed the restriction of the term "Aves" to crown-group birds, that is, extant taxa of birds and all the descendants of their most recent common ancestor. His purpose in doing so was to stabilize the content of the term and to maximize the information to taxonomists of soft parts and other structures not usually available in fossils. Moreover, Linnaeus's original concept of Aves did not include fossil forms, inasmuch as Linnaeus did not know of them.

Acceptance of this definition of Aves, however, has been problematic. *Archaeopteryx* was recognized as a primitive but true bird by the 1880s (because it had feathers, a reduced tail, and other avian features), following several decades of dispute after its initial description in 1861. In standard textbooks in both ornithology and paleontology of the twentieth century, *Archaeopteryx* has been treated unexceptionally as a bird, though placed by the traditional classificatory schemes in its own Subclass Archaeornithes, Order Archaeopterygiformes, and Family Archaeopterygidae to recognize its distinctness from other birds (see also Cracraft, 1981, 1986; Martin, 1983). There seems to be strong reason as well as convention for retaining the term Aves to encompass *Archaeopteryx*, extant (crown-group) birds, and all the descendants of their most recent common ancestor (Padian and Chiappe, 1998). The term Neornithes is normally applied to the node defining crown-group birds. Avialae, as previously stated, is available to define the stem-group consisting of Neornithes and all maniraptorans closer to them than to *Deinonychus*. The name Deinonychosauria, used by Gauthier (1986) to include Dromaeosauridae plus Troodontidae (though he supported its monophyly only tentatively), can now be used as the stem-based sister taxon to Avialae, defined as *Deinonychus* and all maniraptorans closer to it than to Neornithes. This is at least partly consistent with Gauthier's original formulation of Deinonychosauria and Avialae as sister stem-taxa within Maniraptora. Whether or not Troodontidae is included in Deinonychosauria, the meanings of the two groups (Deinonychosauria and Avialae) remain the same because they can be interpreted as stem-based taxa (see Gauthier 1986:fig. 9). The node-based taxon Dromaeosauridae, defined as the most recent common ancestor of *Dromaeosaurus* and *Velociraptor* and all of its descendants, includes Dromaeosaurinae plus Velociraptorinae, both stem-groups formed on the basis of respective proximity to their eponymous genera (see also Currie, 1995). We have proposed here that the name Eumaniraptora should be applied to the node uniting Deinonychosauria with Avialae.

Within Aves (Fig. 2), Ornithurae now comprises Neornithes, Ichthyornithiformes, and Hesperornithiformes, following the taxon-based definition of Martin (1983). For the sake of consistency, we suggest defining Ornithurae as *Hesperornis* and Neornithes plus all descendants of their most recent common ancestor. Carinatae is the name applied to the node encompassing *Ichthyornis* and Neornithes plus all descendants of their most recent common ancestor. *Patagopteryx*, Enantiornithes, and *Iberomesornis* join Ornithurae in another node-based taxon designated Ornithothoraces. We suggest defining Ornithothoraces as *Iberomesornis* and Neornithes plus all descendants of their most recent common ancestor. *Mononykus* plus this group comprise the node Metornithes, and *Archaeopteryx* plus the preceding taxa form Aves. Diagnoses and further remarks can be found in Chiappe (1997) and references therein.

DISCUSSION

We undertook this exercise to suggest a reconciliation of some of the myriad of higher category names that have been proposed for taxa within (mostly non-avian) theropod dinosaurs. We wish to stress again that in so doing we are not advocating any particular phylogeny; rather, we are trying to

standardize names based on what seems to us to be consensus points in theropod phylogeny as well as common use of terminology. Far more names have been proposed for the same (or apparently the same) taxa than are necessary. It seemed practicable to identify and conserve as far as possible the priority of names that have been proposed as nodes or stems, or that can be redefined as such. Some names seem redundant by virtue of previous priority and it seemed necessary to us to erect only one new taxon name (Eumaniraptora).

There are a few obvious insights from this exercise. The widespread use of cladistic methods has revealed the existence of new phylogenetic groupings that are conveniently discussed by recourse to new names; however, only recently has it been realized and accepted that the definitions of these taxa should be explicitly node- or stem-based. In the early days of cladistic analysis it appeared to many workers that if the composition of a group changed by phylogenetic re-analysis, the name would also have to change, but this was a mistake of thinking that group names were based on taxonomic composition rather than a statement of common ancestry. As a result, though, we have far more names for the same groups than we need, and priority (understandably) has not always been respected (Padian and May, 1993). As a result, until the phylogeny of theropods (among many other groups) is better resolved, it seems unnecessary to create additional new names and we advocate refraining from naming every new node and stem that may be suggested by the discovery of every new fossil.

A second, and more far-reaching rationale for the previous statement was voiced by many colleagues who discussed and reviewed our initial proposal (Padian et al., 1997) at the SVP meeting in Chicago. That is, because taxa are defined by ancestry, names of taxa advanced for common usage should be tied to explicit and well-corroborated phylogenetic hypotheses. We agree: the number of names related to node-stem triplets that can be constructed from a simple Hennigian comb diagram of ten species is 28, not counting the species names themselves, and every change in the phylogeny will result in at least two new node and stem names as well as the disuse of at least two others. Given the understandable uncertainties of present phylogenies, it seems pointless to name each stem and node.

The names used here have been based in part on Holtz's (1994, 1996a) phylogeny (which was itself based on earlier work) with emendations, many of which were updated in Currie and Padian (1997), because that was the most extensive treatment of nomenclature at the time we began our study. Other more recent phylogenies deal with a subset or a more expanded range of taxa than in Holtz's (1994) work, however, and if some of their groupings are eventually preferred over Holtz's (see Figure 1), some names will fall into disuse by synonymy with previously established names, while others will become more useful. We review some of these below.

Novas (1997) regards *Giganotosaurus* and *Carcharodontosaurus* as closely related to Abelisauridae, a sister taxon to *Ceratosaurus*. If this phylogeny is valid, it does not change major nodes and stems on the cladogram.

Russell and Dong (1994:fig. 16) grouped tyrannosaurids, dromaeosaurids, *Allosaurus*, *Yangchuanosaurus*, and *Baryonyx* into a monophyletic Carnosauria (Fig. 3A). As long as Carnosauria includes *Allosaurus* and all taxa closer to it than to birds (Russell and Dong did not include birds in their analysis), it is valid by our formulation, and the removal of the other components that Russell and Dong included in it would have no effect on its validity. The comparability of some of their names to ours is contingent on where birds fit in their analysis (e.g., with troodontids, dromaeosaurids, or elsewhere).

Sereno's (1997) analysis integrates previous phylogenetic formulations that he has contributed with other authors, and his is the most thorough of all authors in providing explicit defi-

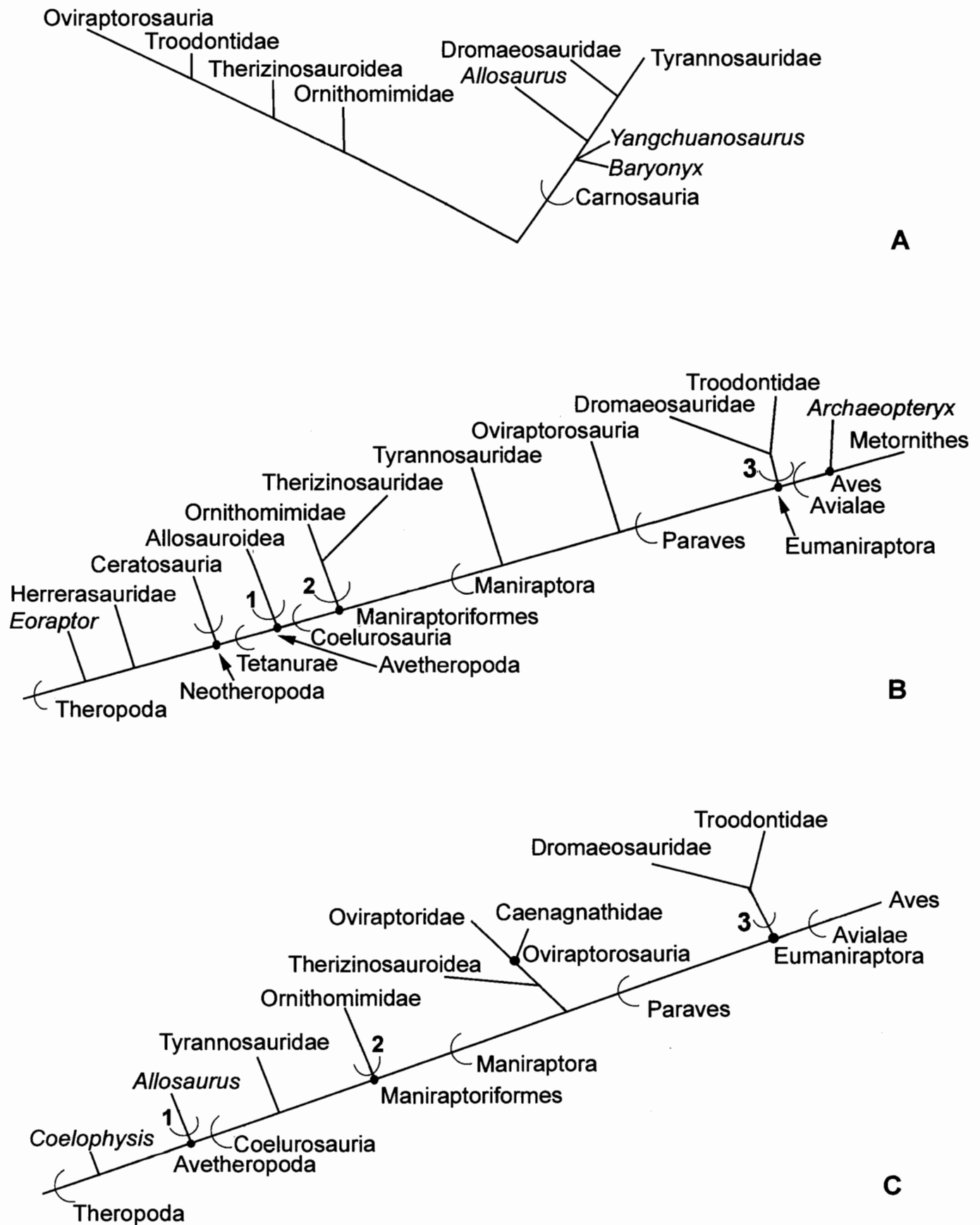


FIGURE 3. Nomenclature suggested here, applied to phylogenies of other authors. **A**, after Russell and Dong (1994). **B**, after Sereni (1997, 1998). **C**, after Sues (1997) and Makovicky and Sues (1998). Numbered stems (1–3) correspond to: 1, Carnosauria; 2, Arctometatarsalia; 3, Deinonychosauria.

nitions for nodes and stems throughout Dinosauria (Fig. 3B). As noted earlier, his use of Neotheropoda is a valid node, regardless of the status of *Eoraptor* and Herrerasauridae. Neotetanurae appears to be a junior objective synonym of Holtz's (1994) Avetheropoda (adapted from Paul, 1988); and Sereno (1997) uses Allosauroidae in the sense of Gauthier's (1986) Carnosauria, which has priority. Sereno's Paraves is a stem-group that contains Deinonychosauria and Aves, and is the sister stem to Oviraptorosauria. In our formulation Maniraptora is a stem, whereas Sereno uses it as a node. As noted above, Holtz (1996b) confirmed that Gauthier (1984, 1986:30, 35) meant it as a stem-taxon. If oviraptorosaurs are accepted as maniraptorans, then Paraves can be a valid stem-taxon within Maniraptora, but the node connecting Paraves and oviraptorosaurs within the stem-group Maniraptora requires a different name than Maniraptora.

Sues (1997) did not explicitly include birds in his phylogeny, though Makovicky and Sues (1998) construct them as the sister group to Deinonychosauria (Dromaeosauridae + Troodontidae) (Fig. 3C). Sues' findings that Troodontidae is the sister taxon to Dromaeosauridae, and Tyrannosauridae is outside Ornithomimidae and other major coelurosaurian groups, would collapse Holtz's (1994) Bullatosauria to Maniraptoriformes, and would reduce the content of the stem Arctometatarsalia to Ornithomimosauria only.

Forster et al. (1998) provided two alternate hypotheses of relationships for some major coelurosaurian groups (Fig. 4). In both, Troodontidae was found to be the sister taxon to Aves, thus bringing Troodontidae to within Maniraptora and Avialae. In one outcome, ornithomimids and oviraptorids formed a trichotomy with dromaeosaurids, troodontids, and Aves; in a second, oviraptorids were closer to this latter group than ornithomimids were. In the second formulation, oviraptorids become maniraptorans. Again, Bullatosauria becomes a redundant term.

The fate of "Tyrannosauroidae" also depends on the phylogeny in question. Following Dong and Russell (1993), it is synonymous with Carnosauria (if birds are closer to troodontids) or Maniraptora (if birds are closer to dromaeosaurids). If the latter case is true in Dong and Russell's phylogeny, tyrannosaurids and dromaeosaurids are coelurosaurs, but oviraptorids, therizinosaurids, troodontids, and ornithomimosaurs are not. In Sues's (1997) phylogeny, assuming a sister-group relationship between Deinonychosauria and Avialae, Tyrannosauroidae is a stem-based name containing only tyrannosaurids as shown (Fig. 3C), just as Arctometatarsalia is a stem-based name containing only ornithomimosaurs. The same is true for the phylogenies expressed by Forster et al. (1998). Following Sereno's (1997) phylogeny, Tyrannosauroidae (*Tyrannosaurus* and everything closer to it than to *Ornithomimus*) is a synonym of Maniraptora (the sister-stem of Arctometatarsalia, which must contain *Ornithomimus*, as noted above). In our view, the definition of "Tyrannosauroidae" and other terms that link tyrannosaurids with other taxa should not be proposed until phylogenetic relationships are better understood. Tyrannosaurids are well diagnosed and their composition is relatively straightforward, but they still are not well defined (Holtz 1994; Sereno 1998) and they probably cannot be until their internal relationships are better understood.

Based on what appear to be consensus conclusions, we propose a "bare-bones" classification of nodes and stems represented in Fig. 5. Names proposed within Ceratosauria (Fig. 1B) will not change, but are not repeated in Fig. 5. In most current phylogenies troodontids and therizinosaurids are minimally regarded as maniraptoriforms and tyrannosaurids as coelurosaurs, but there is enough debate about their precise positions that they cannot be included on a consensus tree at present.

CONCLUSIONS

The nomenclatural scheme proposed above will not solve all potential problems in theropod phylogeny. However, if it is recognized as at least a partial resolution, then further work may recur to it when making decisions about which terms to use for new configurations. An attempt has been made to discriminate between node-based and stem-based taxa, and to provide two sister-taxa that are stem-based for each major node named. The stems in most cases are named for their eponymous genera to avoid confusion. As theropod phylogeny is further resolved, some names may prove congruent with others, and decisions will have to be made based on priority and appropriateness of names. However, in no case should node-based and stem-based names be synonymized: they denote different entities with distinct histories.

NOTE ADDED IN REVISION

The initial development of this manuscript (reflected in Padian et al., 1997 and Currie and Padian, 1997) was done before the publication of Sereno's (1997) review of the Dinosauria, in which he attempted a laudable standardization of some higher category names within Theropoda, arriving at somewhat different results than ours. Our revision of this manuscript was able to incorporate and comment on the findings of his 1997 paper, and in the process of revision he was kind enough to send a copy of his 1998 paper in manuscript, which contains a thorough review of basic taxonomic concepts in the Phylogenetic System. There are further differences between that contribution and ours, which we assess below.

1. Sereno (1998) lists Sauropodomorpha as a node, but Gauthier (1986) used it as a stem with Theropoda as its sister stem-taxon. Saurischia, like Ornithischia, has to be a stem of the node Dinosauria (see Padian and May, 1993; Padian, 1997a). One solution might be to provide a new node name for Prosauropoda + Sauropoda, but this should probably await the continuing discussion about whether Prosauropoda is monophyletic. Oddly enough, with Saurischia and Ornithischia both as stems, there is no node that unites Theropoda + Sauropodomorpha. We suggest "Eusaurischia" for this well-corroborated node. (Von Huene's [1914] "Pachypodosauria" was a group uniting Carnosauria and Sauropodomorpha to the exclusion of Coelurosauria.)
2. Sereno (1998) uses Ceratosauroidae as a stem equivalent to Neoceratosauria, which was proposed as a stem by Holtz (1994) and seems to have priority as well as use by other workers in the literature since then.
3. Abelisaurids sensu lato, as noted in our manuscript, have a great many names of nodes and stems already in the literature, usually based on genera known (or published) on the basis of very partial material. We think caution is in order because this matter is so problematic phylogenetically, but there are already names available that have a different usage than Sereno's (1998; see Bonaparte, 1991; Novas 1991, 1992, 1997). We would prefer to defer the use of higher category names until the material is better described and the phylogeny better understood.
4. Sereno's (1998) Ornithomimosauria is synonymous with Holtz's (1996) Arctometatarsalia in the sense that it includes taxa closer to *Ornithomimus* than to birds. Although Sereno's phylogenetic analysis gives a different content for this stem than Holtz's original phylogeny did, that does not change the definition of the name Arctometatarsalia, which has priority. It is also possible to use Ornithomimosauria as a node uniting Therizinosauridae and Ornithomimidae (i.e., *Erlikosaurus* plus *Ornithomimus* and their common triangle of descendants). This would preserve the important idea that

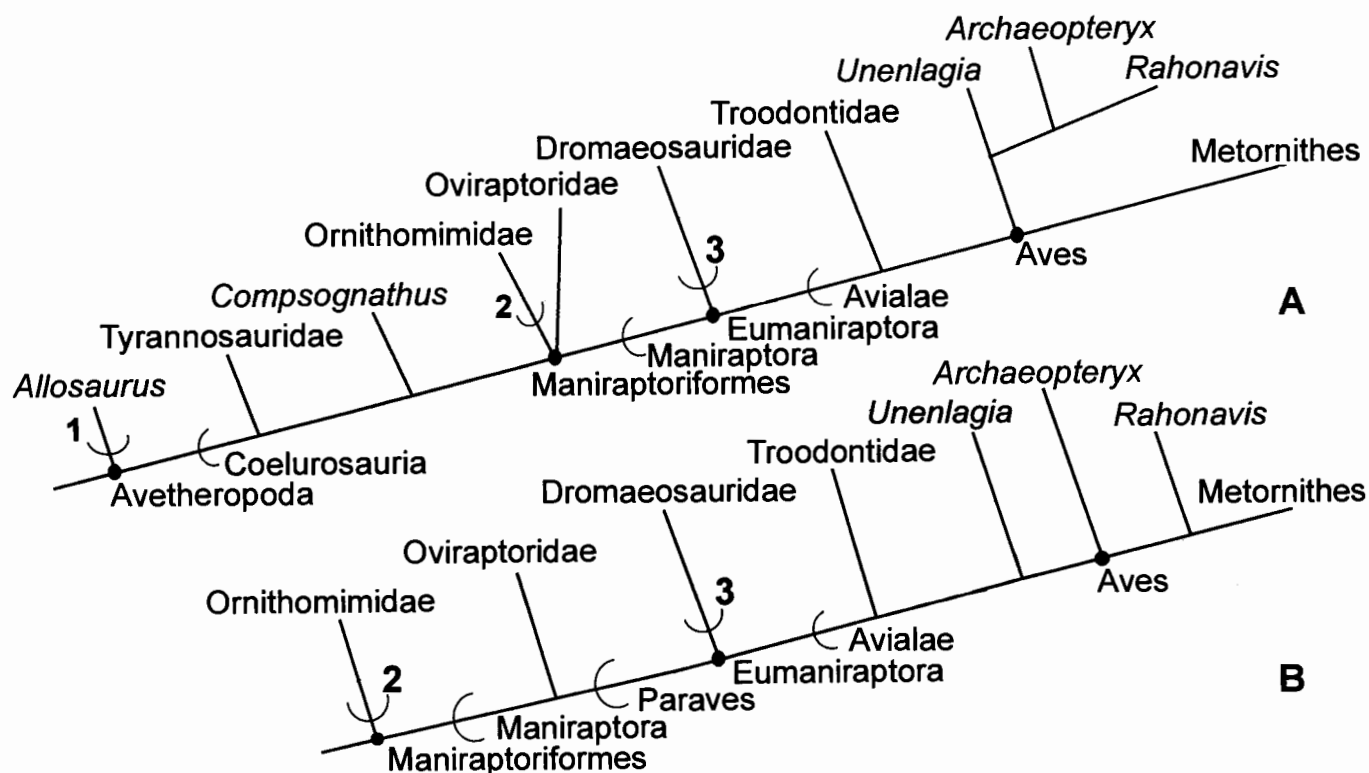


FIGURE 4. Nomenclature suggested here, applied to the phylogenies (Fig. 5A, B respectively) presented in Forster et al. (1998). Numbered stems (1-3) follow Figure 3.

Sereno's phylogenetic result of uniting these groups embodies. Within Sereno's Ornithomimosauria/Arctometatarsalia, there are already some terms in the literature that have been used in a phylogenetic sense of stems and nodes such as Ornithomimosauroida and Therizinosauroida that could be used; we deal with some of these above (see p. 74). Some names require adjustment or precision but they can be conserved and so some sense of priority maintained.

5. It appears that therizinosauroids, tyrannosaurids, and troodontids are going to have mutable phylogenetic positions for

a while, inasmuch as there is some disagreement about where they belong. If and when a single phylogeny is generally accepted, names with earlier priorities could then be retrieved and used. (See our Fig. 5.)

6. Sereno (1998) appears to use Ornithurae as the sister stem-taxon to *Archaeopteryx*, which then by definition is presumably a stem; whereas most other workers, as noted in our paper, accept Martin's (1983; non Gauthier, 1986) use of Ornithurae as *Hesperornis* plus Neornithes and all descendants of their most recent common ancestor. To avoid having

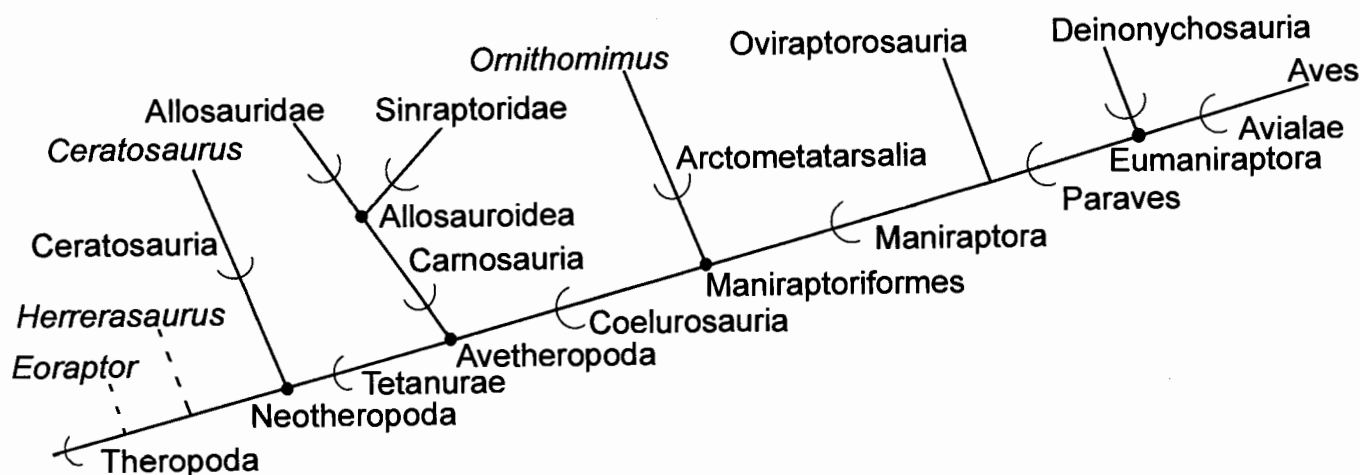


FIGURE 5. Proposed consensus terminology for the major well-situated clades of Theropoda. For consensus terminology of Ceratosauria, see Figure 1B. See text for the positions of troodontids, therizinosauroids, and tyrannosaurs.

Archaeopteryx as a stem-taxon, the term Archaeornithes (in traditional sense, the "subclass" containing *Archaeopteryx*) is available as a stem that could also include new discoveries of birds closer to *Archaeopteryx* than to Neornithes. The complementary stem would then have to be named to include Metornithes (a node).

7. As matters of practice, Sereno in some cases advocates using multiple stem-taxa within a node, and sometimes defines stem taxa as all groups closer to (X) than to any other major taxon. For example, in the first case he suggests a definition of Tyrannosauridae as "all tyrannosauroids closer to *Tyrannosaurus* than to either *Alectrosaurus*, *Aublysodon*, or *Nanotyrannus*," and in the second case he cites a potential definition of Dromornithidae as "all extinct taxa closer to *Dromornis* than to any other ratite." These are both thorny problems of definition that Sereno addresses, and there is no easy solution to them within the philosophically based algorithms of phylogenetic systematics, as he recognizes. In the first case, the interrelationships of taxa within a clade are not well understood because the taxa themselves may be poorly known, and in the second case the closest sister taxon of a morphologically disparate and well diagnosed group is not well established. The first practice has the occasional drawback of promoting instability in some cases, as discussed above (e.g., one of the anchoring taxa may turn out to belong to a different clade). The second practice is inevitably vague in the sense of not being able to anchor a stem taxon to a node or to establish a sister-stem taxon, although until such phylogenies are more robust, it at least provides some idea of constitution.

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