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A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria

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With 9 figures and 4 tables

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Abstract: In traditional Linnaean taxonomy, classifications are constructed and maintained principally as dichotomous hierarchies. In phylogenetic taxonomy, such hierarchies are restricted to monophyletic groups defined explicitly on the basis of common ancestry. A definitional configuration termed a **node-stem triplet** is described that stabilizes the relationship between a given taxon and its subordinate taxa. I outline a rationale within phylogenetic taxonomy for construction of a stable taxonomic framework, as demonstrated by application to the higher-level taxonomy of Dinosauria.

Zusammenfassung: In der traditionellen linneischen Taxonomie werden die Klassifikationen prinzipiell als dichotome Hierarchien erstellt und weitergeführt. In der phylogenetischen Taxonomie sind die Hierarchien dagegen auf monophyletische Gruppen beschränkt, die explizit auf der Basis der gemeinsamen Vorfahrenschaft definiert werden. Um die Verwandtschaft zwischen einem gegebenen Taxon und den ihm untergeordneten Taxa stabil definieren zu können, wird die sogenannte „Knoten-Stamm Triplet"-Konfiguration beschrieben. Diese Konfiguration und Beispiele aus der Taxonomie höherer Gruppen der Dinosaurier werden verwendet, um im Rahmen der phylogenetischen Taxonomie eine Methode zur Konstruktion eines stabilen taxonomischen Rahmens vorzuführen.

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Introduction

The advent of phylogenetic taxonomy has brought into question several taxonomic conventions that were introduced long before evolutionary theory gained currency and taxonomic hierarchies acquired their phylogenetic interpretation (GRIFFITHS 1974, HENNIG 1975, DE QUEIROZ & GAUTHIER 1990, 1992, 1994). In contrast to traditional Linnaean taxa, which are accompanied by formal ranks and character-based definitions, phylogenetic taxa are unranked and delimited on the basis of common ancestry. Taxonomic **definition**, or the delimitation of a clade, is divorced from taxonomic **diagnosis**, which is the characterization of members of a clade based on synapomorphy (GHISELIN 1984, ROWE 1987, DE QUEIROZ & GAUTHIER 1990, 1992).

In phylogenetic taxonomy, two principal kinds of definitions have been described, **node-based** and **stem-based**, the former allied with "crown" groups (taxa bounded by living members with an extinct outgroup) and the latter used for more inclusive clades ("total" groups) that also encompass extinct "stem" taxa (HENNIG 1965, JEFFRIES 1979, 1986, AX 1987, GAUTHIER et al. 1988, DE QUEIROZ & GAUTHIER 1990, 1992).

Despite increasing use of phylogenetic definitions in systematics, no general rationale exists for their application. Are there reasons to prefer node-based or stem-based definitions? And how might these definitional types be employed to stabilize historical usage or taxonomic content?

Traditional (pre-cladistic) taxonomy

The differential diagnosis

In traditional pre-cladistic taxonomy, taxonomic names are defined on the basis of characters that describe members of the taxon, as outlined by architects of "The New Synthesis" (SIMPSON 1961, MAYR 1969). These character-based definitions provided a flexible set of criteria for recognition of members rather than a static list of essential characteristics, as had much earlier been the case with Aristotelian essences. A subset of defining characters, for example, may be sufficient for group membership, so that a taxon exhibiting most or many, but not all, of the defining characters could be included as a member. This flexibility accommodated population variation and evolutionary transformation or loss within lineages of a taxon, so that reduction and loss of limbs in snakes, for example, would not preclude their inclusion within Tetrapoda. In this manner, pre-Darwinian taxonomies adapted to the notion population variation and evolutionary change within taxa, eventually adopting a "cluster concept" for taxonomic definitions (HULL 1974, 1976, GHISELIN 1984, SOBER 1988, DE QUEIROZ & GAUTHIER 1990).

Rather than listing only the derived character-states (synapomorphies) for a particular taxon, the "cluster concept" emerged as a crude, abbreviated phenetic description of the group, with ample allowance for variation, loss, or reversal of "diagnostic" features (DE QUEIROZ & GAUTHIER 1990). Modifiers such as "most," "many" or "typically" often accompany listed features, some of which may actually constitute synapomorphies at lower levels within the group. ROMER's (1956) classification of "reptiles," for example, provides many taxonomic definitions based on the "cluster" model (SERENO 1990). The fundamental role of traditional character-based definitions, which came to be called "differential diagnoses" (MAYR 1969), was to differentiate members of one group from other groups and provide a general description of included members. Traditional differential diagnoses could accommodate paraphyletic, and even polyphyletic, assemblages.

Dichotomous hierarchies

Character-based taxonomic definitions evolved from medieval analytical keys, which evolved from even older hierarchic schemes that used a sequence of features to logically subdivide diversity and create an efficient identification scheme (DARWIN 1859, VOSS 1952, SNEATH & SOKAL 1973, MAYR 1982). The prevalence of dichotomous hierarchies in biological classification, both before and after the ascendance of evolutionary theory, suggests that organismal diversity is most easily understood in contrasting categories arranged in hierarchic order.

Dichotomous hierarchies have been created and maintained in several ways by traditional taxonomists. New, or repositioned, taxa can be absorbed by a traditional dichotomous scheme without changing the rank or relationships of the parent group and its subgroups. The "tidy" subdivision of Dinosauria into Ornithischia and Saurischia, for example, has been maintained over the years by paleontologists who have excluded more distantly related taxa from Dinosauria and allotted newly discovered basal dinosaurs to either Ornithischia or Saurischia.

Raising the rank of a morphologically distinctive or diverse clade and collecting together less diverse "stem" groups into a paraphyletic taxon of equal rank is another common means to reduce complex, or poorly known, branching structure to a simple dichotomous hierarchy ("balancing" taxa; SERENO 1990). These rearrangements of convenience, of course, have no place in a phylogenetic system.

Phylogenetic taxonomy

Definitional structure

Using common ancestry, rather than characters, as the basis for taxonomic definitions is one of several propositions in phylogenetic taxonomy. As outlined by De Queiroz & Gauthier (1990, 1992), node-based and stem-based phylogenetic definitions are constructed by (1) identifying two reference taxa and (2) attaching to them a relational phrase that either includes their most recent common ancestor and all descendants (node-based) or limits inclusion to all descendants closer to one of the reference taxa (stem-based). Thus, "Taxon A, taxon B, their most recent common ancestor and all descendants" is a node-based definition, whereas "All taxa closer to taxon A than to taxon B" is a stem-based definition. Mention of a "common ancestor" and "descendants" is not regarded here as antithetical to phylogenetic systematics or taxonomy; if desired, however, the node-based definition given above can be edited to refer only to "clades" (Lee 1998).

Listing included taxa without a relational phrase about ancestry does not constitute a phylogenetic definition for a taxon, because the boundaries of the clade are not specified (De Queiroz & Gauthier 1990: 309). Gauthier (1986: 11), for example, coined a new taxon "Avialae," mentioning only the included taxa, *Archaeopteryx* and ornithurine birds. Avialae, therefore, has yet to receive a formal phylogenetic definition that specifies whether it is a node- or stem-based taxon. Likewise, the recommendation that a particular taxon, or set of taxa, be associated with a node- or stem-based definition without actually providing that definition also cannot be regarded as sufficient for a formal phylogenetic definition. De Queiroz & Gauthier (1992: 474-475) and Sereno (1997: table 1), for example, presented indented taxonomies of Craniata and Dinosauria, respectively, with guidelines for the inference of node- and stem-based definitions. A formal phylogenetic definition, however, must be provided, so that the intended boundaries (reference taxa) of the taxon are clearly specified.

Other variants of the above formulations for node- and stem-based definitions include (a) the selection of more than two reference taxa and (b) informal reference to "crown" groups (groups bounded by living taxa with extinct outgroups). Gauthier (1986: 14), for example, defined Aves as "all descendants of the most recent common ancestor of Ratitae, Tinami, and Neognathae." Three reference taxa, rather than two, were chosen, ostensibly because the phylogenetic relationships between these three groups of living avians is not resolved with utmost confidence. Listing more than a pair of reference taxa usually does not compromise a phylogenetic definition in any discernible way (Sereno in review b). De Queiroz & Gauthier (1990: 310, 1992: 461) suggest that such definitions should be based on only two reference taxa, although elsewhere in the same paper (De Queiroz & Gauthier 1992: 475) they erect stem-based "total" groups that include the "crown" clade plus "all extinct taxa more closely related to it than to any other crown clade." This phrase presumably excludes subordinate "crown" groups within the "crown" clade under consideration.

"Crown" clades are referenced informally on occasion. Gauthier (1986: 42), for example, defined Archosauria as "all of the descendants of the most recent common ancestor of crocodiles and birds," rather than citing formal "crown" taxa (Crocodylia, Neornithes) or more remote ingroups. The living members of the "crown" group, in this case, are regarded as distinctive on the basis of their survival to the present. The phrase "extant crocodilians" utilizes the extant/extinct status of a taxon as a character, with "extinct" functioning as an irreversible derived state. The most inclusive clade bounded by living taxa defines the "extant" clade. The phrase "extant birds," thus, functions as an informal plesiomorphy-based taxon. The term "extant," however, is somewhat misleading, because "extant birds," for example, must also include many extinct avians located within, or between, traditional avian orders, if it is to constitute a monophyletic, rather than paraphyletic, group. Listing several extant subgroups, as mentioned above, is the preferable alternative for defining a "crown" clade with uncertain basal relationships (Sereno, in review b).

One can also base a phylogenetic definition on the extinct status of a taxon, when outgroup relationships are uncertain. The definition "All extinct taxa closer to *Dromornis* than to any other avian," for example, would define Dromornithidae as the most inclusive clade of extinct birds closely related to the large flightless *Dromornis*, despite the fact that the relationships between dromornithids and other extinct and extant avians are uncertain (Rich 1980). In this case, the "extinct" status of a taxon functions as an irreversible and necessary apomorphy for consideration as a member of the clade – an "extinction criterion," if you will. That phrase has been applied by Lucas (1992) to "crown" clade definitions, although "survivorship criterion" might be more appropriate for the latter.

The utility or necessity of definitions based on the extant or extinct status of taxa is debatable.

Apomorphy-based definitions

Apomorphy-based definitions, although endorsed as a potential definitional style within phylogenetic taxonomy (De Queiroz & Gauthier 1990, 1992), are subject to a number of problems. Consider an apomorphy-based definition for Aves (including *Achaeopteryx* and Ornithurae) based on the presence of "feathers." First, the character coding – "Feathers: absent (0); present (1)" – is only one of several possibilities. A "feather" is a complex, variable structure composed of a rachis, barbs, barbules, and other components. Feathers certainly arose by way of a series of transformations, as recent discoveries are beginning to reveal (Chen et al. 1998), and so it may well be preferable to code these components separately (rather than to assume their correlation).

Second, character-state optimization is often ambiguous. We have little or no data regarding the presence or absence of feathers or their components in taxa immediately outside Aves, such as deinonychosaurian theropods. These taxa may or may not have possessed feathers, and so the placement of the apomorphy on a cladogram and, thus, the boundaries of the apomorphy-based taxon, remain ambiguous.

Finally, homoplasy may result in an ambiguous optimization for a particular apomorphy or in its stable placement at more than one node (Bryant 1994). Formal apomorphy-based definitions, as far as this author is aware, have yet to be implemented in recent phylogenetic studies and should be avoided.

Definitional usage: Absence of a rationale

Despite increasing use of phylogenetic definitions in systematics, a general rationale has yet to be developed for the application of node- and stem-based definitions. Rather, a number of recommendations have been forwarded, all with significant logical or historical shortcomings, and attention, otherwise, has focused on restricting the use of "widely known" names to "crown" taxa and transforming traditional rules governing synonomy and redundancy (e. g., ICZN 1985) to function within a phylogenetic system (De Queiroz & Gauthier 1990, 1992, Brochu 1997). Previous justifications for the use of node- and stem-based definitions are reviewed below.

"Crown" and "total" clades should have node- and stem-based definitions, respectively. A "crown" clade is a taxon bounded by living members with extinct outgroups, and a "total" clade is a "crown" clade plus any extinct outgroups more closely related to it than to another "crown" clade (Jefferies 1979, Hennig 1966, De Queiroz & Gauthier 1990, 1992; Rowe & Gauthier 1992, Bryant 1994, Sereno in review b). A "total" clade, by definition, is stem-based. A "crown" clade, in contrast, need not have a node-based definition to refer to the same group of extant species. Amniota, for example, can be defined as "Any extant tetrapod more closely related to Aves than to Anura." A stem-based definition may be preferable, in fact, if the basal relationships within a "crown" clade (such as Amniota) are poorly established. Given ambiguous or uncertain basal relations, a stem-based definition requires only one ingroup and one distant outgroup to ensure inclusion of all living members, rather than a list of various ingroups with unresolved affinity. Why "crown" taxa should have node-based, rather than equivalent stem-based, definitions has not been clarified. Instead, a superfluous argument has arisen regarding whether "widely used" names, such as Aves, should apply to "crown" versus "total" groups (Norell et al. 1993 versus Patterson 1993).

"Widely," or "universally," used names historically refer to "crown" clades with implicit node-based definitions. For the taxon Mammalia, Rowe & Gauthier (1992: 375-376) state that "its universal usage by comparative biologists, except for some paleontologists, has long been for the crown clade Mammalia, viz., the last common ancestor of Monotremata and Theria, and all of its descendants" and that "Current debate over the name Mammalia highlights the fact that many paleontologists continue to operate in a system influenced in fundamental ways by a pre-Darwinian world view."

Aligning one's preferred usage with that of all "comparative biologists", "neontologists" and, more generally, with the "Darwinian Revolution" (De Queiroz & Gauthier 1990, 1992) draws upon formidable allies. Who, after all, wants to be labeled a "pre-Darwinian"? Yet, Darwin himself was fairly clear regarding what he understood by the terms "Aves," "Mammalia," "Marsupialia," and other groups with living members: for Darwin, these taxa include fossil "stem" groups. In **The Origin**, he wrote (1859: 268), "those groups which have, in known geological periods, undergone much modification, should in the older formations make some slight approach to each other; so that the older members should differ less in some of their characters than do the existing members of the same groups." About mammals, he wrote "They [marsupials] appeared in an earlier geological period, and their range was formerly much more extensive than at present. Hence the Placentata are generally supposed to have been derived from the Implacentata, or Marsupials; not, however, from forms closely resembling the existing Marsupials, but from their early progenitors".

Most extant biologists conceive of the content of Mammalia in a similar fashion, whether they are evolutionary taxonomists, cladists, ecologists, or molecular biologists. In **Chordate Morphology**, Jollie (1973: 76-77) wrote "Many taxonomists are beginning to ask, what is a mammal? An arbitrary line must be drawn across a continuous and overlapping series of species separating mammal from reptile". In **Evolutionary Biology**, Futuyma (1986: 334) wrote "some of the therapsids – the mammal-like reptiles that had arisen in the Permian – approached the mammalian condition so closely that some of them are considered the first mammals." In the most widely used compendium on living mammals, **Mammals of the World**, Walker (1975) clearly included fossil "stem" taxa at all levels within Mammalia.

For most biologists, past or present, higher taxa such as "Mammalia" and "Aves" are associated with "key" characters or sets of such characters – an apomorphy-based definition. A furry, mouse-sized creature with differentiated teeth that lived during the Jurassic will always be considered a "mammal" and, if pressed, allotted to Mammalia by the majority of extant biologists. Likewise, *Archaeopteryx*, with feathers, wings and the capacity for flight, will always be considered a "bird" within Aves. Altering this equation for well established monophyletic taxa will engender greater confusion than encouraging neontologists to use Neornithes or insert an appropriate modifier ("living" or "recent") before Aves, when doing so carries any significance.

Node-based clades maintain the content of the taxon as originally conceived better than stem-based clades. CHIAPPE (1996: 205), for example, has argued that Ornithurae HAECKEL (1866) is better defined as a node-based taxon with Hesperornithiformes and Neornithes as reference taxa than a stem-based definition that includes newly discovered "stem" taxa "because it better reflects the composition of the clade before to [sic] the application of phylogenetic definitions." GAUTHIER (1986: 13), on the other hand, claimed that his stem-based definition of Ornithurae ("Extant birds and all other taxa, such as *Ichthyornis* and Hesperornithes [sic], that are closer to extant birds than is *Archaeopteryx*") was more in keeping with HAECKEL's original intent. Neither definition has historical precedence. The name Ornithurae ("bird tail") was coined for the reduced number of vertebrae and unique coossification (as a pygostyle) that characterizes the tail in all extant birds in contrast to the condition in *Archaeopteryx*. HAECKEL's taxon owes its existence to the then recent discovery of the long-tailed *Archaeopteryx* and predates the description of the extinct short-tailed genera *Ichthyornis* and *Hesperornis*. Ornithurae, as noted by GAUTHIER (1986), has been supplanted by Neornithes (GADOW 1893), a taxon referring to living avians. Based on original intent, an argument could be made that HAECKEL's Ornithurae should supplant Neornithes on grounds of priority, or that it be defined explicitly as an apomorphy-based taxon based on the presence of a pygostyle (now, however, known to be lacking in avians other than *Archaeopteryx*; FORSTER et al. 1998). In both cases, the definition would circumscribe clades other than that identified by CHIAPPE or GAUTHIER. The important point in this connection is that the intent of the original author of historical taxa usually cannot be translated unambiguously into an explicit phylogenetic definition.

Node-based definitions for "crown" taxa enhance stability, informativeness, and accuracy. GAUTHIER (1986:12), for example, states that restricting "Aves" to "living taxa" maximizes "stability and phylogenetic informativeness." In terms of phylogenetic content (see Table 1), however, "crown" groups are no more stable than any other clade. Redefining Mammalia as a "crown" group, for example, does not immediately clarify which **extinct** taxa will be included or excluded. "No one in several centuries has mistakenly assigned a Recent mammal to some other taxon" (ROWE & GAUTHIER 1992:372), not because of some superior attribute of a node-based "crown" definition of Mammalia, but because of the enormous morphologic gap between living mammals and their nearest **living** cousins. If the basal relationships among living taxa within a "crown" group are uncertain, the inclusion of some living subgroups may also be uncertain. Stability of taxonomic content is not related to the living or extinct status of the reference taxa, but rather to the particular choice of reference taxa and, in the case of typical node- based definitions, to the certainty with which the basal dichotomy of the taxon in question has been correctly ascertained (see below).

Justification for reassignment of the taxonomic content of many "widely used" names, such as Aves, seems to reside mainly in the concern that neontologists report their observations accurately, referring only to "crown" clades rather than including extinct "stem" taxa (DE QUEIROZ & GAUTHIER 1992). If one wanted to refer only to the smallest clade including all living birds, for example, "Neornithes" rather than "Aves" would be the appropriate taxon. Neontologists usually insert "Recent" or "living" before the taxon in question when discussing features that are not preserved in fossils, because most adhere to traditional apomorphy-based concepts of higher taxa. Thus, "Recent birds," "living birds," or "extant Aves" are common in the literature when discussing clades bounded by living members. Omitting "Recent" or "living" when such is warranted does not seem to have resulted in unchecked confusion. This distinction between "crown" and "total" groups is arbitrary, in any case, when it involves features that are not preserved in fossils. To suppose that *Archaeopteryx* lacks an apomorphic molecular sequence found in extant birds (Neornithes) is no more justified than to suppose that it was present in the ancient bird. Accelerated character-state transformation, in other words, is not more "correct" or "accurate" than delayed transformation. Likewise, there is nothing more "informative" about "crown" group definitions with regard to phylogeny. These arguments, in any event, do not address whether one should erect a node- or a stem-based definition for a particular group.

Phylogenetic definitions: Rationale

Although two principal kinds of phylogenetic definitions have been clarified, node-based and stem-based, the only discussion regarding their use has involved "crown" and "total" groups. How these definitional structures might aid, more generally, in stabilizing taxonomic content is explored below.

Terminology

The following terminology is introduced to more effectively discuss the structure and arrangement of phylogenetic definitions (Table 1). **Reference taxa** are species or higher taxa that are used to delimit node-based and stem-based phylogenetic definitions. For example, "Taxon A, taxon B, their most recent common ancestor and all descendants" uses A and B as reference taxa to define a node-based taxon.

Phylogenetic definitions are regarded as **complementary** if they utilize the same reference taxa. Thus, the definition "All taxa closer to taxon A than to taxon B" and the definition "Taxon A, taxon B, their most recent common ancestor and all descendants" are complementary. Complementary phylogenetic definitions are also regarded as **reciprocal** if they utilize the same reference taxa in the antipodal positions of a stem-based definition. Thus, the definition "All dinosaurs closer to taxon A than to taxon B" and the definition "All dinosaurs closer to taxon B than to taxon A" are reciprocal.

Table 1. Definitions of terms used in phylogenetic taxonomy.

Term	Definition
Diagnosis	Apomorphies (derived character-states) which identify members of a taxon
Definition	Statement that specifies the taxonomic content of a taxon
Taxonomic content	Existing and potential taxa or individuals that by definition are included within a taxon
Reference taxon	Taxon that serves as a reference in a phylogenetic definition
Node-based taxon	Taxon defined to include a common ancestor (node) and all descendants
Stem-based taxon	Taxon defined to include all descendants closer to one reference descendant taxon than another
Node-stem triplet	Trio of taxa with complementary definitions consisting of a node-based taxon and two subordinate stem-based taxa
Complementary definitions	Phylogenetic definitions that use the same reference taxa (as in a node-stem triplet)
Reciprocal definitions	Phylogenetic definitons that use the same reference taxa but in reverse order (as in opposing stem-based taxa of a node-stem triplet)
Taxonomic equivalence	Statement or equation in which one taxon is equivalent in current and potential taxonomic content to subordinate taxa plus their common ancestor (e. g., A = B + C)

A **node-stem triplet** involves three taxa – a node-based taxon composed of two stem-based subordinate taxa – with complementary definitions (Fig. 1):

> Node: Taxon A, taxon B, their most recent common ancestor and all descendants.
> Stem: All [taxa] closer to taxon A than to taxon B.
> Stem: All [taxa] closer to taxon B than to taxon A.

As an option, reference to the node-based taxon can be inserted (brackets).

Taxonomic content is used here to refer to a statement that includes all existing and potential subordinate taxa included by the phylogenetic definition of a taxon. The smallest number of subordinate taxa that can fulfill this definition of taxonomic content is two; a redundant taxon, that is a single subordinate taxon with an identical phylogenetic definition, is phylogenetically uninformative and has no place in phylogenetic taxonomy. The taxonomic content of taxon C, therefore, could be "Taxon A, taxon B, their most recent common ancestor and all descendants," if taxon A and B are defined to encompass all existing and potential subordinate taxa currently within taxon C.

Taxonomic equivalence is a statement or an equation in which one taxon is shown to be equivalent in current and potential taxonomic content to subordinate taxa plus their common ancestor. A node-stem triplet composed of a node-based taxon (C) and two subordinate stem-based taxa (A, B), for example, can be written as the equivalence statement "C = A + B," because taxon C, by definition, is equivalent to taxon A and B plus their most recent common ancestor.

Reference taxa

Stability of taxonomic content in phylogenetic definitions appears to involve two factors: (1) the phylogenetic distance between the reference taxa and the common ancestor and (2) the effects of the introduction of new taxa. The first is considered in this section and the second in the next.

For a particular phylogenetic definition and pair of reference taxa, taxonomic content can be altered only if an alternative common ancestor is identified. Relocation of a reference taxon on its side of the basal dichotomy does not alter the identification of the common ancestor. Relocation of a reference taxon to the opposing side does. An alternative common ancestor can be identified only if one reference taxon is relocated to the opposite side of the basal dichotomy or outside the basal dichotomy (SERENO, in review b).

For most data sets, a taxon positioned near the basal dichotomy of a cladogram (i. e., near the common ancestor) is easier to relocate to the opposing side (i. e., requires fewer additional steps) than one nested high on one side. Unlike the basal taxon, the nested taxon is held in place by synapomorphies at several nodes, and its phylogenetic distance from the common ancestor is always greater. Thus, stability is generally enhanced in phylogenetic definitions if reference taxa are chosen at some distance (at least several nodes away) from the basal dichotomy.

In current literature, in contrast, the most inclusive reference taxon possible on each side of the basal dichotomy is often chosen for a phylogenetic definition. DE QUEIROZ & GAUTHIER (1992: 475) suggest this pattern of reference taxa for all taxa in their tetrapod classification. SALGADO et al. (1997), to cite an example from the paleontological literature, have chosen Prosauropoda and Sauropoda as reference taxa for Sauropodomorpha (see Figs. 4, 7). Using maximally inclusive reference taxa such as these simply shifts the burden of a more precise definition to less inclusive higher taxa. In the dinosaurian example, it is necessary to determine the definitions for Prosauropoda and Sauropoda to understand more precisely how Sauropodomorpha is defined. SALGADO et al. (1997), however, used Prosauropoda as a terminal taxon, and no definition was given. Sauropoda was defined as a node-based taxon on the basis of two reference taxa, *Vulcanodon* and Eusauropoda (all other sauropods). Thus, if the incompletely known basal sauropod *Vulcanodon* is eventually reinterpreted as more closely related to prosauropods, several taxonomic definitions would be affected. More stable, comprehensible definitions for dinosaurian taxa are established here on the basis of well known, nested reference taxa. Sauropodomorpha is redefined as "*Plateosaurus*, *Saltasaurus*, their most recent common ancestor and all descendants" (Figs. 4, 7; Table 4).

The node-stem triplet

The response of node-based and stem-based definitions to relocation or addition of taxa (which amounts to the same problem) is easy to evaluate. Given taxon A and subordinate taxon B and C (Fig. 1), there are only three resolved positions for relocation or addition of taxa (Fig. 1). If taxon A, B and C have stem-based definitions, the following obtains with introduction of new taxa as shown. Taxon B and C will incorporate an additional taxon with no change in their relationship with the basal dichotomy or with taxon A. When taxon A incorporates a new taxon, however, it is removed from the original basal dichotomy; the taxonomic content of taxon A is no longer taxon B plus taxon C, but rather includes an additional taxon. If taxon A, B and C have node-based definitions, the following obtains with introduction of new taxa as shown. Taxon A remains unaltered because additional taxa are excluded by definition. Taxon B and C, however, are removed from the basal dichotomy; the taxonomic content of taxon A, as a result, is no longer taxon B plus taxon C, but rather includes one or more additional taxa.

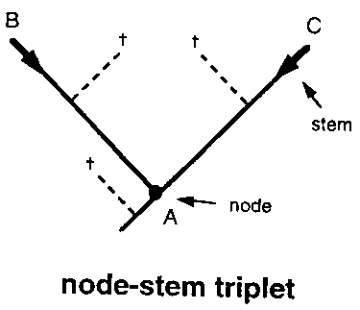


Fig. 1. Phylogenetic/diagram depicting the definitional configuration termed a node-stem triplet, in which a node-based taxon (A, dot) is composed of two subordinate stem-based taxa (B and C, arrows). This definitional triumvirate can incorporate additional or relocated taxa (daggers) without any change in taxonomic content, as expressed by the equivalence statement A = B + C.

There is only one definitional configuration that preserves the taxonomic content of the trio of taxa around a dichotomy – a node-stem triplet (NST). A NST is composed of a node-based taxon and two stem-based subordinate taxa, all three with complementary definitions (the pair of stem-based definitions are reciprocal as well). Addition of taxa around a NST does not alter the definitions of the trio of taxa around the basal dichotomy. Their taxonomic content is stable, as expressed by the equivalence statement A = B + C.

NST's cannot be constructed for adjacent dichotomies on a cladogram. The stem-based subordinate groups of one NST, for example, cannot simultaneously function as the node-based groups of less inclusive NST's. Only a fraction of existing dichotomies in the history of life, however, are labeled with a trio of taxon names. The most significant labeled dichotomies, therefore, can be stabilized in this manner and include those involving balanced diversification, significant morphological transformation, and/or historically associated taxa, as discussed below.

DE QUEIROZ & GAUTHIER (1992: fig. 7) erected a higher classification of tetrapods composed, for the most part, of NST's. This is not readily apparent in their arguments or classification, because they highlighted the association between "crown" clades and their more inclusive "total" clades. Their indented classification highlights this relationship and does not readily show the nested NST's. NST's, nevertheless, are present because all internal node-based "crown" taxa are composed of two subordinate, stem-based "total" taxa. Node-based "Theria," for example, is composed of stem-based "Metatheria" plus "Eutheria." The arrangement of phylogenetic definitions in the classification can be justified on the grounds that it stabilizes taxonomic content within each NST.

Placement Criteria: Diversity, morphology, tradition

Taxon names are applied to organismal diversity as tags for identification and information storage (Farris 1979). Compared to the number of recorded species, relatively few supraspecific names exist for the roughly equal number of branchpoints that map their diversification. These supraspecific taxa have been used by systematists for a limited number of reasons, and their taxonomic content can be stabilized by NST's.

Diversity considerations often figure prominently in the use of higher taxa. Some groups are much more diverse than others, and this difference is often accorded biological significance. On a cladogram, the simplest diversity comparisons are between sister taxa on either side of a dichotomy (Fig. 2A). In this example, several low-diversity taxa are positioned outside a dichotomy with significantly greater diversity on both sides. A diversity-based NST placed at that dichotomy stabilizes the association between taxon names and diversity, despite relocation or addition of taxa near the basal dichotomy.

Morphology plays an important role in the use of higher taxa. Some groups are characterized by more profound morphological transformations than others, and these transformations are often the subject of biological discourse. An uneven distribution of apomorphies is commonplace in phylogenetic studies; a particular node may be separated from outgroups and subordinate taxa by numerous apomorphies (Fig. 2B). A morphology-based NST placed at that dichotomy stabilizes the association between taxon names and morphologic change. The use of node-based definitions for "crown" groups and stem-based definitions for "total" groups (De Queiroz & Gauthier 1990, 1992) often generates a special kind of morphology-based NST, with extinction creating morphologic "gaps" between "crown" groups.

Tradition plays an important role in clade recognition. Some taxonomic names have a long-standing association with a particular dichotomy. Most often this association is based on a "key" character or set of characters and may involve a taxon that is transitional in form (i. e., a "missing link" bounded by morphologic "gaps"). For the past century, for example, "Aves" has been associated with a clade composed of *Archaeopteryx* and Ornithurae, a taxon comprising all birds more advanced than *Archaeopteryx* (Fig. 2C; Table 4). *Archaeopteryx* has been widely recognized as an important transitional form preserving the earliest evidence of feathers and wings, the hallmarks of living birds. Although "feathers" may be optimized, scored or interpreted in different ways by systematists, the general associ-

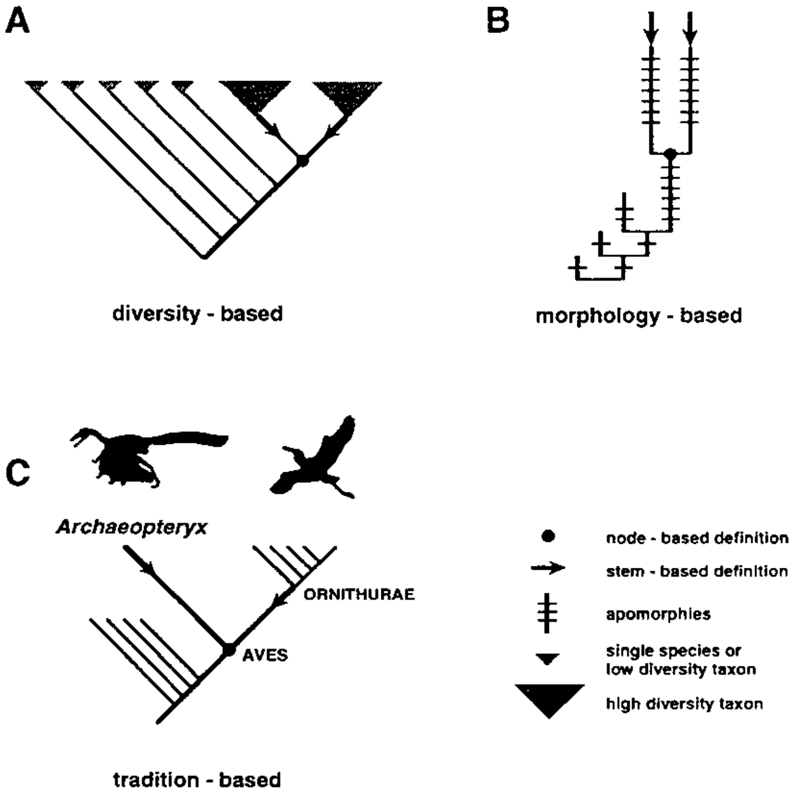
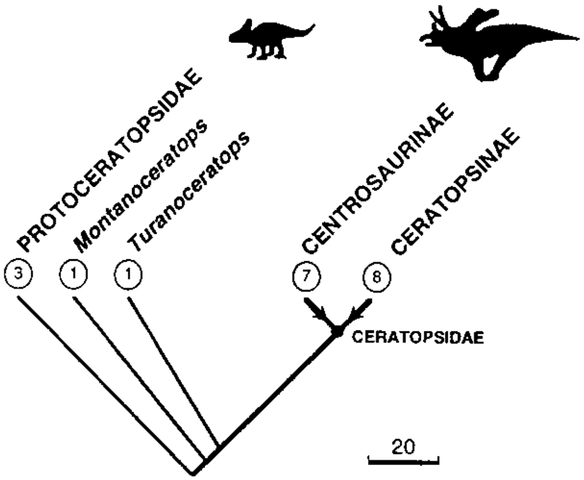


Fig. 2. Phylogenetic diagrams showing the logical basis for stabilizing particular nodes with node-stem triplet (NST) definitions. **A**: diversity-based NST with low-diversity outgroups to a taxon composed of two high-diversity subgroups; **B**: character-based NST with plesiomorphic outgroups to an apomorphic taxon composed of two apomorphic subgroups; **C**: tradition-based NST in which a taxon and its two subgroups have a long historical association.



Ceratopsidae Marsh 1890
Centrosaurinae Lambe 1915
Ceratopsinae (Marsh 1988)

Fig. 3. A node-stem triplet among ceratopsian dinosaurs based on the criteria outlined in Figure 2. Number of genera for each terminal taxon are shown within circles, which highlights ceratopsid diversity as compared to its outgroups. The thickened clade lines are scaled according to the number of synapomorphies that diagnose each clade, which underscores the morphologic distinction of Ceratopsidae and its two subgroups compared to adjacent, more inclusive nodes (scale bar equals 20 apomorphies; SERENO, in press, unpublished data). The indented classification below includes the original authors, revealing a century-long tradition that recognizes Ceratopsidae and its two subgroups, Centrosaurinae and Ceratopsinae (boldface indicates a node-based definition; regular typeface indicates a stem-based definition).

ation between "key" characters and a traditional taxonomic name should be respected, if only to avoid confusion on the part of the majority of biologists. A tradition-based NST placed at the dichotomy between *Archaeopteryx* and Ornithurae stabilizes the longstanding historical interpretation of the taxonomic content of Aves and maintains the proximate association between Aves and apomorphies involving modern feather and wing design.

The three criteria outlined above for placement of NST'S are neither exact nor mutually exclusive. The best case for location of a NST is when these criteria identify the same dichotomy. Among ceratopsian dinosaurs, for example, ceratopsids are significantly more diverse than their nearest outgroups, with at least seven genera in each ceratopsid subgroup (Fig. 3). Morphologically speaking, ceratopsids are easily distinguished from their nearest outgroups by their larger body size and many cranial and postcranial synapomorphies. The subgroups Ceratopsinae and Centrosaurinae are also morphologically distinct and are characterized by more synapomorphies than at adjacent nodes within Ceratopsia (Fig. 3). Finally, Ceratopsidae and its pair of subordinate taxa have been in use for nearly a century.

Conclusions

1. Node- and stem-based definitions require at minimum two reference taxa and a relational phrase regarding membership.

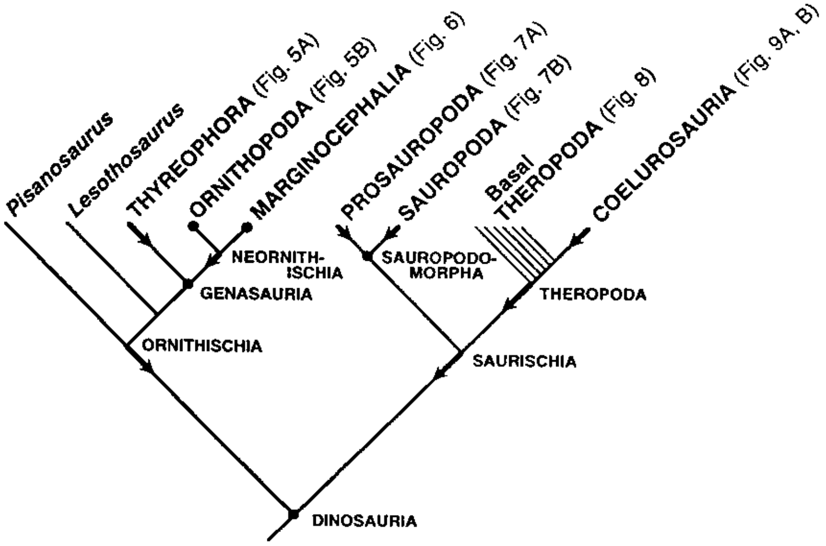


Fig. 4. Phylogenetic diagram for basal groups within Dinosauria showing the distribution of node-based (dot) and stem-based (arrow) taxa (for definitions, see Table 4).

2. Apomorphy-based definitions are fraught with character-related instability and ambiguity and should not be used in phylogenetic taxonomy.
3. "Crown" and "total" clades are recognized on the basis of current survivorship, with living and extinct states functioning as an irreversible character.
4. "Widely used" names for monophyletic groups such as "Aves" are generally understood as apomorphy-based taxa and are best redefined in a manner that does not greatly alter traditional taxonomic content.
5. No general rationale has been forwarded for the application of node- and stem-based definitions in phylogenetic taxonomy.
6. A definitional configuration termed a node-stem triplet stabilize the taxonomic content of a phylogenetic dichotomy.

Table 2. Tabulation of suprageneric taxa within Dinosauria with previous phylogenetic definitions compared to that recommended in Table 4 (and SERENO 1997: table 1). Taxa without asterisks conform in taxonomic content and definitional type with that proposed in the initial phylogenetic definition.
* = alternate definitional type recommended for stability with respect to neighboring taxa
** = alternate node recommended to maintain continuity with historical usage

Taxon	Initial Definition	Present Definition	Initial Author(s)
Saurischia	stem	stem	GAUTHIER 1986
Sauropodomorpha	node	node	SALGADO et al. 1997
Neosauropoda	node	node	SALGADO et al. 1997
Titanosauriformes	node	node	SALGADO et al. 1997
Theropoda	stem	stem	GAUTHIER 1986
Tetanurae	stem	stem	GAUTHIER 1986
Maniraptoriformes	node	node	HOLTZ 1996
Coelurosauria	stem	stem	GAUTHIER 1986
Ornithurae	stem	stem	GAUTHIER 1986
Ornithothoraces	node	node	CHIAPPE 1996
Sauropoda*	node	stem	SALGADO et al. 1997
Eusauropoda*	node	stem	SALGADO et al. 1997
Titanosauria*	node	stem	SALGADO et al. 1997
Saltasaurinae*	node	stem	SALGADO et al. 1997
Maniraptora*	stem	node	GAUTHIER 1986
Aves**	node	node	GAUTHIER 1986

7. Stability of taxonomic content in phylogenetic definitions is also enhanced by choosing reference taxa remote from the common ancestor.
8. Diversity, morphology, and tradition constitute the principal criteria for placement of node-stem triplets.

Appendix

Twenty-six node-stem triplets (NST's) are established within Dinosauria utilizing well known, deeply nested, reference taxa (Table 3) to provide a stable framework for dinosaurian taxonomy (Figs. 4-9; Table 4). Only the most basal clades within Aves are considered. These NST's are positioned within the taxonomic hierarchy based on considerations of diversity, morphology and tradition (Fig. 2). Several higher taxa within Dinosauria already have been assigned explicit phylogenetic definitions (Table 2). As much as possible, the definitions proposed here (Table 4) accommodate these previous definitions (Table 3).

Dinosauria: Antipodal reference taxa

The genus *Triceratops* and the higher taxon Neornithes (living birds) were chosen as antipodal reference taxa for phylogenetic definitions within Dinosauria, given their deeply nested position within Ornithischia and Saurischia, respectively. A hadrosaurid genus could have served equally well in place of *Triceratops*, given the equally deeply nested position of hadrosaurids within Ornithischia. Among saurischians, living birds (Neornithes) comprise a distant and convenient reference taxon, here defined phylogenetically as *Struthio* (ostrich), *Passer* (sparrow), their common ancestor and all descendants. The reference taxa for all 26 NST's are given in Table 3.

Dinosauria: Basal node-stem triplet

SEELEY (1888) divided OWEN's (1842) Dinosauria into two groups, Ornithischia and Saurischia, which he believed had evolved independently. This subdivision gained currency nearly a century ago (HUENE 1914), although it was not until the advent of cladistics that the monophyly of Dinosauria, Ornithischia, and Saurischia was established (BAKKER & GALTON 1974, GAUTHIER 1986, SERENO et al. 1993, NOVAS 1993). A tradition-based NST (Dinosauria = Ornithischia + Saurischia) recognizes and stabilizes this historical subdivision (Fig. 4). This NST also acknowledges the great diversity of ornithischians and saurischians, as opposed to immediate dinosaurian outgroups, and the greater number of synapomorphies that unite these clades, as opposed to immediate outgroup nodes. This basal dinosaurian NST, therefore, is supported by all three criteria (diversity, morphology, tradition; Fig. 2).

Table 3. Reference taxa for phylogenetic definitions within Dinosauria, exclusive of Neornithes (living birds). The node-based taxon of each of the 26 node-stem triplets recognized here within Dinosauria are given with the corresponding reference taxa. For the node-based taxon Maniraptoriformes (asterisk), only one of the two stem-based subordinate taxa has been named (Ornithomimosauria).

Node	Reference Taxa
Dinosauria	*Neornithes, Triceratops*
Genasauria	*Ankylosaurus, Triceratops*
Eurypoda	*Ankylosaurus, Stegosaurus*
Ornithopoda	*Heterodontosaurus, Parasaurolophus*
Ankylopollexia	*Camptosaurus, Parasaurolophus*
Hadrosauriformes	*Iguanodon, Parasaurolophus*
Hadrosauridae	*Saurolophus, Parasaurolophus*
Marginocephalia	*Pachycephalosaurus, Triceratops*
Pachycephalosauridae	*Stegoceras, Pachycephalosaurus*
Coronosauria	*Protoceratops, Triceratops*
Ceratopsidae	*Pachyrhinosaurus, Triceratops*
Sauropodomorpha	*Plateosaurus, Saltasaurus*
Plateosauria	*Plateosaurus, Massospondylus*
Neosauropoda	*Diplodocus, Saltasaurus*
Titanosauriformes	*Brachiosaurus, Saltasaurus*
Saltasauridae	*Opisthocoelicaudia, Saltasaurus*
Neotheropoda	*Coelophysis, Neornithes*
Abelisauridae	*Abelisaurus, Carnotaurus*
Coelophysidae	*Coelophysis, Procompsognathus*
Spinosauroidea	*Spinosaurus, Torvosaurus*
Neotetanurae	*Allosaurus, Neornithes*
Maniraptoriformes*	*Ornithomimus, Neornithes*
Maniraptora	*Oviraptor, Neornithes*
Deinonychosauria	*Troodon, Velociraptor*
Aves	*Archaeopteryx, Neornithes*
Ornithothoraces	*Sinornis, Neornithes*

Ornithischia

Within Ornithischia, two genera have been recognized as outgroups to remaining ornithischians. The more primitive, *Pisanosaurus* (Bonaparte 1976, Sereno 1991, 1997), demonstrates that the majority of ornithischian synapomorphies were already in place; *Lesothosaurus*, the more derived and complete of the two, is linked with later ornithischians by only a few features. The most inclusive NST within Ornithischia is best positioned after the divergence of these basal genera. A diversity-based

Table 4. Indented taxonomic hierarchy and phylogenetic definitions for Dinosauria exclusive of Neornithes (living birds). Boldface indicates node-based definitions, and regular typeface indicates stem-based definitions. Parentheses indicate the original author of the family group and are followed by the author that recognized a new rank within the group. All are listed in the literature citations.

Taxonomic Hierarchy	Definition
Dinosauria Owen 1842	*Triceratops*, Neornithes, their most recent common ancestor and all descendants.
Ornithischia Seeley 1888	All dinosaurs closer to *Triceratops* than to Neornithes.
Genasauria Sereno 1986	*Ankylosaurus, Triceratops*, their most recent common ancestor and all descendants.
Thyreophora Nopcsa 1915	All genasaurs closer to *Ankylosaurus* than to *Triceratops*.
Eurypoda Sereno 1986	*Stegosaurus, Ankylosaurus*, their most recent common ancestor and all descendants.
Stegosauria Marsh 1877	All eurypods closer to *Stegosaurus* than to *Ankylosaurus*.
Stegosauridae Marsh 1880	All stegosaurs closer to *Stegosaurus* than to *Huayangosaurus*.
Stegosauruinae (Marsh 1880) Abel 1919	All stegosaurids closer to *Stegosaurus* than to *Dacentrurus*.
Ankylosauria Osborn 1923	All eurypods closer to *Ankylosaurus* than to *Stegosaurus*.
Ankylosauridae Brown 1908	All ankylosaurs closer to *Ankylosaurus* than to *Panoplosaurus*.
Ankylosaurinae (Brown 1908) Nopcsa 1918	All ankylosaurids closer to *Ankylosaurus* than to either *Shamosaurus* or *Minmi*.
Nodosauridae Marsh 1890	All ankylosaurs closer to *Panoplosaurus* than to *Ankylosaurus*.
Nodosaurinae (Marsh 1890) Abel 1919	All nodosaurids closer to *Panoplosaurus* than to either *Sarcolestes* or *Hylaeosaurus*.
Neornithischia Cooper 1985	All genasaurs closer to *Triceratops* than to *Ankylosaurus*.
Ornithopoda Marsh 1881	*Heterodontosaurus, Parasaurolophus*, their most recent common ancestor and all descendants.
Heterodontosauridae Romer 1966	All ornithopods closer to *Heterodontosaurus* than to *Parasaurolophus*.
Euornithopoda Sereno 1986	All ornithopods clsoer to *Parasaurolophus* than to *Heterodontosaurus*.
Hypsilophodontidae Dollo 1882	All euornithopods closer to *Hypsilophodon* than to *Parasaurolophus*.
Iguanodontia Dollo 1888	All euornithopods closer to *Parasaurolophus* than to *Hypsilophodon*.
Dryosauridae Milner & Norman 1984	All iguanodontians closer to *Dryosaurus* than tho *Parasaurolophus*.

Table 4 (cont.)

Ankylopollexia Sereno 1986	*Camptosaurus*, *Parasaurolophus*, their most recent common ancestor and all descendants
Camptosauridae Marsh 1885	All ankylopollexians closer to *Camptosaurus* than to *Parasaurolophus*.
Styracosterna Sereno 1986	All ankylopollexians closer to *Parasaurolophus* than to *Camptosaurus*.
Hadrosauriformes Sereno 1997	*Iguanodon*, *Parasaurolophus*, their most recent common ancestor and all descendants.
Iguanodontidae Cope 1869	All hadrosauriforms closer to *Iguanodon* than to *Parasaurolophus*.
Hadrosauroidea (Cope 1869) Sereno 1986	All hadrosauriforms closer to *Parasaurolophus* than to *Iguanodon*.
Hadrosauridae Cope 1869	*Saurolophus*, *Parasaurolophus*, their most recent common ancestor and all descendants.
Hadrosaurinae (Cope 1869) Lambe 1918	All hadrosaurids closer to *Saurolophus* than to *Parasaurolophus*.
Lambeosaurinae Parks 1923	All hadrosaurids closer to *Parasaurolophus* than to *Saurolophus*.
Marginocephalia Sereno 1986	*Pachycephalosaurus*, *Triceratops*, their most recent common ancestor and all descendants.
Pachycephalosauria Maryanska & Osmolska 1974	All marginocephalians closer to *Pachycephalosaurus* than to *Triceratops*.
Pachycephalosauridae Sternberg 1945	*Stegoceras*, *Pachycephalosaurus*, their most recent common ancestor and all descendants.
Stegoceras Lambe 1902	All pachycephalosaurids closer to *Stegoceras validus* than to *Pachycephalosaurus*.
Pachycephalosaurinae (Sternberg 1945) new taxon	All pachycephalosaurids closer to *Pachycephalosaurus* than to *Stegoceras*.
Ceratopsia Marsh 1890	All marginocephalians closer to *Triceratops* than to *Pachycephalosaurus*.
Neoceratopsia Sereno 1986	All ceratopsians closer to *Triceratops* than to *Psittacosaurus*.
Coronosauria Sereno 1986	*Protoceratops*, *Triceratops*, their most recent common ancestor and all descendants.
Protoceratopsidae Granger & Gregory 1923	All coronosaurs closer to *Protoceratops* than to *Triceratops*.
Ceratopsoidea (Marsh 1888) Hay 1902	All coronosaurs closer to *Triceratops* than to *Protocertops*.
Ceratopsidae Marsh 1888	*Pachyrhinosaurus*, *Triceratops*, their most recent common ancestor and all descendants.
Centrosaurinae Lambe 1915	All ceratopsids closer to *Pachyrhinosaurus* than to *Tricertops*.
Ceratopsinae (Marsh 1888) Abel 1919	All ceratopsids closer to *Triceratops* than to *Pachyrhinosaurus*.

Table 4 (cont.)

Saurischia Seeley 1888	All dinosaurs closer to Neornithes than to *Triceratops*.
Sauropodomorpha Huene 1932	*Plateosaurus*, *Saltasaurus*, their most recent common ancestor and all descendants.
Prosauropoda Huene 1920	All sauropodomorphs closer to *Plateosaurus* than to *Saltasaurus*.
Plateosauria Tornier 1913	*Plateosaurus*, *Massospondylus*, their most recent common ancestor and all descendants.
Plateosauridae Marsh 1895	All plateosaurs closer to *Plateosaurus* than to *Massospondylus*.
Massospondylidae Huene 1914	All plateosaurs closer to *Massospondylus* than to *Plateosaurus*.
Sauropoda Marsh 1878	All sauropodomorphs closer to *Saltasaurus* than to *Plateosaurus*.
Eusauropoda Upchurch 1995	All sauropods closer to *Saltasaurus* than to *Vulcanodon*.
Neosauropoda Bonaparte 1986	*Diplodocus*, *Saltasaurus*, their most recent common ancestor and all decendants.
Diplodocoidea (Marsh 1884) Upchurch 1995	All neosauropods closer to *Diplodocus* than to *Saltasaurus*.
Dicraeosauridae (Janensch 1929) Huene 1956	All diplodocoids closer to *Dicraeosaurus* than to *Diplodocus*.
Diplodocidae Marsh 1884	All diplodocoids closer to *Diplodocus* than to *Dicraeosaurus*.
Macronaria Wilson & Sereno 1998	All neosauropods closer to *Saltasaurus* than to *Diplodocus*.
Titanosauriformes Salgado et al. 1997	*Brachiosaurus*, *Saltasaurus*, their most recent common ancestor and all descendants.
Brachiosauridae Riggs 1904	All titanosauriforms closer to *Brachiosaurus* than to *Saltasaurus*.
Somphospondyli Wilson & Sereno 1998	All titanosauriforms closer to *Saltasaurus* than to *Brachiosaurus*.
Titanosauria Bonaparte & Coria 1993	All somphospondyls closer to *Saltasaurus* than to *Euhelopus*.
Saltasauridae (Powell 1992) new taxon	*Opisthocoelicaudia*, *Saltasaurus*, their most recent ancestor and all descendants.
Saltasaurinae Powell 1992	All saltasaurids closer to *Saltasaurus* than to *Opisthocoelicaudia*.
Opisthocoelicaudinae new taxon	All saltasaurids closer to *Opisthocoelicaudia* than to *Saltasaurus*.

Table 4 (cont.)

Theropoda MARSH 1881	All saurischians closer to Neornithes than to *Saltasaurus*.
Herrerasauridae BENEDETTO 1973	All theropods closer to *Herrerasaurus* than to Neornithes.
Neotheropoda BAKKER 1986	*Coelophysis*, Neornithes, their most recent common ancestor and all descendants.
Ceratosauria MARSH 1884	All neotheropods closer to *Coelophysis* than to Neornithes.
Ceratosauroidea (MARSH 1884) BONAPARTE et al. 1990	All ceratosaurs closer to *Carnotaurus* than to *Coelophysis*.
Abelisauridae BONAPARTE & NOVAS 1985	*Abelisaurus*, *Carnotaurus*, their most recent common ancestor and all descendants.
Abelisaurinae (BONAPARTE & NOVAS 1985) new taxon	All abelisaurids closer to *Abelisaurus* than to *Carnotaurus*.
Carnotaurinae new taxon	All abelisaurids closer to *Carnotaurus* than to *Abelisaurus*.
Coelophysoidea (NOPCSA 1928) HOLTZ 1994	All ceratosaurs closer to *Coelophysis* than to *Carnotaurus*.
Coelophysidae (NOPCSA 1928) PAUL 1988	*Coelophysis*, *Procompsognathus*, their most recent common ancestor and all descendants.
Coelophysinae NOPCSA 1928	All coelophysis closer to *Coelophysis* than to *Procompsognathus*.
Procompsognathinae (HUENE 1929) NOPCSA 1923	All coelophysids closer to *Procompsognathus* than to *Coelophysis*.
Tetanurae GAUTHIER 1986	All neotheropods closer to Neornithes than to *Torvosaurus*.
Spinosauroidea (STROMER 1915) OLSHEVSKY 1995	*Spinosaurus*, *Torvosaurus*, their most recent common ancestor and all descendants.
Torvosauridae JENSEN 1985	All spinosauroids closer to *Torvosaurus* than to *Spinosaurus*.
Spinosauridae STROMER 1915	All spinosauroids closer to *Spinosaurus* than to *Torvosaurus*.
Neotetanurae SERENO et al. 1994	*Allosaurus*, Neornithes, their most recent common ancestor and all descendants.
Allosauroidea (MARSH 1878) CURRIE & ZHAO 1993	All neotetanurans closer to *Allosaurus* than to Neornithes.
Allosauridae MARSH 1878	All allosauroids closer to *Allosaurus* than to either *Sinraptor*, *Monolophosaurus*, *Cryolophosaurus* or *Carcharodontosaurus*.
Sinraptoridae CURRIE & ZHAO 1993	All allosauroids closer to *Sinraptor* than to either *Allosaurus*, *Monolophosaurus*, *Cryolophosaurus* or *Carcharodontosaurus*.
Carcharodontosauridae STROMER 1931	All allosauroids closer to *Carcharodontosaurus* than to either *Allosaurus*, *Monolophosaurus*, *Cryolophosaurus* or *Sinraptor*.
Coelurosauria HUENE 1914	All neotetanurans closer to Neornithes than to *Allosaurus*.

Table 4 (cont.)

Maniraptoriformes HOLTZ 1996	*Ornithomimus*, Neornithes, their most recent common ancestor and all descendants.
Ornithomimosauria BARSBOLD 1976b	All maniraptoriforms closer to *Ornithomimus* than to Neornithes.
Therizinosauridae MALEEV 1954	All ornithomimosaurs closer to *Erlikosaurus* than to *Ornithomimus*.
Ornithomimidae MARSH 1890	All ornithomimosaurs closer to *Ornithomimus* than to *Erlikosaurus*.
Ornithomiminae (MARSH 1890) NOPCSA 1923	All ornithomimids closer to *Ornithomimus* than to either *Pelicanimimus* or *Harpymimus*.
Tyrannosauroidea (OSBORN 1905) BONAPARTE et al. 1990	All maniraptoriforms closer to *Tyrannosaurus* than to Neornithes.
Tyrannosauridae OSBORN 1905	All tyrannosauroids closer to *Tyrannosaurus* than to either *Alectrosaurus*, *Aublysodon*, or *Nanotyrannus*.
Tyrannosaurinae (OSBORN 1905) MATTHEW & BROWN 1922	All tyrannosaurids closer to *Tyrannosaurus* than to either *Albertosaurus*, *Daspletosaurus*, or *Gorgosaurus*.
Maniraptora GAUTHIER 1986	*Oviraptor*, Neornithes, their most recent common ancestor and all descendants.
Oviraptorosauria BARSBOLD 1976a	All maniraptorans closer to *Oviraptor* than to Neornithes.
Caenagnathidae STERNBERG 1940	All oviraptorosaurs closer to *Caenagnathus* than to *Oviraptor*.
Oviraptoridae BARSBOLD 1976a	All oviraptorosaurs closer to *Oviraptor* than to *Caenagnathus*.
Paraves SERENO 1997	All maniraptorans closer to Neornithes than to *Oviraptor*.
Deinonychosauria COLBERT & RUSSELL 1969	*Troodon*, *Velociraptor*, their most recent common ancestor and all descendants.
Troodontidae GILMORE 1924	All deinonychosaurs closer to *Troodon* than to *Velociraptor*.
Dromaeosauridae (MATTHEW & BROWN 1922) RUSSELL 1969	All deinonychosaurs closer to *Velociraptor* than to *Troodon*.
Dromaeosaurinae MATTHEW & BROWN 1922	All dromaeosaurids closer to *Dromaeosaurus* than to *Velociraptor*.
Velociraptorinae BARSBOLD 1978	All dromaeosaurids closer to *Velociraptor* than to *Dromaeosaurus*.
Aves LINNE 1758	*Archaeopteryx*, Neornithes, their most recent common ancestor and all descendants.
Archaeopteryx MEYER 1861	All avians closer to *Archaeopteryx lithographica* than to Neornithes.
Ornithurae HAECKEL 1866	All avians closer to Neornithes than to *Archaeopteryx*.
Ornithothoraces CHIAPPE & CALVO 1994	*Sinornis*, Neornithes, their most recent common ancestor and all descendants.
Enantiornithes WALKER 1981	All ornithothoracines closer to *Sinornis* than to Neornithes.
Euornithes new taxon	All ornithothoracines closer to Neornithes than to *Sinornis*.

NST (Genasauria = Thyreophora + Neornithischia) is recognized for Genasauria and its diverse subgroups. Thyreophora and Neornithischia, each with more than 40 genera (Fig. 4). Thyreophora (Nopcsa 1915) has long been used to unite armored ornithischians, although there are few additional synapomorphies for the group. Neornithischia (= Cerapoda) includes all remaining ornithischians and is united by more synapomorphies (Neornithischia Cooper 1985 was coined to unite some of these derived ornithischians and predates Cerapoda Sereno 1986). Diversity considerations, however, provide the principal support for this NST.

Two NST's stabilize taxonomic content among traditional ornithischian suborders. Ornithopods are defined to include the distinctive subgroup Heterodontosauridae and its diverse sister taxon Euornithopoda (sensu Weishampel 1990) (Ornithopoda = Heterodontosauridae + Euornithopoda; Fig. 5B). Marginocephalians are defined as a combination of the diverse and distinct clades Pachycephalosauria and Ceratopsia (Marginocephalia = Pachycephalosauria + Ceratopsia) (Fig. 6). If defined in this manner 40 years ago on the basis of taxa known at that time, these NST's would have absorbed all neornithischians described or repositioned since, without any change in taxonomic content as expressed in the equivalence statements above.

Thyreophora

Three genera (*Scutellosaurus*, *Emausaurus*, *Scelidosaurus*) comprise much of what is known about basal thyreophorans and are positioned as successive outgroups to Eurypoda (Fig. 5A). None of these most inclusive clades within Thyreophora warrant special recognition on the basis of diversity, morphology, or traditional nomenclature. Nearly all armored ornithischians belong to the broad-footed clade Eurypoda, which is composed of two clades, Stegosauria and Ankylosauria (Fig. 5A). A NST involving these taxa recognizes their diversity and distinctive form, as shown by the significant number of synapomorphies that unite each clade (Eurypoda = Stegosauria + Ankylosauria). *Stegosaurus* and *Ankylosaurus*, well known and deeply nested genera, constitute the antipodal reference taxa for Thyreophora (Table 3).

Among stegosaurs, *Huayangosaurus* and *Dacentrurus* are positioned as successive outgroups to more derived stegosaurs (Sereno & Dong 1992). Stegosauridae and Stegosaurinae are defined as stem-based taxa, the former including *Dacentrurus* and the latter restricted to more derived stegosaurs (Fig. 5A, Table 4). Stegosaurines include *Stegosaurus* and seven additional genera, but their incompleteness precludes further reliable phylogenetic resolution. The synapomorphies that unite Stegosauridae and Stegosaurinae comprise what little is currently known about stegosaurian phylogeny. A NST within Stegosauria is not warranted based on current patterns of diversity, morphology or traditional nomenclature.

Fig. 5. Phylogenetic diagram for Thyreophora (**A**) and Ornithopoda (**B**) showing the distribution of node-based (dot) and stem-based (arrow) taxa (for definitions, see Table 4).

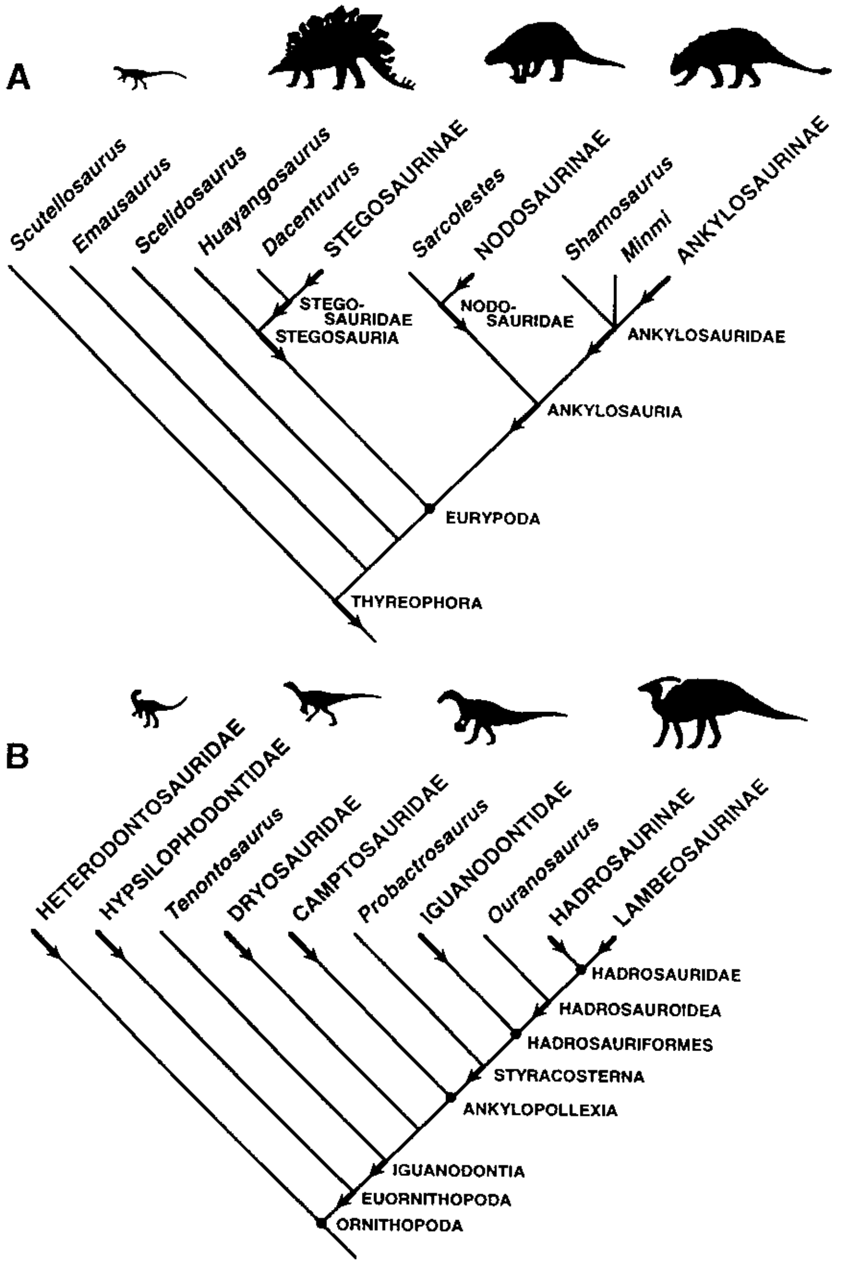


Fig. 5 (Legend see p. 66)

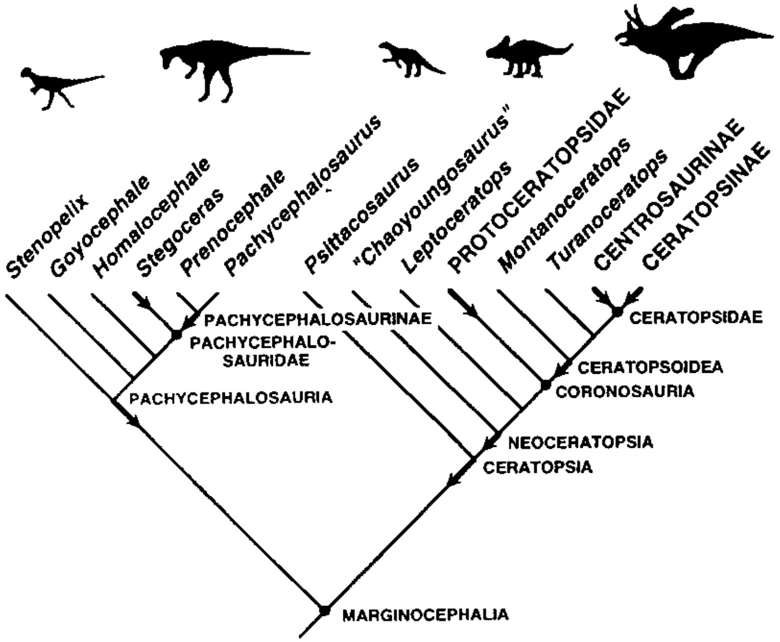


Fig. 6. Phylogenetic diagram for Marginocephalia showing the distribution of node-based (dot) and stem-based (arrow) taxa (for definitions, see Table 4).

Among ankylosaurs, two equally diverse subgroups have long been recognized, Nodosauridae and Ankylosauridae, each of which are characterized by numerous synapomorphies (SERENO 1986, 1997, COOMBS & MARYANSKA 1990). The obvious position for a NST within Ankylosauria would be at the base of the clade, with stem-based definitions for Nodosauridae and Ankylosauridae. Ankylosauria, however, was defined above as a stem-based taxon of a more basal NST (Eurypoda = Stegosauria + Ankylosauria). The eurypod NST, arguably, is the more useful of the two; recent discovery of a basal ankylosaur (*Mymoorapelta*; KIRKLAND & CARPENTER 1994), in this regard, will reduce significantly the number of synapomorphies that currently diagnose Ankylosauridae or Ankylosauria (depending on its phylogenetic position). Stem-based definitions for Nodosauridae and Ankylosauridae stabilize these taxa as they are currently understood and leave open the possibility of erecting a NST in the future within Ankylosauria (Fig. 5A). Within Nodosauridae and Ankylosauridae, several genera have been described (*Sarcolestes* and *Hylaeosaurus* among nodosaurids; *Shamosaurus* and *Minmi* among ankylosaurids) that lie outside the more derived subgroups, Nodosaurinae and Ankylosaurinae. Stem-based definitions for Nodosaurinae and Ankylosaurinae effectively encompass the more derived genera without requiring ingroup resolution.

Ornithopoda

Within Ornithopoda, a series of relatively low-diversity taxa constitute successive outgroups to Hadrosauridae (Fig. 5B), with successive nodes supported by approximately the same number of synapomorphies (SERENO 1997). Iguanodontia is not a particularly effective location for a NST, given the unresolved relationships between the basal genera *Tenontosaurus* (FORSTER 1990), *Muttaburrasaurus* (MOLNAR 1996), and other iguanodontians (SERENO 1986, 1997). Although better resolved, other nodes closer to hadrosaurids are difficult to distinguish on the basis of diversity, morphology and tradition; all involve low-diversity "stem" taxa, roughly the same number of synapomorphies, and taxonomic names with little or no historical usage (SERENO 1986, 1997). Traditionally, these "stem" groups were gathered to compose a paraphyletic "Iguanodontidae."

Two NST's are situated among nonhadrosaurid iguanodontians largely on the basis of well known apomorphies. Ankylopollexia and its subgroups (Ankylopollexia = Camptosauridae + Styracosterna) were chosen because two of the three taxa exhibit striking apomorphies that have been subject to extended comment in the literature (Fig. 5B). Ankylopollexians evolved tooth-supported dentitions and hands that bear a unique thumb spike; styracosternans have sternal bones with an elongate ventrolateral process, a bound metacarpus, and hoof-shaped unguals. Likewise, Hadrosauriformes and its subgroups (Hadrosauriformes = Iguanodontidae + Hadrosauroidea) are defined as a NST because of notable features of hadrosauriforms (enlarged external nares, lattice pattern of ossified tendons) and, particularly, hadrosauroids (duck-shaped bill, loss of manual digit I). The taxa involved in these NST's, it should be underscored, do not have apomorphy-based definitions (Table 4). They are node- and stem-based taxa that function as an aid in discourse on the evolution and adaptations of advanced iguanodontians. They are not strongly supported by the standard criteria of diversity, morphology and tradition, because Camptosauridae is a low-diversity taxon compared to Styracosterna; because the number of synapomorphies distinguishing these clades is not discordantly greater than at adjacent nodes; and because the higher taxa involved have little historical usage.

Hadrosaurids present the clearest case for a NST based on diversity, morphology and tradition (Fig. 5B). The two hadrosaurid subgroups, Hadrosaurinae and Lambeosaurinae, are considerably more diverse than immediate hadrosaurid outgroups; two of the clades (Hadrosauridae, Lambeosaurinae) are united by many synapomorphies; and, with some variation, these taxonomic names have achieved broad usage. Certain genera formally regarded as hadrosaurids (WEISHAMPEL et al. 1993, HEAD 1996, FORSTER 1997) may lie outside Hadrosauridae, when this taxon is defined on the nested reference genera *Saurolophus* and *Parasaurolophus* (Tables 3, 4).

Marginocephalia

Within Pachycephalosauria, one NST is identified (Pachycephalosauridae = *Stegoceras* + Pachycephalosaurinae) (Fig. 6). With this NST, domed species (pachycephalosaurids) are distinguished from basal genera that retain the flat-headed condition (whether or not these flat-headed forms constitute a monophyletic clade); fully-domed forms (pachycephalosaurines) are distinguished from all other pachycephalosaurs; and the well known genera *Stegoceras* and *Pachycephalosaurus* function as reference taxa (Tables 3, 4). The partial and fully-domed condition may not always constitute synapomorphies for Pachycephalosaurinae and Pachycephalosauridae, respectively, because these taxa do not have apomorphy-based definitions. Nonetheless, the partial and fully-domed condition would have been associated with these taxonomic names for the last 50 years on the basis of the present definitions.

Basal ceratopsians comprise a series of low-diversity "stem" groups to Ceratopsidae (SERENO 1986, in press) (Fig. 6). The first NST (Coronosauria = Protoceratopsidae + Ceratopsoidea) is diversity-based, recognizing protoceratopsids (at least three genera) as somewhat more diverse than other ceratopsid outgroups. Coronosauria, in addition, is currently associated with the two striking synapomorphies, the parietosquamosal frill and nasal horn. Thus, although Coronosauria does not have an apomorphy-based definition, its association with these apomorphies provides a convenient reference. The second NST (Ceratopsidae = Centrosaurinae + Ceratopsinae) is supported by the substantial diversity of each subgroup, as compared to ceratopsid outgroups; the morphologic distinction of all three clades, as reflected by the number of synapomorphies; and the long-standing usage of these taxonomic names (Fig. 3). A formal effort should be made to preserve. The names Ceratopsidae and Ceratopsinae should be preserved. Although the genus *Ceratops* has been considered a junior synonym (DODSON & CURRIE 1990) and may not be based on diagnostic material at the generic or species level, it clearly belongs with other "chasmosaurines" (MARSH 1888).

Saurischia

Within Saurischia, a NST is positioned at the base of Sauropodomorpha in recognition of its diverse, distinct, and traditional subgroups, Prosauropoda and Sauropoda (Sauropodomorpha = Prosauropoda + Sauropoda) (Fig. 4).

Prosauropoda

Most prosauropods belong to a long-necked clade (plateosaurs), composed of low-skulled genera (massospondylids) and genera which have lowered the jaw articulation (plateosaurids) (Fig. 7A; Tables 3, 4). A diversity- and morphology-based NST stabilizes this dichotomy, utilizing the well known genera *Massospondylus* and *Plateosaurus* as reference taxa (Plateosauria = Massospondylidae + Plateosauridae).

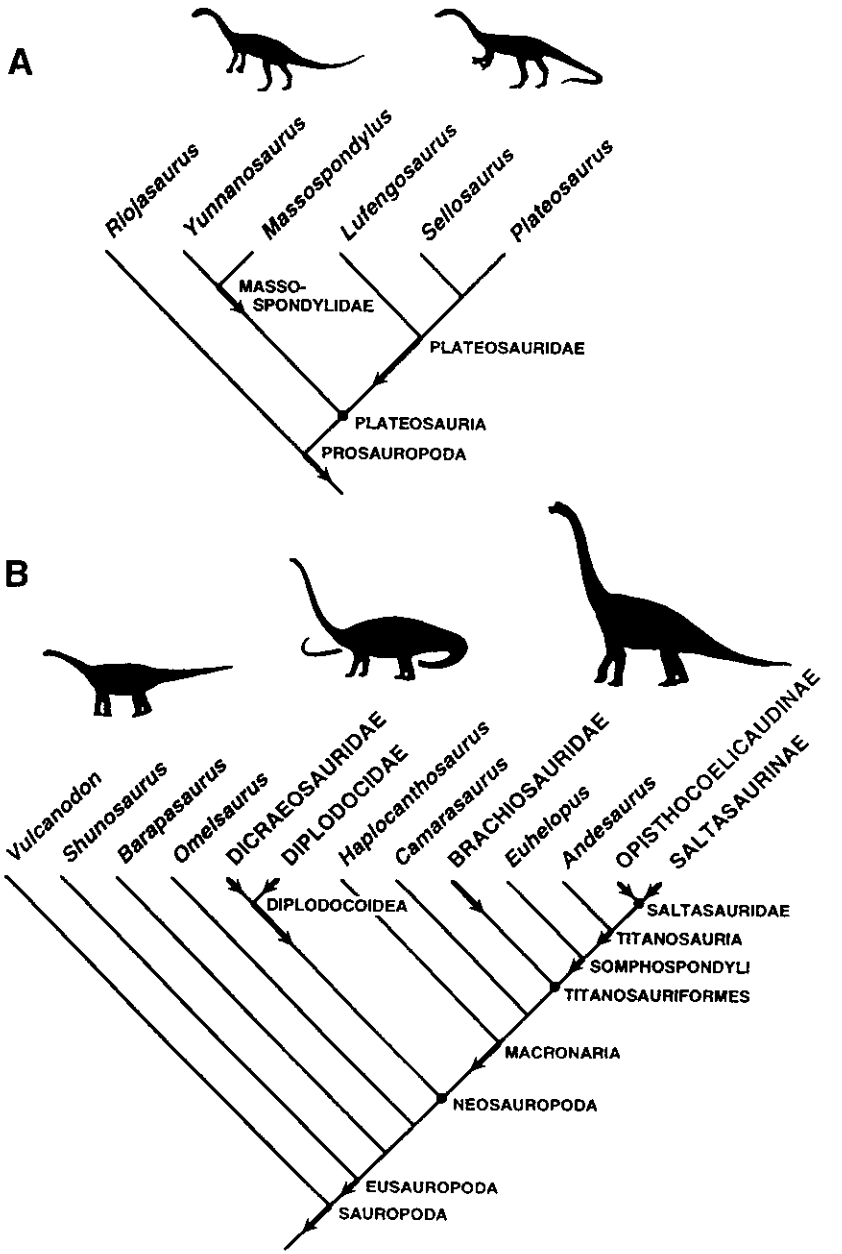


Fig. 7. Phylogenetic diagram for Prosauropoda (A) and Sauropoda (B) showing the distribution of node-based (dot) and stem-based (arrow) taxa (for definitions, see Table 4). Phylogenetic definitions within Sauropoda follow WILSON & SERENO (1998).

Sauropoda

Several sauropod genera constitute basal "stem" taxa to Neosauropoda, a diverse clade subdivided into diplodocoids and macronarians (Wilson & Sereno 1998) (Fig. 7B). A diversity-based-NST (Neosauropoda = Diplodocoidea + Macronaria) recognizes this fundamental dichotomy in sauropod phylogeny. Diplodocoidea and Macronaria, in addition, function best as stem-based taxa, because they incorporate several "stem" genera on either side of the dichotomy.

Two NST's are established among more derived sauropods (Fig. 7B). The first is a diversity-based NST (Titanosauriformes = Brachiosauridae + Somphospondyli) situated at the dichotomy between brachiosaurids and a diverse clade of "spongy-boned" sauropods (somphospondyls) that include titanosaurs (Salgado et al. 1997, Wilson & Sereno 1998).

The second NST (Saltasauridae = Opisthoceolicaudinae + Saltasaurinae) is situated within the titanosaurian radiation (Fig. 7B). A NST at the base ofTitanosauria is not particularly heuristic, because it requires the use of poorly known basal titanosaurs, such as *Andesaurus* (Salgado et al. 1997) as a reference taxon. Better known titanosaurs constitute successive "stem" genera toward the derived genus *Saltasaurus* (Salgado et al. 1997, Wilson unpublished data). A NST utilizing the well known genera *Opisthoceolicaudia* and *Saltasaurus* as reference taxa encompasses nearly all titanosaurs with the unusual biconvex caudal vertebra. Although not based on diversity, morphology or tradition, a saltasaurid NST stabilizes the higher taxonomy of derived titanosaurs and supplants use of the taxon "Titanosauridae," which is not based on a valid genus.

Basal Theropoda

Among theropods, two low-diversity taxa (*Eoraptor*, Herrerasauridae) are positioned as successive sister taxa to a major dichotomy within the group, similar to the pattern at the base of Ornithischia (Gauthier 1986, Sereno et al. 1993) (Figs. 4, 8). The most inclusive diversity-based NST within Theropoda, therefore, is not at the basal node of the taxon, but rather at the junction that recognizes the fundamental dichotomy among theropods (Neotheropoda = Ceratosauria + Tetanurae) (Gauthier 1986, Holtz 1994, Sereno 1997, Padian et al., in review). Furthermore, two of these taxa (Neotheropoda, Tetanurae) are united by more synapomorphies than at other nodes linking major groups of theropods (Sereno 1997: fig. 3).

Ceratosauria

Ceratosaurs are divided roughly equally between ceratosauroids and coelophysoids (Rowe & Gauthier 1990, Holtz 1994; Fig. 8). A diversity-based NST for Ceratosauria is warranted, with stem-based definitions for Ceratosauroidea (= Neoceratosauria) and Coelophysoidea. Ceratosauria, however, has already been defined as a stem-based taxon of a more fundamental NST. Ceratosauroidea and Coelophysoidea, nevertheless, are effective stem-based taxa, because several "stem" genera are present within each group (Fig. 8). One NST is recognized at a higher level within each subgroup of Ceratosauria. Among ceratosauroids, an abelisaurid NST (Abelisauridae = Abelisaurinae + Carnotaurinae) recognizes the basal split between the less modified genus *Abelisaurus* and the very characteristic horned abelisaurids, the carnotaurines. This NST is not diversity-based, given the singleton genus *Abelisaurus* on one side of the dichotomy. Rather, this NST is recognized to stabilize the taxonomy of abelisaurids and carnotaurines, in particular, which have become the best known subgroup among ceratosauroids (Bonaparte et al. 1990, Chatterjee & Rudra 1996). A parallel diversity-based NST is recognized among coelophysoids (Coelophysidae = Coelophysinae + Procompsognathinae), dividing a closely knit clade of small-bodied genera (coelophysids) into those more closely related to either *Coelophysis* or *Procompsognathus* (Fig. 8).

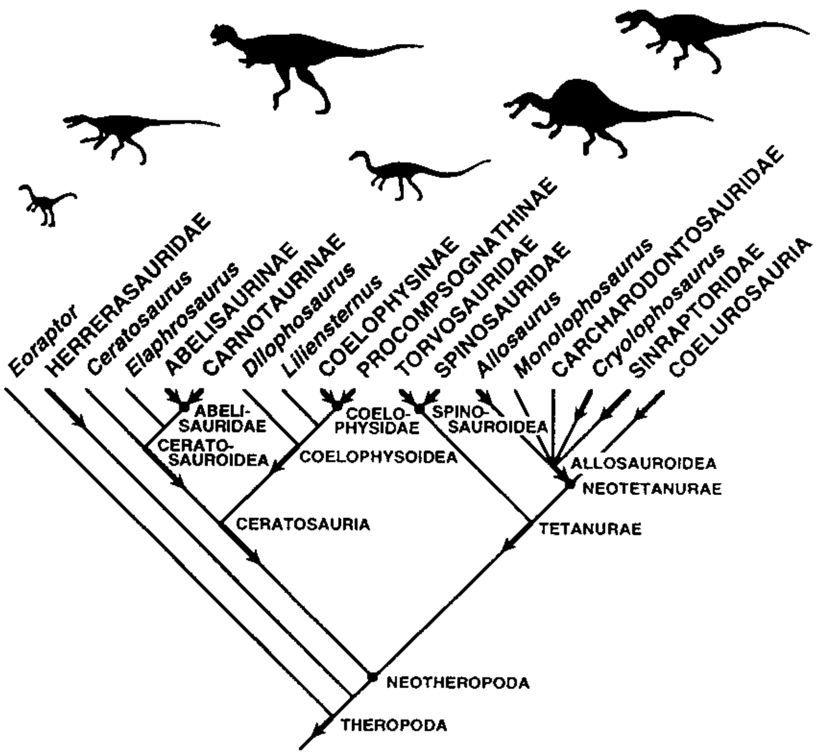


Fig. 8. Phylogenetic diagram for basal Theropoda showing the distribution of node-based (dot) and stem-based (arrow) taxa (for definitions, see Table 4).

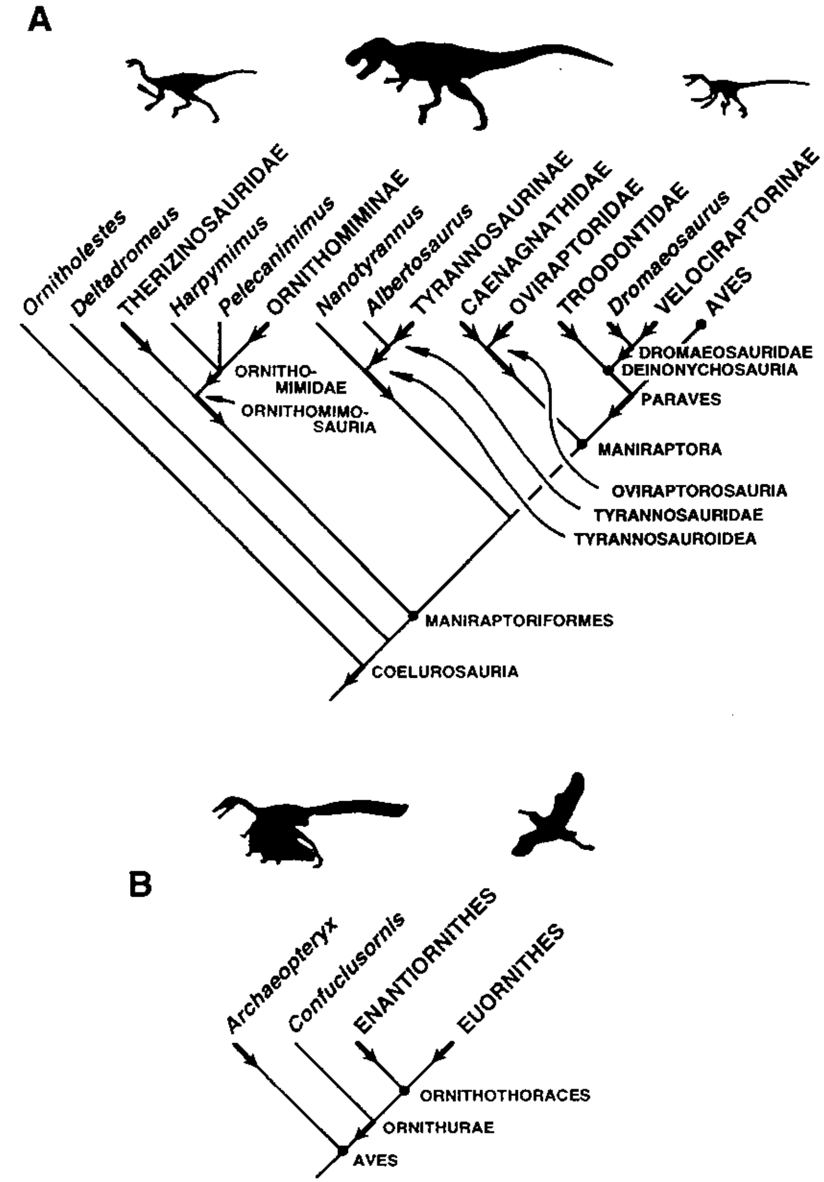


Fig. 9. Phylogenetic diagram for Coelurosauria (A) and basal Aves (B) showing the distribution of node-based (dot) and stem-based (arrow) taxa (for definitions, see Table 4).

Basal Tetanurae

Basal tetanurans comprise a large number of large-bodied genera, one subgroup of which is clearly more derived than the others. This derived subgroup, Allosauroidea, is the sister taxon to Coelurosauria, which together compose Neotetanurae (Fig. 8). Neotetanurae (SERENO et al. 1994) is used here rather than "Avetheropoda" (PAUL 1988) for two reasons. As originally used, the latter was not clearly distinguished from Coelurosauria (sensu GAUTHIER 1986), which PAUL (1988) did not use, and included taxa with affinities outside Neotetanurae (e. g., *Indosuchus*, *Chilantaisaurus*). Two diversity-based NST's are recognized, the first involving Neotetanurae (Neotetanurae = Allosauroidea + Coelurosauria). This stabilized scheme has the capability to absorb several poorly known genera, often referred to as "megalosaurids" or "allosaurids," when their anatomy and relationships are better resolved. Torvosaurids and spinosaurids are the best known tetanurans outside the neotetanuran radiation (Fig. 8). A diversity-based NST recognizes the basal split within this clade (Spinosauroidea = Torvosauridae + Spinosauridae).

Coelurosauria

Coelurosaurs comprise a very diverse taxon (Fig. 9A). Because there are few coelurosaurian synapomorphies and a number of "stem" genera at the base of the clade, Coelurosauria is most effectively defined as a stem-based taxon within a more inclusive NST (Neotetanurae = Allosauroidea + Coelurosauria) (Fig. 8).

Three NST's are recognized among nonavian coelurosaurs (Fig. 9A). Maniraptoriformes identifies the first dichotomy among coelurosaurs with significant diversity on each side. A diversity-based NST is positioned here, with *Ornithomimus* and Neornithes as reference taxa (Maniraptoriformes = Ornithomimosauria + Tyrannosauroidea + Maniraptora) (Tables 3, 4). With these reference taxa, alternative opinions regarding the affinities of therizinosaurs and tyrannosauroids within Coelurosauria are of little taxonomic consequence. For this reason, I have left unnamed a potential stem-based taxon uniting tyrannosauroids and maniraptorans.

The second and third diversity-based NST's within Coelurosauria are located among maniraptorans (Fig. 9A). Maniraptora and basal nodes within this clade are united by substantial character data, although none stand above the rest as discordantly divergent (SERENO 1997: fig. 3). A diversity-based NST is recognized for Maniraptora and its subordinate clades (Maniraptora = Oviraptorosauria + Paraves). Paraves was coined as a stem-based taxon that would unite Aves with the most closely related nonavian coelurosaurs (SERENO 1997). Maniraptora, rather than Paraves, was chosen as a NST to allow recognition of an avian NST at a less inclusive level (a paravian NST would require a stem-based definition for Aves and thus preclude an avian NST). There are no other grounds for recognizing Maniraptora rather than Paraves as a NST. The reference taxa for Paraves (*Oviraptor*, Neornithes) accommodate alternative hypotheses that exclude troodontids (HOLTZ 1994), are the dromaeosaurid *Velociraptor* and Neornithes (Tables 3, 4).

Deinonychosauria and its distinct subclades, Troodontidae and Dromaeosauridae, are recognized as a diversity-based NST (Deinonychosauria = Troodontidae + Dromaeosauridae) (Fig. 9A). The stem-based Troodontidae and Dromaeosauridae will absorb new basal members without change in the taxonomic content of Deinonychosauria.

Basal Aves

I have defined Aves in the traditional sense, recognizing a tradition-based NST to anchor the definition (Aves = *Archaeopteryx* + Ornithurae) (Fig. 9B). In this formulation, Ornithurae is a stem-based taxon, as proposed in its initial phylogenetic definition (Gauthier 1986) (Tables 2, 4).

A diversity- and morphology-based NST is established for the principal dichotomy among Mesozoic avians, the divergence of Enantiornithes ("opposite birds") from Euornithes ("true birds"), a taxon coined here (Fig. 9B, Table 4). The three taxa composing this NST (Ornithothoraces = Enantiornithes + Euornithes) are very distinct morphologically, as shown by long lists of synapomorphies (Chiappe 1996, Sereno in review). *Iberomesornis* served as a reference taxon in the original definition of Ornithothoraces (initially referenced as the "Las Hoyas bird" for a taxon initially named "Ornithopectae"; Chiappe 1991). *Sinornis*, rather than *Iberomesornis*, is used here as a reference taxon for Ornithothoraces, because the phylogenetic interpretation of *Sinornis* is not in dispute; *Sinornis* is a member of Enantiornithes and is known from many specimens. *Iberomesornis*, on the other hand, has been regarded either as a basal avian outside Enantiornithes (Chiappe 1996) or as an enantiornithine (Kurochkin 1996, Sereno in review a), and the single partial skeleton may not be complete enough to reach consensus. Ornithothoraces, defined here by the reference taxa *Sinornis* and Neornithes (Tables 3, 4), identifies the major dichotomy in avian diversity during the Mesozoic.

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