

The phylogenetic taxonomy of Diplodocoidea (Dinosauria: Sauropoda)

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Despite some continuing controversies, sauropod phylogeny is now the subject of broad agreement. Against this backdrop of relatively stable phylogenetic hypotheses, however, the nomenclature of the sauropod clade that includes *Diplodocus* and its relatives remains confused. Not all of the named groups within this clade have suitable phylogenetic definitions; others have multiple names; and some names have multiple conflicting definitions. We survey the taxonomic history of this clade, consider the suitability for phylogenetic taxonomy of various candidate definitions from the literature, and discuss some sources of confusion. Finally, we recommend “best practice” in the use of the relevant clade names.

INTRODUCTION

The phylogeny and taxonomy of the Mesozoic dinosaur clade Sauropoda has been the subject of several recent major studies. A broad consensus on a well-established higher-level phylogeny of Sauropoda has now been achieved (Upchurch 1995, 1998, 1999, Calvo and Salgado 1995, Salgado et al. 1997, Wilson and Sereno 1998, Wilson 2002, Upchurch et al. 2004). However, while the topology of the sauropod tree is relatively well resolved, the same cannot be said of the names used for the various sauropod groups. Sauropod taxonomy remains confused, particularly for the groups including and immediately surrounding *Diplodocus*. Some groups have been given multiple names and some names have been given multiple conflicting definitions. Many of these names, having been coined some years ago, are in broad use despite never having been given a rigorous phylogenetic definition. In the light of the stable topology within this group, inspired by the recommendations of Brochu and Sumrall (2001), and in the spirit of Padian et al.’s (1999) paper on the phylogenetic taxonomy of theropods, we feel that now is an appropriate time to establish a coherent set of clade names and definitions within the phylogenetic nomenclatural system (de Queiroz and Gauthier 1990, 1992, 1994).

This paper describes the phylogenetic framework within which high-level sauropod taxon names are now interpreted, reviews the history of the relevant names, discusses the intent of the names and problems with some existing definitions, and finally recommends a set of consistent definitions for existing names that may usefully be employed. We do not erect any new names, though we do provide explicit definitions for some names that currently lack them. We have not fully adhered to the recommendations of the draft PhyloCode (Cantino and de Queiroz 2000), because a definitive version of this taxonomic system has yet to be agreed upon and accepted within the community.

The following notation is used for clade definitions:

(A + B) = the node-based clade consisting of the most recent common ancestor of A and B, together with all of its descendants (that is, the least inclusive clade containing both A and B);

(A not B) = the stem-based clade consisting of the most remote ancestor of A that is not also an ancestor of B, together with all of its descendants (that is, the clade of all individuals more closely related to A than to B).

PHYLOGENETIC FRAMEWORK

While some details of sauropod phylogeny remain the subject of disagreement, most phylogenetic studies recover the same relationships between the better understood genera. The results presented by Salgado et al. (1997), Upchurch (1999), Wilson (2002) and Upchurch et al. (2004) are all compatible with the cladogram shown in Fig. 1. The following historical review and discussion will refer to the relationships illustrated here. The recommendations with which we conclude are based on the assumption that this consensus phylogeny is correct but with the intention that, if it should prove mistaken, the definitions should remain unambiguous, useful, and as far as possible stable in content.

TAXONOMIC HISTORY

Neosauropoda

Bonaparte (1986a) discussed sauropod evolution in terms of three paraphyletic grades of increasingly derived animals and a more advanced group of Late Jurassic sauropods. The grades were “vulcanodontids,” “primitive cetiosaurids,” and “advanced cetiosaurids,” but the advanced group was not named in that paper. Bonaparte (1986b) named this group Neosauropoda; however, his usage did not include titanosaurs and he did not provide a definition.

Neosauropoda was first used in the modern sense by Upchurch (1994), but again no definition was provided. The first phylogenetically significant use of this name was by Upchurch (1995) who, though not providing an explicit phylogenetic definition, described the group as follows: “The ‘Neosauropoda’ [his use of quotes]...contains the Brachiosauridae, Camarasauridae, and the new superfamilies Titanosauroidae and Diplodocoidea. The Cetiosauridae...is also provisionally included within the Neosauropoda, but may be removed in future studies” (p. 365). This description was later revised

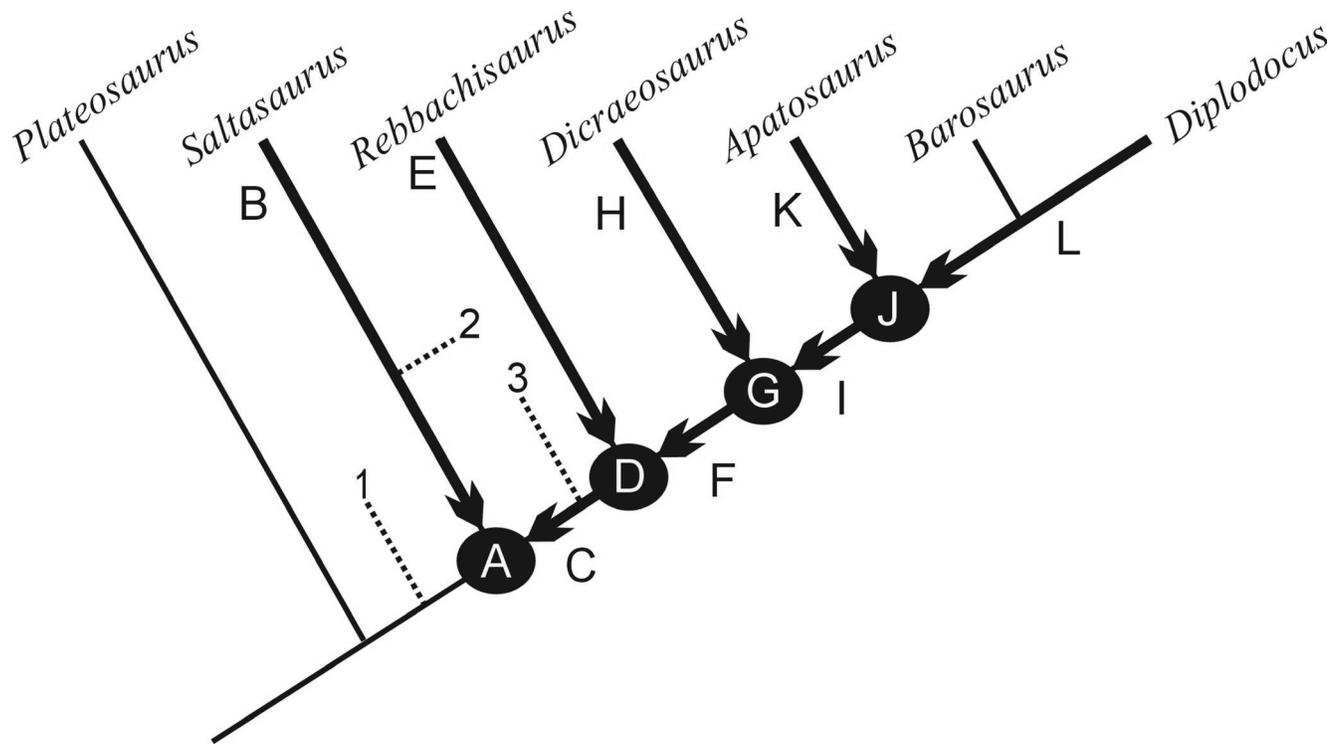


Fig. 1. Relationships between sauropods showing successive outgroups to *Diplodocus*. Includes basal sauropodomorphs (represented by *Plateosaurus*), Macronaria (represented by *Saltasaurus*) and Diplodocoidea (represented by all other genera named in the figure). The numbers 1, 2 and 3 indicate possible positions for *Haplocanthosaurus*, discussed in the text. The letters A to L indicate nodes and stems in this phylogeny, the names and definitions of which are discussed in the text.

with Cetiosauridae omitted (Upchurch 1998, p. 81). Again no explicit phylogenetic definition was provided, but fig. 19 of that paper indicated that Upchurch used Neosauropoda for the node containing diplodocoids and the camarasaur/brachiosaur/titanosaur clade that he termed “Brachiosauria” (now generally known as Macronaria; see below).

The first published explicit phylogenetic definition of Neosauropoda was that of Salgado et al. (1997), who defined it as “the clade including the most recent common ancestor of Diplodocidae and Camarasauromorpha and all of its descendants” (p. 8; see below on Camarasauromorpha). This definition, however, has not been widely used.

Wilson and Sereno (1998, p. 55) provided a more explicit definition of Neosauropoda as “*Diplodocus* [Marsh 1878], *Saltasaurus* [Bonaparte and Powell 1980], their common ancestor and all descendants.” While this definition is equivalent to that of Salgado et al. (1997) in all phylogenies where *Camarasaurus* Cope 1877a is closer to *Saltasaurus* than it is to *Diplodocus*, its greater explicitness has won it wide acceptance. We recommend the use of this definition.

Macronaria

This group is relevant to the current study as it is the sister-group to Diplodocoidea. The name Macronaria was first used in Wilson and Sereno (1998) where it was described

as the stem-based sister-clade to Diplodocoidea and defined (p. 55) as “All neosauropods closer to *Saltasaurus* than to *Diplodocus*.” Two other names have been proposed for clades with similar memberships. Salgado et al. (1997) coined Camarasauromorpha for “the clade including the most recent common ancestor of Camarasauridae and Titanosauriformes and all of its descendants” (p. 9). Camarasauromorpha is node-based, and less inclusive than the stem-based Macronaria. Upchurch (1998) used ‘Brachiosauria’ (his use of quotes) to describe the same node (“*Camarasaurus*, brachiosaurids and titanosaurs”). Neither Camarasauromorpha nor Brachiosauria has been widely used by sauropod workers since they were named, whereas Macronaria has won widespread acceptance. However, we emphasize that Macronaria and Camarasauromorpha are not equivalent and we recommend that both be provisionally retained.

Diplodocoidea

The name Diplodocoidea is credited to Marsh (1884) because the Principle of Coordination (ICZN 1999, article 36) stipulates that coinage of the family name Diplodocidae implied the creation of the superfamily Diplodocoidea and subfamily Diplodocinae. In terms of phylogenetic taxonomy, however, Marsh’s “definition” is useless. The first use of Diplodocoidea in a phylogenetic context was in Upchurch’s

(1993) dissertation, but this was not published. It was next used simultaneously in three papers within the same volume (Upchurch 1994, Barrett and Upchurch 1994, Hunt et al. 1994), but, as discussed below, none of these provides a definition that is satisfactory for the purposes of phylogenetic taxonomy. The usual citation for Diplodocoidea is Upchurch (1995). In this work (p. 380), Diplodocoidea was described as “a new superfamily which contains the Diplodocidae, Dicraeosauridae and the new family, Nemegtosauridae.” As explained in the Discussion section, however, this definition is also problematic.

Wilson and Sereno (1998) defined Diplodocoidea as “All neosauropods closer to *Diplodocus* than to *Saltasaurus*” (p. 55).

Diplodocimorpha

The name Diplodocimorpha was coined by Calvo and Salgado (1995, p. 14) who defined it as “*Rebbachisaurus tessonei* sp. nov., Diplodocidae, and all descendants of their common ancestor.” Since the publication of this definition, the species *tessonei* has been referred to *Rayososaurus* Bonaparte 1996 (Wilson and Sereno 1998, p. 18) and has recently been given its own new genus, *Limaysaurus* (Salgado et al. 2004). Diplodocimorpha has been used by Salgado (1999, 2001) and Salgado et al. (2004) but has not otherwise been employed, even by authors referring to the same clade (e.g., Upchurch 1999, p. 118). Wilson and Sereno (1998, p. 6) and Pereda Suberbiola et al. (2003, p. 475) considered Diplodocimorpha and Diplodocoidea equivalent, thus implying that Diplodocimorpha was redundant.

Rebbachisauridae

Although *Rebbachisaurus garasbae* Lavocat 1954 was first described by Lavocat (1954), and related genera and species were identified by Lapparent (1960), Calvo and Salgado (1995), and Bonaparte (1996), the taxon Rebbachisauridae was not erected until Bonaparte (1997). However, since this was only an abstract, some sources (e.g., Upchurch et al. 2004) have preferred to cite Sereno et al.’s (1999) use of this name, and we follow this choice. Neither Bonaparte (1996) nor Sereno et al. (1999) provided a phylogenetic definition of Rebbachisauridae, but one is found in Salgado et al. (2004), which cites a personal communication from Wilson defining this clade as *Rebbachisaurus garasbae* not *Diplodocus*. Given the poor quality of the *R. garasbae* material, it would perhaps be better to anchor the taxon on *Limaysaurus tessonei* Salgado et al. 2004, but for now we accept Salgado et al.’s definition.

Flagellicaudata

The taxon Flagellicaudata was defined by Harris and Dodson (2004, p. 198) as “a node-based taxon consisting of the most recent common ancestor of *Dicraeosaurus* [Janensch 1914] and *Diplodocus* and all of its descendants.” They went on (p. 206) to suggest that, according to some of the most

parsimonious trees produced by their cladistic analysis, the new taxon *Suuwassea emilieae* Harris and Dodson 2004 may occur “as the sister taxon to all *other* flagellicaudatans” (our emphasis). This has been interpreted by some to mean that a different definition may have been intended, with *Suuwassea emilieae* itself included as a specifier in Flagellicaudata. Harris (personal communication, 2004) confirms that this was not the intention: the published definition is the intended one.

Diplodocidae

This group was introduced by Marsh (1884) as the third of his three families of sauropods along with Atlantosauridae and Morosauridae. Marsh (1884) did not comment on the content of the new family beyond *Diplodocus* itself, and his definition is phylogenetically uninformative. Diplodocidae has historically been used in at least three rather different ways. Traditionally, it has been used to mean a broad group more or less equivalent to the modern concept of Diplodocoidea and Diplodocimorpha (e.g., Bonaparte 1986a, McIntosh 1990). Secondly, some authors have used Diplodocidae for the clade that includes both diplodocids *sensu stricto* and dicraeosaurids (e.g., Janensch 1929, Calvo and Salgado 1995, Salgado 1999), a grouping equivalent to Flagellicaudata. More recently, it has generally been understood to include *Diplodocus*, *Barosaurus* Marsh 1890, *Apatosaurus* Marsh 1877 and closely related forms, but not *Dicraeosaurus*, *Rebbachisaurus* Lavocat 1954 and other more distantly related taxa. This latter usage was codified by Sereno’s (1998, p. 63) definition of Diplodocidae as “all diplodocoids closer to *Diplodocus* than to *Dicraeosaurus*.”

Dicraeosaurinae

In the future, the name Dicraeosaurinae might be used for a clade uniting *Dicraeosaurus* with *Brachytrachelopan* Rauhut, Remes, Fechner, Cladera and Puerta 2005, to the exclusion of *Amargasaurus* Salgado and Bonaparte 1991. At present, however, relationships within Dicraeosauridae are not sufficiently resolved for this to be appropriate: Salgado (1999) has suggested that *Dicraeosaurus sattleri* may be closer to *Amargasaurus* than to *D. hansemanni*, and it is possible, though unlikely, that *D. hansemanni* is closer to *Brachytrachelopan* than to *D. sattleri*. While the balance of evidence suggests that the genus *Dicraeosaurus* is monophyletic (Rauhut, personal communication 2005) and related more closely to *Brachytrachelopan* than to *Amargasaurus* (Rauhut et al. 2005), further study is required before a clade is named.

Diplodocinae

This name was erected by Janensch (1929) as the sister group to Dicraeosaurinae, these two groups in his usage roughly corresponding to the modern concepts of Diplodocidae and Dicraeosauridae. In modern use, Diplodocinae denotes a more restricted group, typically uniting *Diplodocus* and *Barosaurus* to the exclusion of *Apatosaurus*, with Apato-

saurinae being its sister group. No phylogenetic definition has been published of either Diplodocinae or Apatosaurinae: we propose Diplodocinae = (*Diplodocus* not *Apatosaurus*), and Apatosaurinae = (*Apatosaurus* not *Diplodocus*), to complete the node-stem triplet.

DISCUSSION

Of all these taxa, the most problematic is Diplodocoidea, which has been used in several different and incompatible ways. Aside from Marsh's (1884) implication of the name when he coined Diplodocidae, its earliest widely accepted publication is in Upchurch (1995), and this is the citation used in, for example, Wilson (2002). In a special volume devoted to sauropods and published in 1994, and thus prior to Upchurch's (1995) establishment of Diplodocoidea, three papers used the term. However, none of them published it in a phylogenetically satisfactory way. In the first of these three papers, Upchurch (1994) used 'Diplodocoidea' in quotes; he wrote (p. 251), of this and other newly coined names, "These are included purely as convenient 'labels' and will be properly diagnosed elsewhere (Upchurch, in press)," referring to Upchurch (1995). Secondly, Barrett and Upchurch (1994) included a brief appendix on sauropod classification and noted that their classification of diplodocoids followed Upchurch (1993). They also noted (p. 203) that "formal definitions...are given in this reference." The contents of Diplodocoidea in this sense were implied but not stated, and no definition was given. Because Upchurch 1993 is an unpublished dissertation, its contents do not affect formal phylogenetic taxonomy. Finally, Hunt et al. (1994, p. 264) independently proposed that "diplodocids and dicraeosaurids share similar cranial features and probably together constitute a monophyletic superfamily Diplodocidae [sic]" — a misspelling that also occurs in Upchurch's (1998, p. 74) caption to his fig. 19. Hunt (personal communication, 2004) confirms that the misspelling was inadvertent. The misspelled name should not be used.

However, Upchurch's widely cited (1995, p. 380) definition is also unsatisfactory for the purposes of phylogenetic taxonomy: "The Diplodocoidea is a new superfamily which contains the Diplodocidae, Dicraeosauridae and the new family, Nemegtosauridae." If this is read as a phylogenetic definition, then it is a three-element node. However, the position of one of the specifiers, Nemegtosauridae, remains controversial. Although Upchurch (1998, 1999) recovered Nemegtosauridae as the sister group to the (Diplodocidae + Dicraeosauridae) clade, other analyses (e.g., Salgado and Calvo 1997, Curry Rogers and Forster 2001, Wilson 2002) find these animals in Titanosauria. Although Upchurch et al. (2004) recovered Nemegtosauridae as the sister group to a (*Rebbachisaurus* + Diplodocidae) clade, Upchurch now favours a titanosaurian position for this group (personal communication, 2004). The diplodocoid position of Nemegtosauridae in the 2004 analysis is probably due to the omission of *Rapetosaurus* Curry Rogers and Forster 2001 from the

matrix, as cranial similarities between it and nemegtosaurs were responsible for Curry Rogers and Forster's (2001) recovery of Nemegtosauridae within Titanosauria. If nemegtosaurs are indeed titanosaurs, then Diplodocoidea *sensu* Upchurch (1995) is equivalent to Neosauropoda. In the light of these developments, a definition that depends on so unstable a specifier is not suitable.

Despite the lack of a clear definition, the intent of Diplodocoidea as representing a superset of Diplodocidae plus Dicraeosauridae seems to have been quickly adopted. Wilson and Smith (1996), for example, described *Amphicoelias* Cope 1877b as having "a basal position within Diplodocoidea", being "sister group to a well supported diplodocid plus dicraeosaurid clade."

The earliest wholly satisfactory definition of Diplodocoidea is that of Wilson and Sereno (1998, p. 55): "All neosauropods closer to *Diplodocus* than to *Saltasaurus*." This is explicit, and the specifier taxa appear to be well resolved, yielding a definition that is likely to remain stable in content even if significantly different topologies are recovered by future analyses.

If we employ Wilson and Sereno's (1998) stem-based definition of Diplodocoidea, then Calvo and Salgado's (1995) node-based Diplodocimorpha ("*Rebbachisaurus*" [= *Limaysaurus*] *tessonei* + Diplodocidae) is nested inside it according to current phylogenies. This will remain the case so long as *Limaysaurus tessonei* is found to be closer to *Diplodocus* than is *Saltasaurus*. In Linnean taxonomy, the -oidea suffix usually indicates a "superfamily" in vertebrates and -morpha usually indicates the more inclusive rank of "infrasuborder." However, the clade Diplodocimorpha is less inclusive than Diplodocoidea. Since these ranks are essentially meaningless, we do not perceive this as a problem in the definitions of the clade names.

Diplodocoidea and Diplodocimorpha, then, are not equivalent, *contra* Wilson and Sereno (1998). This has important ramifications. For example, one of the possible positions of *Haplocanthosaurus* Hatcher 1903 is as a non-diplodocimorph diplodocoid; that is, an animal closer to *Diplodocus* than is *Saltasaurus*, but less close to *Diplodocus* than is *Rebbachisaurus*. This corresponds to position 3 in Fig. 1, and is recovered by Wilson (2002, fig. 13A, p. 240). In other analyses, *Haplocanthosaurus* is found in position 2, in which case it is either a non-camarasauromorph macronarian (Wilson and Sereno 1998, fig. 44A, p. 54) or a camarasauromorph (Upchurch et al. 2004, fig. 13.18, p. 297); yet in others, it is found in position 1, in which case it is not a neosauropod at all (Upchurch 1999, fig. 19, p. 74).

RECOMMENDATIONS

In pursuit of the optimum balance between elegance, consistency with traditional usage, and stability of content as phylogenetic hypotheses change, Table 1 proposes "best practice" in the use of names for groups of sauropods close to *Diplodocus*. For each clade, we use the earliest published

Table 1. Phylogenetic definitions for the sauropod clades discussed in this work. Clades are listed in their node-stem triplets, with the nodes in decreasing order of inclusiveness.

Clade name	Author of name	Recommended definition	Author of definition	Figure 1
Neosauropoda	Bonaparte 1986b	(<i>Diplodocus</i> + <i>Saltasaurus</i>)	Wilson and Sereno 1998	Node A
Macronaria	Wilson and Sereno 1998	(<i>Saltasaurus</i> not <i>Diplodocus</i>)	Wilson and Sereno 1998	Stem B
Diplodocoidea	Marsh 1884; Upchurch 1995 ¹	(<i>Diplodocus</i> not <i>Saltasaurus</i>)	Wilson and Sereno 1998	Stem C
Diplodocimorpha	Calvo and Salgado 1995	(<i>Diplodocus</i> + <i>Rebbachisaurus</i>)	[New] ²	Node D
Rebbachisauridae	Sereno et al. 1999	(<i>Rebbachisaurus</i> not <i>Diplodocus</i>)	Salgado et al. 2004	Stem E
[no name] ³		(<i>Diplodocus</i> not <i>Rebbachisaurus</i>)		Stem F
Flagellicaudata	Harris and Dodson 2004	(<i>Dicraeosaurus</i> + <i>Diplodocus</i>)	Harris and Dodson 2004	Node G
Dicraeosauridae	Huene 1927	(<i>Dicraeosaurus</i> not <i>Diplodocus</i>)	Sereno 1998	Stem H
Diplodocidae	Marsh 1884	(<i>Diplodocus</i> not <i>Dicraeosaurus</i>)	Sereno 1998	Stem I
[no name] ⁴		(<i>Diplodocus</i> + <i>Apatosaurus</i>)		Node J
Apatosaurinae	Huene 1927; Janensch 1929 ⁵	(<i>Apatosaurus</i> not <i>Diplodocus</i>)	[New]	Stem K
Diplodocinae	Marsh 1884; Janensch 1929 ⁶	(<i>Diplodocus</i> not <i>Apatosaurus</i>)	[New]	Stem L

¹ The name Diplodocoidea is attributed both to Marsh 1884 (due to the Principle of Coordination) and to Upchurch 1995 (due to the first explicit use).

² Since the publication of the name Diplodocimorpha in Calvo and Salgado 1995 as (*Rebbachisaurus tessonei* + Diplodocidae), the species *tessonei* has been removed from *Rebbachisaurus*, so that the old combination *Rebbachisaurus tessonei* is no longer valid (Salgado et al. 2004). Our new definition of Diplodocimorpha as (*Diplodocus* + *Rebbachisaurus*) is equivalent to the original definition, but uses the type species of *Rebbachisaurus*, *R. garasbae*, and is more obviously part of a node-stem triplet.

³ Stem F (*Diplodocus* not *Rebbachisaurus*) needs no name, but would have been an alternative definition for the name Flagellicaudata.

⁴ Node J (*Diplodocus* + *Apatosaurus*) needs no name. It would be an alternative definition for Diplodocidae, but we prefer the stem version of Diplodocidae as it is stable in content if future phylogenies recover *Apatosaurus* closer to *Diplodocus* than *Barosaurus* is.

⁵ The name Apatosaurinae is attributed both to Huene 1927 (due to the Principle of Coordination) and to Janensch 1929 (due to the first explicit use).

⁶ The name Diplodocinae is attributed both to Marsh 1884 (due to the Principle of Coordination) and to Janensch 1929 (due to the first explicit use).

definition suitable for phylogenetic taxonomy, introducing our own definitions only where necessary. We prefer to use genera rather than clades as specifiers, as this approach yields more transparent definitions that do not depend on interpretations of other clade names. We did not find it necessary to define any new clade names.

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LITERATURE CITED

- Barrett, P.M., and P. Upchurch. 1994. Feeding mechanisms of *Diplodocus*. *Gaia* 10:195–203.
- Bonaparte, J.F. 1986a. The early radiation and phylogenetic relationships of the Jurassic sauropod dinosaurs, based on vertebral anatomy. Pp. 247–258 in K. Padian (ed.). *The Beginnings of the Age of Dinosaurs*. Cambridge University Press, Cambridge, UK.
- Bonaparte, J.F. 1986b. Les dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétiosaures) du Jurassique moyen de Cerro Cóndor (Chubut, Argentina). *Annales de Paléontologie* 72: 325–386.
- Bonaparte, J.F. 1996. Cretaceous tetrapods of Argentina. *Münchener Geowissenschaftliche Abhandlungen (A)* 30:73–130.
- Bonaparte, J.F. 1997. *Rayososaurus agrioensis* Bonaparte 1995. *Ameghiniana* 34:116.
- Bonaparte, J.F., and J.E. Powell. 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda—Coelurosauria—Carnosauria—Aves). *Memoires de la Société Géologique de France, Nouvelle Série* 139:19–28.
- Brochu, C.A., and C.D. Sumrall. 2001. Phylogenetic nomenclature and paleontology. *Journal of Paleontology* 75:754–757.
- Calvo, J.O., and L. Salgado. 1995. *Rebbachisaurus tessonei* sp. nov. a new Sauropoda from the Albian-Cenomanian of Argentina; new evidence on the origin of the Diplodocidae. *Gaia* 11:13–33.
- Cantino, P.D., and K. de Queiroz. 2000. PhyloCode: a phylogenetic code of biological nomenclature. <http://www.ohiou.edu/phylocode/>.
- Cope, E.D. 1877a. On a gigantic saurian from the Dakota epoch of Colorado. *Paleontology Bulletin* 25:5–10.
- Cope, E.D. 1877b. On *Amphicoelias*, a genus of saurian from the Dakota epoch of Colorado. *Proceedings of the American Philosophical Society* 17:242–246.
- Curry Rogers, K., and C.A. Forster. 2001. The last of the dinosaur titans: a new sauropod from Madagascar. *Nature* 412:530–534.
- de Queiroz, K., and J. Gauthier. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. *Systematic Zoology* 39:307–322.
- de Queiroz, K., and J. Gauthier. 1992. Phylogenetic taxonomy. *Annual Review of Ecology and Systematics* 23:449–480.
- de Queiroz, K., and J. Gauthier. 1994. Toward a phylogenetic system of biological nomenclature. *Trends in Ecology and Evolution* 9:27–31.
- Harris, J.D., and P. Dodson. 2004. A new diplodocoid sauropod dinosaur from the Upper Jurassic Morrison Formation of Montana, USA. *Acta Palaeontologica Polonica* 49:197–210.
- Hatcher, J.B. 1903. A new name for the dinosaur *Haplocanthus* Hatcher. *Proceedings of the Biological Society of Washington* 16: 100.
- Huene, F. 1927. Short review of the present knowledge of the Sauropoda. *Memoirs of the Queensland Museum* 9:121–126.
- Hunt, A.P., M.G. Lockley, S.G. Lucas, and C.A. Meyer. 1994. The global sauropod fossil record. *Gaia* 10:261–279.
- International Commission on Zoological Nomenclature. 1999. *International Code of Zoological Nomenclature—Fourth Edition*. The International Trust for Zoological Nomenclature, London. 306 pp.
- Janensch, W. 1914. Übersicht über die Wirbeltierfauna der Tendaguru-Schichten, nebst einer kurzen Charakterisierung der neu aufgeführten Arten von Sauropoden. *Archiv für Biontologie* 3: 81–110.
- Janensch, W. 1929. Die Wirbelsäule der gattung *Dicraeosaurus*. *Palaeontographica (Supplement 7)* 3:39–133.
- Lapparent, A.F. de. 1960. Les dinosauriens du “Continental Intercalaire” du Sahara central. *Memoires de la Société Géologique de France (Nouvelle Serie)* 88A:1–56.
- Lavocat, R. 1954. Sur les Dinosauriens du continental intercalaire des Kem-Kem de la Daoura. *Comptes Rendus 19th International Geological Congress, 1952*. Part 15(3):65–68.
- Marsh, O.C. 1877. Notice of some new dinosaurian reptiles from the Jurassic Formation. *American Journal of Science, Series 3* 14:514–516.
- Marsh, O.C. 1878. Principal characters of American Jurassic dinosaurs. Part I. *American Journal of Science, Series 3* 16:411–416.
- Marsh, O.C. 1884. Principal characters of American Jurassic dinosaurs. Part VII. On the Diplodocidae, a new family of the Sauropoda. *American Journal of Science, Series 3* 27:160–168.
- Marsh, O.C. 1890. Description of new dinosaurian reptiles. *American Journal of Science, Series 3* 39:81–86.
- McIntosh, J.S. 1990. Sauropoda. Pp. 345–401 in D. B. Weishampel, P. Dodson and H. Osmólska (eds.). *The Dinosauria*. University of California Press, Berkeley.
- Padian, K., J.R. Hutchinson, and T.R. Holtz, Jr. 1999. Phylogenetic definitions and nomenclature of the major taxonomic categories of the carnivorous Dinosauria (Theropoda). *Journal of Vertebrate Paleontology* 19:69–80.
- Pereda Suberbiola, X., F. Torcida, L.A. Izquierdo, P. Huerta, D. Montero, and G. Perez. 2003. First rebbachisaurid dinosaur (Sauropoda, Diplodocoidea) from the Early Cretaceous of Spain: palaeobiogeographical implications. *Bulletin de la Société Géologique de France* 174:471–479.

- Rauhut, O.W.M., K. Remes, R. Fechner, G. Cladera, and P. Puerta. 2005. Discovery of a short-necked sauropod dinosaur from the Late Jurassic period of Patagonia. *Nature* 435:670–672.
- Salgado, L. 1999. The macroevolution of the Diplodocimorpha (Dinosauria; Sauropoda): a developmental model. *Ameghiniana* 36:203–216.
- Salgado, L. 2001. Los saurópodos de Patagonia: sistemática, evolución y paleobiología. Pp. 139–168 in Colectivo Arqueológico-Paleontológico de Salas (eds.). Actas de Las II Jornadas de Paleontología de Dinosaurios y su Entorno. Salas de los Infantes, Burgos, España.
- Salgado, L., and J.F. Bonaparte. 1991. Un nuevo saurópodo Dicraosauridae, *Amargasaurus cazau* gen. et sp. nov., de la Formación La Amarga, Neocomiano de la Provincia del Neuquén, Argentina. *Ameghiniana* 28:333–346.
- Salgado, L., and J.O. Calvo. 1997. Evolution of titanosaurid sauropods. II: the cranial evidence. *Ameghiniana* 34:33–48.
- Salgado, L., R.A. Coria, and J.O. Calvo. 1997. Evolution of titanosaurid sauropods. I: phylogenetic analysis based on the postcranial evidence. *Ameghiniana* 34:3–32.
- Salgado, L., A. Garrido, S.E. Cocca, and J.R. Cocca. 2004. Lower Cretaceous rebbachisaurid sauropods from Cerro Aguada Del Leon (Lohan Cura Formation), Neuquén Province, northwestern Patagonia, Argentina. *Journal of Vertebrate Paleontology* 24: 903–912.
- Sereno, P. 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 210:41–83.
- Sereno, P.C., A.L. Beck, D.B. Dutheil, H.C.E. Larsson, G.H. Lyon, B. Moussa, R.W. Sadleir, C.A. Sidor, D.J. Varricchio, G.P. Wilson, and J.A. Wilson. 1999. Cretaceous sauropods from the Sahara and the uneven rate of skeletal evolution among dinosaurs. *Science* 282:1342–1347.
- Upchurch, P. 1993. The anatomy, phylogeny and systematics of sauropod dinosaurs. Ph.D. diss. University of Cambridge, Cambridge, UK. 489 pp.
- Upchurch, P. 1994. Sauropod phylogeny and palaeoecology. *Gaia* 10:249–260.
- Upchurch, P. 1995. The evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society of London, Series B* 349:365–390.
- Upchurch, P. 1998. The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society* 124:43–103.
- Upchurch, P. 1999. The phylogenetic relationships of the Nemegtosauridae (Saurischia, Sauropoda). *Journal of Vertebrate Paleontology* 19:106–125.
- Upchurch, P., P.M. Barrett, and P. Dodson. 2004. Sauropoda. Pp. 259–322 in D.B. Weishampel, P. Dodson, and H. Osmólska (eds.). The Dinosauria, 2nd edition. University of California Press, Berkeley and Los Angeles.
- Wilson, J.A. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of the Linnean Society* 136: 217–276.
- Wilson, J.A., and P.C. Sereno. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Society of Vertebrate Paleontology Memoir* 5:1–68.
- Wilson, J.A., and M. Smith. 1996. New remains of *Amphicoelias* Cope (Dinosauria: Sauropoda) from the Upper Jurassic of Montana and diplodocid phylogeny. *Journal of Vertebrate Paleontology* 16(3 Suppl.):73A.