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The early evolution of titanosauriform sauropod dinosaurs

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Titanosauriformes was a globally distributed, long-lived clade of dinosaurs that contains both the largest and smallest known sauropods. These common and diverse megaherbivores evolved a suite of cranial and locomotory specializations perhaps related to their near-ubiquity in Mesozoic ecosystems. In an effort to understand the phylogenetic relationships of their early (Late Jurassic–Early Cretaceous) members, this paper presents a lower-level cladistic analysis of basal titanosauriforms in which 25 ingroup and three outgroup taxa were scored for 119 characters. Analysis of these characters resulted in the recovery of three main clades: Brachiosauridae, a cosmopolitan mix of Late Jurassic and Early Cretaceous sauropods, Euhelopodidae, a clade of mid-Cretaceous East Asian sauropods, and Titanosauria, a large Cretaceous clade made up of mostly Gondwanan genera. Several putative brachiosaurids were instead found to represent non-titanosauriforms or more derived taxa, and no support for a Laurasia-wide clade of titanosauriforms was found. This analysis establishes robust synapomorphies for many titanosauriform subclades. A re-evaluation of the phylogenetic affinities of fragmentary taxa based on these synapomorphies found no body fossil evidence for titanosaurs before the middle Cretaceous (Aptian), in contrast to previous reports of Middle and Late Jurassic forms. Purported titanosaur track-ways from the Middle Jurassic either indicate a substantial ghost lineage for the group or – more likely – represent non-titanosaurs. Titanosauriform palaeobiogeographical history is the result of several factors including differential extinction and dispersal. This study provides a foundation for future study of basal titanosauriform phylogeny and the origins of Titanosauria.

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ADDITIONAL KEYWORDS: cladistic analysis – Mesozoic – phylogeny – titanosaur.

INTRODUCTION

Titanosauriformes is a large clade (*c.* 90 genera) of sauropod dinosaurs whose members were present and common in most Mesozoic ecosystems. The smallest, largest, geologically youngest, and most geographically widespread sauropods are titanosauriforms. Some genera are known from complete skeletons and ontogenetic series (e.g., Janensch, 1950; Curry Rogers, 2005), but most named species are poorly known. In particular, skulls are exceedingly rare in Titanosauriformes, although recent discoveries have begun to remedy this problem (Curry Rogers, 2005; Chure *et al.*, 2010; Zaher *et al.*, 2011). Despite the patchy nature of much of their fossil record, several evolutionary patterns are apparent in titanosauriform evolution, including a trend towards decreasing tooth size (Chure *et al.*, 2010), development of a 'wide gauge' gait and concomitant appendicular specializations (Wilson & Carrano, 1999), and several episodes of gigantism (Bonaparte & Coria, 1993; Wedel, Cifelli & Sanders, 2000a) and dwarfing (Sander *et al.*, 2006; Stein *et al.*, 2010). More derived titanosauriforms – lithostrotian titanosaurs – are characterized by a number of apomorphies that might seem counterintuitive for giant animals, including non-ossification of the carpus and manual phalanges (Curry Rogers, 2005), increased skeletal pneumaticity (Wedel, Cifelli & Sanders, 2000b), and the development of large osteoderms (D'Emic, Wilson & Chatterjee, 2009; Curry Rogers *et al.*, 2011).

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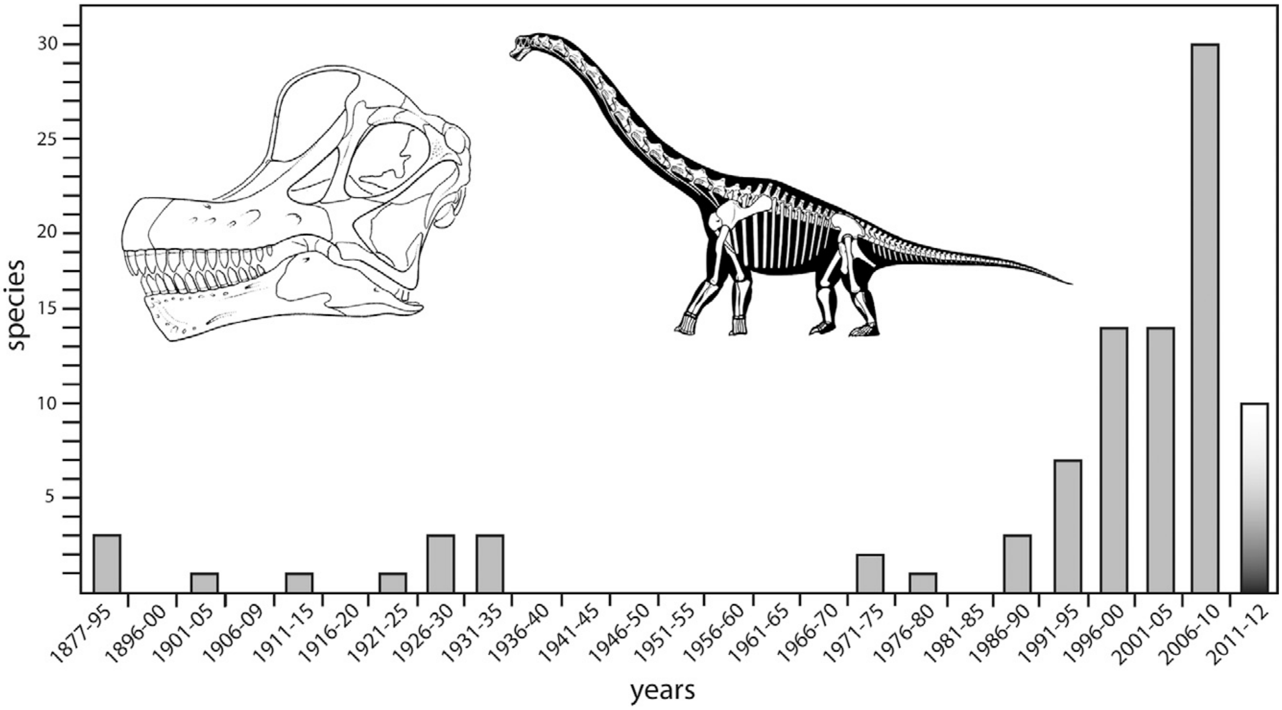

Figure 1. Titanosauriform discoveries plotted in five-year bins. Note the dramatic increase in naming in recent years. The skull and body of *Giraffatitan* (modified from Wilson & Sereno, 1998) highlight basal titanosauriform anatomy.

The number of named titanosauriforms has dramatically increased in recent years (Fig. 1), as has the number of taxonomic revisions adding information about previously named genera (e.g. Wilson & Upchurch, 2003; Wilson *et al*., 2009; D'Emic & Wilson, 2011; Mannion, 2011; Mannion & Calvo, 2011; Carballido *et al*., 2011a, b). The bulk of new discoveries have come from Asia and South America, but several North American, African, and Australian forms have come to light as well (see list in Mannion & Calvo, 2011).

Titanosauriforms are important to Mesozoic palaeobiogeography because of their diversity and ubiquity, but their impact on palaeobiogeography has not been fully realized owing to confusion over their phylogenetic relationships (e.g. Krause *et al*., 2006). For example, East Asian endemism has been suggested for sauropods during various time periods, from the Middle Jurassic to the Cretaceous (Russell, 1993; Upchurch, Hunn & Norman, 2002; Wilson & Upchurch, 2009). Recently, all Cretaceous East Asian sauropods have been recognized as titanosauriforms, in contrast to an array of non-neosauropods that characterized the Jurassic of Asia (Wilson, 2005; Whitlock, D'Emic & Wilson, 2011). Resolving the role of endemism and the details of this faunal turnover for the sauropods of East Asia also depends on their lower-level phylogenetic relationships.

Titanosauriformes and its subclades are stable because they are defined by phylogenetic nomenclature (e.g. the sister clades Brachiosauridae and Somphospondyli; Table 1), but the content of and interrelationships within these clades vary substantially depending on the analysis. These analyses in turn are sensitive to taxon inclusion, and with the inclusion of characters outpaced by the inclusion of taxa, few topologies are repeatedly recovered amongst analyses with small changes in taxonomic or character content (e.g. Royo-Torres, 2009).

In the following contribution, I review previous cladistic analyses focusing on basal titanosauriforms in order to identify areas of agreement and conflict. I then present a lower-level cladistic analysis of 25 ingroup taxa using a combination of previously formulated and novel characters. I then explore the phylogenetic affinities of taxa represented by fragmentary specimens and comment on the palaeobiogeographical patterns revealed, with a focus on the origins of Titanosauria.

ABBREVIATIONS

Institutions: FMNH PR, Field Museum of Natural History, Chicago; MB (HMN MB.R), Humboldt Museum für Naturkunde, Berlin; MACN PV, Museo Argentino de Ciencias Naturales, Buenos Aires; MCF PVPH, Museo Cármen Funes, Paleontología de Vertebrados, Plaza Huincul; NHMUK, British Museum of Natural History, London; NSM, National Science Museum, Daejeon; YPM, Yale Peabody Museum, New Haven.

Table 1. Recommended phylogenetic nomenclature for selected clades within Titanosauriformes and its outgroups. Definitions follow Wilson & Sereno (1998), Wilson & Upchurch (2003), and Taylor (2009)

Clade	Definition	Reference/author
Neosauropoda	*Diplodocus longus*, *Saltasaurus loricatus*, MRCA and all its descendants	Bonaparte, 1986
Macronaria	Neosauropods more closely related to *Saltasaurus loricatus* than to *Diplodocus longus*	Wilson & Sereno, 1998
Euhelopodidae	Neosauropods more closely related to *Euhelopus zdanskyi* than to *Neuquensaurus australis*	Romer, 1956 (name); this study (definition)
Titanosauriformes	*Brachiosaurus altithorax*, *Saltasaurus loricatus*, MRCA and all its descendants	Salgado, Coria & Calvo 1997
Brachiosauridae	Neosauropods more closely related to *Brachiosaurus altithorax* than to *Saltasaurus loricatus*	Riggs, 1903
Somphospondyli	Neosauropods more closely related to *Saltasaurus loricatus* than to *Brachiosaurus altithorax*	Wilson & Sereno, 1998
Titanosauria	*Andesaurus delgadoi*, *Saltasaurus loricatus*, MRCA and its descendants	Bonaparte & Coria, 1993
Lithostrotia	*Malawisaurus dixeyi*, *Saltasaurus loricatus*, MRCA and its descendants	Upchurch *et al*., 2004

MRCA, most recent common ancestor.

Table 2. Comparison of the current and seven other recent cladistic analyses including a substantial number of basal titanosauriform sauropod dinosaurs. Character numbers in parentheses indicate the total number of characters included (i.e. including constant and parsimony-uninformative ones); number outside parenthesis indicates the number of parsimony-informative characters only

Analysis	No. of ingroup taxa	No. recovered as non-titanosaur TSFs	No. of characters	MPTs
Salgado *et al*., 1997	10	2	38	1
Wilson, 2002 (Wilson & Upchurch, 2009)	27	2	234	3
Canudo *et al*., 2008	17	3	217 (246)	9
González Riga *et al*., 2009	22	6	84 (102)	2
Upchurch *et al*., 2004 (Wilson & Upchurch, 2009)	34	4	309 (311)	97
Royo-Torres, 2009	24	6	295 (399)	5
Carballido *et al*., 2011a	28	6	227 (289)	12
This analysis	25	16	119	9

MPTs, most parsimonious trees; TSFs, Titanosauriformes.

Abbreviations for vertebral laminae and fossae follow Wilson (1999) and Wilson *et al*. (2011), respectively. Anatomical nomenclature is 'Romerian,' following that traditionally applied to reptiles (Wilson, 2006).

PREVIOUS CLADISTIC ANALYSES

'Basal' (non-titanosaur) titanosauriforms have been included in a number of cladistic analyses, including those investigating global sauropod relationships (e.g. Wilson, 2002; Upchurch, Barrett & Dodson, 2004) and those specifically aimed at resolving the relationships of newly described basal titanosauriforms (e.g. Rose, 2007; Canudo, Royo-Torres & Cuenca-Bescós, 2008). The latter types of analyses employ largely unmodified versions of the data matrices of the two global phylogenetic analyses mentioned above, so their taxonomic and character scope (sensu Sereno, 2009) have been somewhat homogenous. One advantage of these analyses having a similar taxonomic scope is that their results are more comparable than they would be otherwise. However, the addition of new taxa to analyses has outpaced the addition of characters and thus outpaced discovery of stable (i.e. repeatedly recovered) synapomorphies (Whitlock *et al*., 2011). Many of the analyses aimed at resolving basal titanosauriform relationships have included a substantial number of characters that were parsimony-uninformative (Table 2), or informative only to the relationships of non-titanosauriforms such as diplodocoids. This dilution of the available synapomorphy pool developed for global sauropod analyses (e.g. Upchurch, 1998; Wilson, 2002; Upchurch *et al*., 2004) results in reduced phylogenetic resolution and robustness relative to the original global analyses (Whitlock *et al*., 2011).

Of the many cladistic analyses that have included investigation of early titanosauriform relationships in their scope, six have contributed the bulk of new characters and taxon data (Fig. 2). These analyses show only coarse agreement in the phylogenetic relationships of basal titanosauriforms (Fig. 2). Between two and six genera have been resolved as non-titanosaur titanosauriforms in these previous analyses (Table 2). Brachiosaurids and titanosaurs are always united to the exclusion of *Camarasaurus*, and these three taxa are always united to the exclusion of Diplodocoidea. When included, *Chubutisaurus* and *Ligabuesaurus* are recovered as non-titanosaur somphospondylans (e.g. González Riga, Previtera & Pirrone, 2009; Royo-Torres, 2009; Carballido *et al*., 2011a). *Phuwiangosaurus* occupies a variety of positions in these analyses, including a non-titanosaur somphospondylan (e.g. González Riga *et al*., 2009), a brachiosaurid (Royo-Torres, 2009), and a titanosaur (Carballido *et al*., 2011a). Brachiosauridae is usually only composed of *Brachiosaurus* (including scorings for the now generically separate *Giraffatitan*; Taylor, 2009), but some analyses have recovered other genera (e.g. *Cedarosaurus*, '*Pleurocoelus*') within the clade as well. Figure 3 shows a strict consensus of simplified versions of the trees (those taxa present in more than half of the six analyses) depicted in Figure 2. This consensus cladogram fails to recover many commonly recovered sauropod clades as monophyletic, including Macronaria, Titanosauriformes, and Brachiosauridae. The base of Titanosauria is likewise unresolved, as a polytomy amongst *Andesaurus*, *Ligabuesaurus*, and *Chubutisaurus*. In order to explore the reasons behind this lack of resolution, one taxon at a time was removed from the matrix and the strict consensus re-computed. Most of the lack of resolution in the strict consensus appears to be the result of the unstable position of just a single taxon, *Euhelopus* (Fig. 3). Removing *Euhelopus* from the trees yields a better-resolved cladogram more consistent with previous studies (e.g. Wilson, 2002; Upchurch *et al*., 2004). In this cladogram, *Tastavinsaurus* is recovered as the sister taxon to Titanosauriformes, in contrast to its original description as a titanosauriform (Canudo *et al*., 2008). *Malawisaurus* is consistently recovered as a titanosaur intermediate in position between *Andesaurus* and more derived forms.

Many authors have published more than one iteration of a given matrix, usually varying the taxonomic content to accommodate new discoveries, with changes to characters and/or scoring in some cases (e.g. Calvo & González Riga, 2003; Calvo, González Riga & Porfiri, 2008; González Riga *et al*., 2009). Each of these sets of analyses will be discussed together, with focus on the most recent analysis of each set that contributed substantial modification to the data matrix. For more detailed comments on previous iterations of the matrices discussed here (e.g. Upchurch, 1995, 1998; Wilson & Sereno, 1998), see Wilson (2002).

SALGADO, CORIA & CALVO (1997)

The results of Salgado *et al*. (1997) allied *Camarasaurus*, brachiosaurids, and titanosaurs to the exclusion of diplodocoids (Fig. 2). Salgado *et al*. (1997) coined the node-based clades Titanosauriformes and Camarasauromorpha, and provided a phylogenetic definition for Titanosauria and several included clades. Their analysis included detailed descriptions of synapomorphies that have been inherited by more recent analyses. Consequently, the analysis of Salgado *et al*. (1997) has served as a higher-level 'backbone' of character data, topology, and phylogenetic nomenclature that has been modified for studies of lower-level titanosauriform affinities. Several synapomorphies were cited as support for each node of Salgado *et al*. (1997), but decay indices (Bremer, 1994) were not reported. Re-analysis of the matrix of Salgado *et al*. (1997) produces decay indices of 2 and 3 for Titanosauria and Titanosauriformes, respectively; all other decay indices were equal to 1. Salgado *et al*. (1997) included material pertaining to three non-titanosaur titanosauriforms in their analysis: *Giraffatitan*/*Brachiosaurus* (both scored under *Brachiosaurus*) and *Chubutisaurus*. They recovered *Giraffatitan* and *Andesaurus* as the most basal titanosauriform and titanosaur, respectively, with *Chubutisaurus* as the sister taxon to Titanosauria. They recovered a monophyletic 'Titanosauridae' (equivalent to Lithostrotia of Upchurch *et al*., 2004) and Saltasaurinae, as in most subsequent titanosauriform cladistic analyses.

WILSON (2002); WILSON & UPCHURCH (2009)

The analysis of Wilson (2002) aimed to study the lower-level relationships of representatives of all major sauropod clades, including basal forms, diplodocoids, and titanosaurs and their relatives (Fig. 2). Wilson (2002) included two non-titanosauriform titanosaurs in his analysis: *Brachiosaurus* (including *Giraffatitan*) and *Euhelopus*, which were recovered as successive sister taxa to Titanosauria, following Wilson & Sereno (1998). Wilson & Sereno (1998) named Somphospondyli, a stem-based node uniting titanosauriforms more closely related to *Saltasaurus* than to *Brachiosaurus* (i.e. non-brachiosaurid titanosauriforms). Wilson & Upchurch (2009) recommended modification for some of the scores for *Euhelopus* in the Wilson (2002) matrix. These alterations do not alter the topology found by Wilson (2002), but do weaken support for the node uniting *Euhelopus* + Titanosauria

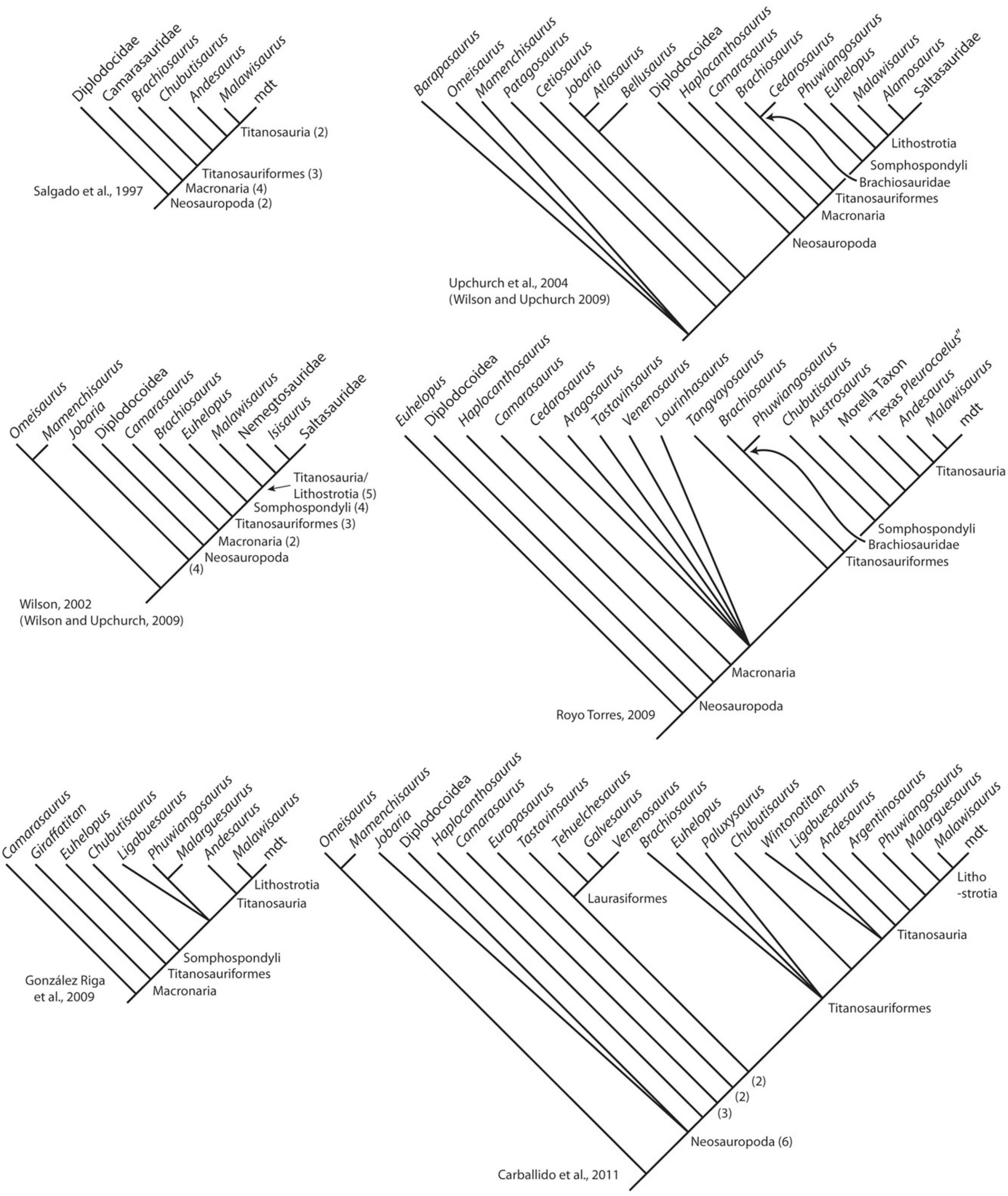

Figure 2. Selected previous cladistic hypotheses for the relationships of basal titanosauriforms, with their authors listed near their root. mdt, more derived titanosaurs. Numbers near each node indicate decay indices calculated in PAUP*.

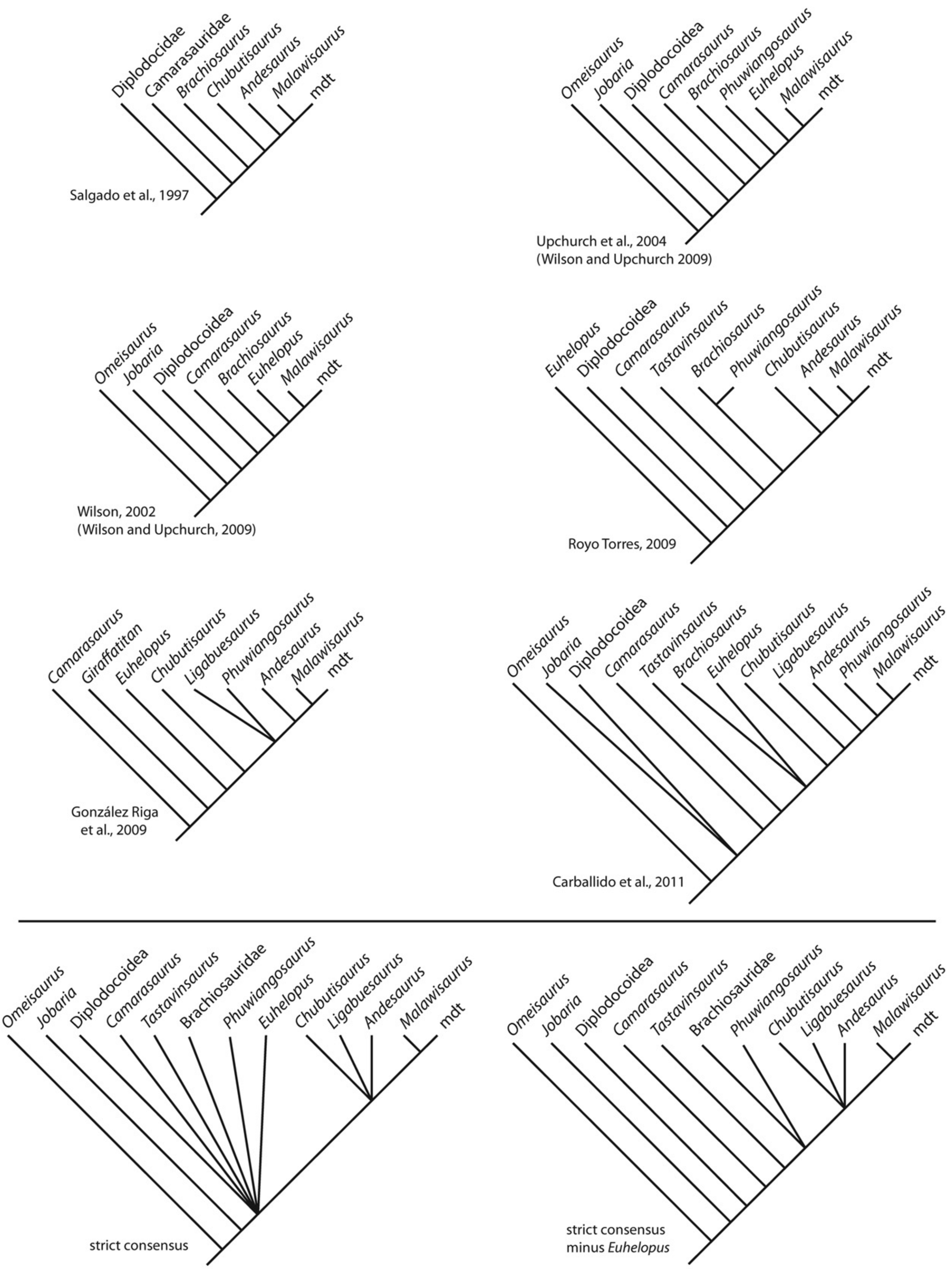

Figure 3. Parsed versions of the cladograms presented in Figure 2, with their authors listed near their root. Only taxa appearing in at least half of those analyses are included here. A strict consensus of these analyses with and without *Euhelopus* is shown at the bottom left and bottom right of the figure, respectively. mdt, more derived titanosaurs.

(Fig. 2). Most of the other titanosauriform nodes in this modified analysis of Wilson (2002) are robustly supported (Fig. 2).

The relationships of most taxa included in both Wilson (2002) and Salgado *et al*. (1997) are identical. Wilson (2002) did not include *Andesaurus* in his analysis, but like Salgado *et al*. (1997), recovered *Malawisaurus* in a basal position relative to other titanosaurs.

UPCHURCH *ET AL*. (2004); WILSON & UPCHURCH (2009)

Upchurch *et al*. (2004) presented an expanded and updated version of the matrices presented in Upchurch (1995, 1998). Like Wilson (2002), the scope of analysis in Upchurch *et al*. (2004) was broad (Sauropoda). That analysis included a variety of taxa regarded as non-titanosaur titanosauriforms by most authors (e.g. *Euhelopus*, *Phuwiangosaurus*; González Riga *et al*., 2009; Suteethorn *et al*., 2010), but only two were recovered as such in Upchurch *et al*. (2004): *Brachiosaurus* (including *Giraffatitan*) and *Cedarosaurus* (Fig. 2). As *Andesaurus* was absent from the analysis of Upchurch *et al*. (2004) and is one of the specifiers for the definition of Titanosauria (Wilson & Upchurch, 2003; Table 1), the labelling of Titanosauria by Upchurch *et al*. (2004) at any node between Titanosauriformes and Lithostrotia was arbitrary. Consequently, the titanosaur membership of *Phuwiangosaurus* posited by Upchurch *et al*. (2004) was ambiguous according to their results.

As in previous analyses (e.g. Salgado *et al*., 1997), *Brachiosaurus* was more closely related to titanosaurs than *Camarasaurus* in the analysis of Upchurch *et al*. (2004). Upchurch *et al*. (2004) presented the first cladistic support for Brachiosauridae, uniting the Early Cretaceous North American *Cedarosaurus* with *Brachiosaurus* (including *Giraffatitan* in the scorings for the latter). The purported *Brachiosaurus*-like Middle Jurassic sauropod *Atlasaurus* (Allain *et al*., 1999) was found to be a non-titanosauriform neosauropod closely allied with *Jobaria* (Sereno *et al*., 1999). *Tehuelchesaurus* was found to be a non-neosauropod closely related to *Omeisaurus* following the original description of the former taxon (Rich *et al*., 1999).

The scorings for *Euhelopus* in the Upchurch *et al*. (2004) matrix were modified by Wilson & Upchurch (2009) with substantial consequences for the phylogenetic position of several taxa. *Euhelopus* was recovered as the sister taxon of Titanosauria in agreement with Wilson & Sereno (1998) and Wilson (2002). The sister-taxon relationship between *Brachiosaurus* and *Cedarosaurus* was unchanged, but *Atlasaurus* and *Jobaria* moved outside of Neosauropoda. *Tehuelchesaurus* was deleted from the revised matrix of Upchurch *et al*. (2004) presented in Wilson & Upchurch (2009). Upchurch *et al*. (2004) recovered similar titanosaur inter-relationships as other analyses (e.g. Salgado *et al*., 1997), including a basal position for *Malawisaurus*.

ROYO-TORRES (2009); ROYO-TORRES, ALCALÁ & COBOS (2012)

Royo-Torres (2009) described a sauropod from the Early Cretaceous of Spain, *Tastavinsaurus sanzi*, and investigated its phylogenetic affinities with a matrix containing a broad sample of basal titanosauriforms and 65 new characters. This influx of novel taxon and character data resulted in substantial differences between the results of Royo-Torres (2009) and previous analyses, despite the fact that over one quarter of the included characters (104/399) were parsimony uninformative. The topologies recovered by Royo-Torres (2009) are highly sensitive to taxon inclusion (compare his figs 4.208, 4.209, and 4.212), and few steps are needed to collapse any given node. Royo-Torres (2009) included 15 taxa traditionally regarded as non-titanosaur titanosauriforms in two separate analyses. The first analysis only included characters for anatomical regions preserved in *Tastavinsaurus*; the second contained characters sampled from the entire skeleton. The discussion below will focus on the latter, more comprehensive analysis.

The data matrix (25 ingroup taxa, 399 characters) was re-run in PAUP* (Swofford, 2002), which produced five most parsimonious trees of tree length 752, identical to the results of Royo-Torres (2009). Royo-Torres (2009) did not present a strict consensus of these trees. I computed a strict consensus in PAUP*, which yielded a large polytomy at the base of Titanosauriformes (Fig. 2). Royo-Torres (2009: fig. 4.212) presented a 50% majority consensus of his five most parsimonious trees, which included a novel clade for which he coined the name Laurasiformes. Laurasiformes was defined as a stem-based taxon containing taxa more closely related to *Tastavinsaurus* than *Saltasaurus*. The existence of Laurasiformes is highly sensitive to taxon and character inclusion; the clade is absent from the strict consensus of the tree built from 25 taxa, but is present when 28 taxa are included and many characters are excluded (compare Royo-Torres, 2009: figs 4.209, 4.212).

Several novel relationships are hypothesized according to the strict consensus of the results of Royo-Torres (2009). Most of these novel hypotheses are also present in his 50% majority rule tree (fig. 4.212), including *Euhelopus* as the outgroup to Neosauropoda, *Tangvayosaurus* as the sister taxon of Titanosauriformes, and a close relationship between

Phuwiangosaurus and *Brachiosaurus*. '*Pleurocoelus*' from Texas was recovered just outside of Titanosauria. The scorings for '*Pleurocoelus*' from Texas in the matrix of Royo-Torres (2009: table 4.97) include material from several specimens [i.e. dorsal and caudal vertebrae (SMU 61732), hindlimb (FMNH PR 977)]. As shown by D'Emic (in press), these specimens pertain to more than one species, making this operational taxonomic unit a chimera in the matrix of Royo-Torres (2009). Finally, *Andesaurus* and *Malawisaurus* are recovered as the basal-most titanosaurs in Royo-Torres' (2009) analysis, in keeping with the results of previous analyses (e.g. Salgado *et al*., 1997). Decay indices could not be calculated for the results of Royo-Torres (2009) because of computing limitations.

Canudo *et al*. (2008) presented a restricted version of the same matrix used by Royo-Torres (2009), and obtained a different set of relationships for the Laurasiformes than any recovered by Royo-Torres (2009). Specifically, only *Venenosaurus* and *Tastavinsaurus* were members of Laurasiformes, and *Phuwiangosaurus* was not recovered as a brachiosaurid, but in a clade with *Andesaurus* and *Cedarosaurus*. One most parsimonious cladogram was reported by Canudo *et al*. (2008), but the polytomies those authors depict implies that the number of most parsimonious cladograms is equal to at least nine. The decay indices reported by Canudo *et al*. (2008) are implausibly high given the data at hand (e.g. 24 for Titanosauriformes). In sum, Canudo *et al*. (2008) and Royo-Torres (2009) presented many novel characters, yet these analyses do not result in a stable set of relationships for basal titanosauriforms. Likewise, there are problems with several of the characters in the analyses of Canudo *et al*. (2008) and Royo-Torres (2009), which will be discussed below (see 'Characters'). The existence of Laurasiformes will be tested below (see 'Laurasiformes').

GONZÁLEZ RIGA *ET AL*. (2009)

González Riga *et al*. (2009), in their description of the mid-Cretaceous Argentine taxon *Malarguesaurus florenciae*, presented a phylogenetic analysis of Titanosauriformes focusing on titanosaurs (Fig. 2). This matrix represents the latest iteration of the matrix used by Calvo & González Riga (2003), González Riga (2003), Bonaparte, González Riga & Apesteguía (2006), and Calvo, González Riga & Porfiri (2007, 2008). In turn, the original matrix of Calvo & González Riga (2003) is largely based on characters culled from previous analyses (Wilson, 2002; Upchurch *et al*., 2004). As such, they largely agree with the results of those cladistic analyses of Titanosauriformes, always recovering a traditional Titanosauriformes and Titanosauria, as well as positioning *Euhelopus* as the most basal somphospondylan and *Andesaurus* and *Malawisaurus* as basal titanosaurs. Several taxa not generally included in other analyses were included in the González Riga *et al*. (2009) family of analyses (e.g. *Ligabuesaurus*). In these analyses, *Ligabuesaurus*, *Phuwiangosaurus*, and *Chubutisaurus* are positioned as somphospondylans outside of Titanosauria.

The results presented by González Riga *et al*. (2009; two most parsimonious trees of 199 steps) could not be reproduced when their data matrix was re-run in PAUP*. Instead, 94 most parsimonious trees were recovered of tree length 206. The reasons for this discrepancy are unknown, as the analysis was repeated with the same parameters as those mentioned in González Riga *et al*. (2009). Eighteen of the 102 characters presented by González Riga *et al*. (2009) were parsimony uninformative. A strict consensus of these trees yielded a large polytomy amongst *Phuwianogsaurus*, *Ligabuesaurus*, *Malarguesaurus*, *Andesaurus*, and Lithostrotia, as well as a polytomy amongst the node uniting those taxa, *Euhelopus*, and *Chubutisaurus*. A 50% majority rule of these trees was identical to the results of González Riga *et al*. (2009), except that *Ligabuesaurus*, *Phuwiangosaurus*, and *Malarguesaurus* formed a polytomy. The reasons for these discrepancies are unknown.

CHURE *ET AL*. (2010)

Chure *et al*., 2010 described abundant cranial material of the Early Cretaceous North American sauropod *Abydosaurus mcintoshi* and conducted a phylogenetic analysis in which they recovered *Abydosaurus* as the sister taxon of *Brachiosaurus* (Fig. 2) (note that their scorings for *Brachiosaurus altithorax* included data from *Giraffatitan brancai*). The matrix was a modified version of Wilson (2002), tailored to analyse the phylogenetic position of *Abydosaurus.* Apart from the addition of *Abydosaurus*, the only other topological difference between the results of Wilson (2002) and Chure *et al*. (2010) is that the latter could not resolve the position of *Jobaria*, *Haplocanthosaurus*, and Diplodocoidea with respect to Neosauropoda. In the results of Chure *et al*. (2010) the decay index of Brachiosauridae is 3, whereas those for Titanosauriformes, Somphospondyli, and Lithostrotia (*Malawisaurus* + more derived forms) are 5, 4, and 5, respectively.

CARBALLIDO *ET AL*., 2011a, b

Carballido *et al*. (2011a, b) conducted the most taxonomically comprehensive analyses of basal titanosauriform inter-relationships to date, including a substantial number of taxa included in cladistic analysis for the first time (Fig. 2). Carballido *et al*. (2011a) recovered a Laurasiformes that included *Tastavinsaurus*, *Venenosaurus*, *Techuelchesaurus*, and *Galvesaurus*. This result is similar to that recovered by Royo-Torres (2009), who originally named Laurasiformes. In contrast, Carballido *et al*. (2011b) found only *Janenschia* and *Tastavinsaurus* to lie within the Laurasiformes.

Carballido *et al*. (2011a) recovered *Euhelopus*, *Brachiosaurus* (including *Giraffatitan*), and '*Paluxysaurus*' (now referred to *Sauroposeidon*, D'Emic, in press; D'Emic & Foreman, 2012) in a polytomy. Some taxa recovered outside of Titanosauria in previous analyses (*Phuwiangosaurus*, *Malarguesaurus*) were recovered within that clade by Carballido *et al*. (2011a). Finally, Carballido *et al*. (2011a, b) resolved the Late Jurassic dwarf *Europasaurus* as a basal macronarian, in keeping with its original description (Sander *et al*., 2006). Support for nearly all nodes was low (decay index = 1) in Carballido *et al*.'s (2011a, b) analyses.

Re-running the character matrix of Carballido *et al*. (2011a) in PAUP* showed that of the 289 characters presented, 79% (227) were parsimony-informative. When their data set was re-run in PAUP*, three unambiguous laurasiform synapomorphies were recovered. All three recovered laurasiform synapomorphies (characters 101, 158, 173) have a homoplastic distribution amongst basal titanosauriforms, and all three are mis-scored in some way. For example, a 'supraneural camera' (character 101; a centroprezygapophyseal fossa that deeply invades the neural arch; Wilson *et al*., 2011) was scored as absent in *Brachiosaurus* and was left unscored in *Galvesaurus*, but the former taxon has this fossa (Wilson *et al*., 2011), whereas the latter does not (Barco, 2009). Likewise, Laurasiformes was recovered with a specialized 'platycoelous/distoplatyan' anterior caudal vertebral centrum articulation (character 158), but anterior caudal vertebral centra with slightly concave anterior faces and concave-to-flat posterior faces are common amongst non-titanosaurs, including *Brachiosaurus*, *Sauroposeidon*, *Camarasaurus*, and *Haplocanthosaurus*, all of which were incorrectly scored as having different articulations to Laurasiformes. The same criticism applies to the final laurasiform synapomorphy (character 173), 'middle caudal vertebral neural spines vertical' – this feature characterizes *Camarasaurus*, *Haplocanthosaurus*, *Brachiosaurus*, and *Giraffatitan* as well as Laurasiformes, but was scored differently for these taxa. Changing these scorings in the matrix of Carballido *et al*. (2011a) and running it in PAUP* could not replicate results obtained with the original scorings – no result was obtained because of limitations in computing power. However, based on these scoring changes, there does not seem to be support for Laurasiformes in the corrected data set.

CLADISTIC ANALYSIS OF LOWER-LEVEL RELATIONSHIPS OF BASAL TITANOSAURIFORM SAUROPODS

Below I present a lower-level cladistic analysis focusing on the relationships of basal titanosauriforms. I outline the operational taxonomic units employed, present the results and robustness of the analysis, and discuss its implications. See appendices for the character-taxon matrix (Appendix 1), character list (Appendix 2), synapomorphy list (Appendix 3), and autapomorphy list (Appendix 4).

OUTGROUP CHOICE

Character polarity was determined on the basis of outgroup comparison. Some ingroup taxa (e.g. Diplodocoidea, *Camarasaurus*) are universally regarded as non-titanosauriforms (e.g. Wilson, 2002; Upchurch *et al*., 2004), but were included in the ingroup so as to not assume the titanosauriform affinities of these or other taxa a priori. Three taxa were selected as outgroups: *Shunosaurus lii* (Dong, Zhou & Zhang, 1983), *Omeisaurus* (including *Omeisaurus tianfuensis He, Li & Cai*, 1988 and *Omeisaurus maoianus Tang et al*., 2001) and *Jobaria tiguidensis* (Sereno *et al*., 1999). These taxa were selected for their completeness and because they have been recovered as non-neosauropod eusauropods by nearly all authors (Sereno *et al*., 1999; Wilson, 2002; Upchurch *et al*., 2004 when scores were corrected for the latter as per Wilson & Upchurch, 2009). *Jobaria* was originally thought to be Early Cretaceous in age (Sereno *et al*., 1999), but may be older, perhaps Middle Jurassic (Rauhut & Lopez-Arbarello, 2009). *Omeisaurus* is Middle Jurassic in age (Tang *et al*., 2001), pre-dating any of the taxa in the ingroup with the exception of *Atlasaurus imelaki* (Allain *et al*., 1999).

TERMINAL TAXA

Twenty-five terminal taxa were selected for phylogenetic analysis (Table 3). These taxa were selected in an effort to sample the spatiotemporal distribution (Middle Jurassic–Late Cretaceous) and morphologies of possible basal titanosauriforms. Several taxa were not included in the analysis because their validity could not be evaluated or substantiated (e.g. *Aragosaurus*, *Fukuititan*, *Fusuisaurus*, *Pukyongosaurus*) see 'Relationships of fragmentarily represented taxa' below). Fragmentarily represented taxa were not excluded a priori because anatomical completeness

Table 3. Geological age, geographical range, per cent missing data, and original reference (i.e. data sources aside from personal observation) for three outgroups (*Shunosaurus*, *Omeisaurus*, *Jobaria*) and terminal taxa analysed

Taxon	Geological age (stage)	Geographical range	References
Shunosaurus lii	Middle Jurassic (Bathonian–Callovian)	Asia (China)	Dong *et al*., 1983
Omeisaurus	Middle Jurassic (Bathonian–Callovian)	Asia (China)	Young, 1939
Jobaria tiguidensis	Middle or Late Jurassic (Bathonian–Oxfordian)	Africa (Niger)	Sereno *et al*., 1999
Atlasaurus imelaki	Middle Jurassic (Bathonian–Callovian)	Africa (Morocco)	Monbaron *et al*., 1999
Diplodocoidea	Late Jurassic–Late Cretaceous (Kimmeridgian–Coniacian)	North America (USA), Europe (various), Africa (Niger), South America (Argentina)	Marsh, 1884; Upchurch, 1995; Whitlock, 2011
Camarasaurus	Late Jurassic (Kimmeridgian–Tithonian)	North America (USA)	Cope, 1877
Tehuelchesaurus benitezii	Late Jurassic (Kimmeridgian–Tithonian)	South America (Argentina)	Rich *et al*., 1999; Carballido *et al*., 2011b
Europasaurus holgeri	Late Jurassic (Kimmeridgian)	Europe (Germany)	Sander *et al*., 2006
Giraffatitan brancai	Late Jurassic (Kimmeridgian–Tithonian)	Africa (Tanzania)	Janensch, 1914, 1929, 1950, 1961; Paul, 1988
Brachiosaurus altithorax	Late Jurassic (Kimmeridgian–Tithonian)	North America (USA)	Riggs, 1903
Cedarosaurus weiskopfae	Early Cretaceous (Aptian–Albian)	North America (USA)	Tidwell *et al*., 1999
Venenosaurus dicrocei	Early Cretaceous (Aptian–Albian)	North America (USA)	Tidwell *et al*., 2001; Tidwell and Wilhite, 2005
Abydosaurus mcintoshi	Early Cretaceous (late Albian)	North America (USA)	Chure *et al*., 2010
Ligabuesaurus leanzi	Early Cretaceous (Aptian–Albian)	South America (Argentina)	Bonaparte *et al*., 2006
Sauroposeidon proteles	Early Cretaceous (Aptian–Albian)	North America (USA)	Wedel *et al*., 2000a, b; Rose, 2007; D'Emic & Foreman, 2012
Chubutisaurus insignis	Early or Late Cretaceous (Aptian–Cenomanian)	South America (Argentina)	del Corro, 1975; Carballido *et al*. 2011a
Tastavinsaurus sanzi	Early Cretaceous (Aptian)	Europe (Spain)	Canudo *et al*., 2008; Royo-Torres, 2009; Royo-Torres *et al*., 2012
Qiaowanlong kangxii	Early Cretaceous (Aptian–Albian)	Asia (China)	You & Li, 2009
Erketu ellisoni	Late Cretaceous (Cenomanian–Santonian)	Asia (Mongolia)	Ksepka & Norell, 2006, 2010
Daxiatitan binglingi	Early Cretaceous	Asia (China)	You *et al*., 2008
Euhelopus zdanskyi	Early Cretaceous (Barremian–Aptian)	Asia (China)	Wiman, 1929; Wilson & Upchurch, 2009
Phuwiangosaurus sirindhornae	Early Cretaceous (Barremian–Aptian)	Asia (Thailand)	Martin *et al*., 1994; Suteethorn *et al*., 2009, 2010
Tangvayosaurus hoffeti	Early Cretaceous (Aptian–Albian)	Asia (Laos)	Allain *et al*., 1999
Andesaurus delgadoi	Early or Late Cretaceous (Albian–Cenomanian)	South America (Argentina)	Calvo & Bonaparte, 1991, Mannion & Calvo, 2011
Malawisaurus dixeyi	Early Cretaceous (Aptian)	Africa (Malawi)	Haughton, 1928; Jacobs *et al*., 1993; Gomani, 2005
Opisthocoelicaudia skarzynskii	Late Cretaceous (Maastrichtian)	Asia (Mongolia)	Borsuk-Bialynicka, 1977
Alamosaurus sanjuanensis	Late Cretaceous (Maastrichtian)	North America (USA)	Gilmore, 1922; Lehman & Coulson, 2002; D'Emic *et al*., 2011
'Saltasaurini' (*Saltasaurus, Neuquensaurus, Rocasaurus*)	Late Cretaceous (Campanian–Maastrichtian)	South America (USA)	Powell, 1992; Lydekker, 1893; Salgado & Azpilicueta, 2000; D'Emic & Wilson, 2011

does not necessarily equal phylogenetic informativeness (Smith, 1994; Upchurch, 1998; Kearney, 2002). However, several fragmentary taxa were excluded because the ratio of available (i.e. described or personally observed) to preserved information was low (e.g. *Daanosaurus*, *Dongyangosaurus*, *Huanghetitan*, *Lusotitan*). Including these taxa would have resulted in a large amount of unnecessarily missing data and a likely loss of resolution. This analysis did not aim to resolve the relationships of all titanosauriforms, only the basal (non-titanosaur) ones. Consequently, taxonomic sampling of derived titanosaurs (i.e. lithostrotians) was limited to well-preserved taxa that are representative of several previously recovered 'grades' of titanosaurs. These representatives include purported basal titanosaurs (*Andesaurus*, *Phuwiangosaurus, Venenosaurus, Tangvayosaurus*) and one of the specifiers of Lithostrotia (*Malawisaurus*; Upchurch *et al*., 2004).

All taxa were scored on the basis of personal observation and original descriptions with the exception of *Qiaowanlong*, *Daxiatitan*, *Atlasaurus*, *Omeisaurus*, *Euhelopus*, and *Tastavinsaurus*. These latter taxa were scored on the basis of published descriptions and monographs and supplemented with photographs from colleagues (see Acknowledgements). The monophyly of each terminal taxon is justified with autapomorphies (see Appendix 4). Many terminal taxa are taxonomically simple, but some terminal taxa require further discussion (see below) because their content and/or diagnosis differ from their original or traditional definition. Likewise, two ingroup taxa are composites of several sauropod genera (Diplodocoidea and 'Saltasaurini') and one ingroup taxon contains several species (*Camarasaurus*); justification for these higher-level groupings is also provided below.

ALAMOSAURUS SANJUANENSIS

Alamosaurus sanjuanensis was named on the basis of a holotypic scapula and paratypic ischium from the Maastrichtian Kirtland Formation of New Mexico, USA (Gilmore, 1922). Referred remains from Utah (Gilmore, 1946) and Texas (Lehman & Coulson, 2002) are substantiated by autapomorphies amongst the exemplars (D'Emic *et al*., 2011) and were included in scoring for *Alamosaurus*. Teeth (Kues, Lehman & Rigby, 1980) and a pes (D'Emic *et al*., 2011) from the holotypic area and horizon were also included in the scoring for *Alamosaurus* because they most likely pertain to *Alamosaurus*, the only sauropod genus recognized from the Maastrichtian of North America.

BRACHIOSAURUS ALTITHORAX AND *GIRAFFATITAN BRANCAI*

Riggs (1903) coined the name *Brachiosaurus altithorax* for what was then the world's largest-known dinosaur. *Brachiosaurus altithorax* was founded on a single partial skeleton from the Late Jurassic Morrison Formation of Colorado, USA, represented by several dorsal vertebrae, a sacrum with ilia, two caudal vertebrae, a coracoid, humerus, femur, and some dorsal ribs. Some other materials from the Morrison Formation may belong to *Brachiosaurus altithorax* (see review in Taylor, 2009), but many of these materials do not overlap anatomically with the holotype, and those materials that do overlap have not currently been united with the holotype using autapomorphies. Consequently, scoring for *Brachiosaurus altithorax* is limited to the holotype.

Janensch (1914) named two additional species of *Brachiosaurus* from the Late Jurassic Tendaguru beds of Tanzania, *Brachiosaurus brancai* and *Brachiosaurus fraasi*, which were later synonymized by Janensch (1929). Paul (1988) proposed that the Tanzanian form be regarded as a separate subgenus, *Brachiosaurus* (*Giraffatitan*) *brancai*, which Taylor (2009) formalized by referring the Tanzanian brachiosaur material to a separate genus, *Giraffatitan brancai*. Many of the differences cited by Taylor (2009) do not differ substantially between the Morrison and Tendaguru specimens when serial and individual variation are taken into account [e.g. caudal vertebral neural spine shape; compare Taylor (2009: fig. 3) with Ikejiri *et al*. (2005: fig. 5)]. In addition, some of the differences cited in support of generic separation of the Morrison and Tendaguru brachiosaurids are erroneous owing to misinterpretation of broken or deformed features (e.g. the cited tubercle on the posterior ilium of *Brachiosaurus altithorax* is a fragment of a sacral rib; the cited block-like hyposphene of the caudal vertebrae of *Brachiosaurus altithorax* is the broken remainder of the postzygapophyses; pers. observ.), or have a wider distribution amongst sauropods (e.g. the laterally deflected coracoid glenoid; see Wilson & Sereno, 1998). However, several features suggested by previous authors (Janensch, 1950; Paul, 1988; Taylor, 2009) do distinguish the Tendaguru and Morrison brachiosaurid exemplars in a substantive way. The following features do not vary within other sauropod genera when deformation, breakage, within-individual, and within-species sources of variation are accounted for: the centra of dorsal vertebrae are broader transversely than dorsoventrally in *Giraffatitan brancai*, rather than subcircular in cross-section in *B. altithorax*; anterior caudal vertebrae are about 30% taller relative to centrum length in *Brachiosaurus altithorax*; transverse processes are only half of the neural spine length in the posterior dorsal vertebrae of *Brachiosaurus altithorax*, whereas they are subequal to neural spine length in *Giraffatitan brancai* (Janensch, 1950; Paul, 1988; Taylor, 2009). These three features justify the generic separation of *Giraffatitan* and *Brachiosaurus*. Consequently, the name *Giraffatitan brancai* will be used to refer to the hypodigm brachiosaur material from Tendaguru.

CAMARASAURUS

The genus *Camarasaurus* is known from dozens of skeletons found across the western USA (Ikejiri, 2005). Four species of *Camarasaurus* are currently recognized: *Camarasaurus grandis*, *Camarasaurus lewisi*, *Camarasaurus supremus*, and *Camarasaurus lentus* (Upchurch *et al*., 2004). Perhaps owing to its broad spatial distribution and the presence of four species in the terminal taxon, some characters are polymorphic for *Camarasaurus* in this analysis. Where polymorphisms were present, the state present in the Gunma specimen (McIntosh *et al*., 1996) of *Camarasaurus* was favoured, because it is found stratigraphically lower (and is several million years older) than most other specimens of *Camarasaurus*, and so it is more likely to approximate the ancestral condition for the genus (Ikejiri, 2005).

CEDAROSAURUS WEISKOPFAE

Tidwell, Carpenter & Brooks (1999) named *Cedarosaurus weiskopfae* on the basis of a partial skeleton from the Early Cretaceous Cedar Mountain Formation of Utah, USA. D'Emic (in press) demonstrated that a sauropod hind limb from the Glen Rose Formation of Texas (FMNH PR 977) is referable to *Cedarosaurus*, so this material was included in the scores as well.

DIPLODOCOIDEA

Diplodocoidea is a diverse, geographically widespread clade that evolved alongside Titanosauriformes until the mid-Cretaceous. The phylogeny of the group is mostly based on their derived cranial anatomy, with few appendicular specializations (Whitlock, 2011). Scoring for Diplodocoidea was mostly based on the most primitive diplodocoid, *Haplocanthosaurus*, or the basal-most taxon available if data were missing for that genus, following the phylogeny of Whitlock (2011).

EUHELOPUS ZDANSKYI

Euhelopus zdanskyi is represented by cranial and postcranial material from the Mengyin Formation of China. *Euhelopus* is likely to be Early Cretaceous in age, although a Late Jurassic age is possible (Wilson & Upchurch, 2009). *Euhelopus* has been the subject of several detailed descriptions (Wiman, 1929; Mateer & McIntosh, 1985; Wilson & Upchurch, 2009) and studies of its phylogenetic affinities (Wilson & Sereno, 1998; Wilson & Upchurch, 2009), which have suggested that it is a basal somphospondylan. In the present analysis, exemplars 'a' and 'c' of *Euhelopus* are regarded as pertaining to one individual following Wilson & Upchurch (2009).

LIGABUESAURUS LEANZI

Bonaparte, González Riga & Apesteguía (2006) named *Ligabuesaurus leanzi* on the basis of abundant material from the Aptian Lohan Cura Formation of Argentina. Only the holotypic individual (MCF PHV 233, formerly MCF PHV 261) was considered for scoring *Ligabuesaurus* in this matrix; other, isolated materials were excluded (e.g. the tooth described by Bonaparte *et al*., 2006; MCF PHV 744).

PHUWIANGOSAURUS SIRINDHORNAE

Phuwiangosaurus sirindhornae was named by Martin, Buffetaut & Suteethorn (1994) on the basis of a partial skeleton from the Early Cretaceous Sao Khua Formation of north-east Thailand. Suteethorn *et al*. (2010) described new bones attributable to the holotype individual, and Suteethorn *et al*. (2009) described a new, juvenile individual. Personal observation confirms these referrals, so both the holotype and juvenile ('K11' specimen) skeletons were used for scoring.

SAUROPOSEIDON PROTELES

Sauroposeidon proteles was named by Wedel *et al*. (2000a) on the basis of four mid-cervical vertebrae from the Early Cretaceous Antlers Formation of Oklahoma, USA. Wedel *et al*. (2000a, b), and Wedel & Cifelli (2005) tentatively referred a cervical vertebral centrum from the penecontemporaneous Cloverly Formation of Wyoming to *Sauroposeidon proteles*. Revision of the Cloverly Formation sauropod material has confirmed this referral (D'Emic, in press; D'Emic & Foreman, 2012), as well as provided a basis for referral of material from the Cloverly Formation and the Twin Mountains Formation of Texas (material formerly referred to as '*Paluxysaurus jonesi*'). Autapomorphies, the absence of meaningful differences, and their similar age support referral of *Paluxysaurus* and the Cloverly Formation sauropod material to *Sauroposeidon proteles*, so all three sets of exemplars were used for scoring that taxon in this analysis.

'SALTASAURINI'

Saltasaurus, *Neuquensaurus*, and *Rocasaurus* form a clade when all three are included in cladistic analyses (e.g. Curry Rogers, 2005; González Riga *et al*., 2009).

I informally refer to these taxa as 'Saltasaurini' instead of Saltasaurinae, because Saltasaurinae is a stem-based taxon and may contain some of the other terminal taxa depending on the results of the analysis. The saltasaurine status of *Bonatitan* (Martinelli & Forasieppi, 2004) remains to be adequately tested by cladistic analysis, so it was excluded from scorings for 'Saltasaurini'. Data for *Neuquensaurus* were based on only holotypic and definitively referred materials as outlined in D'Emic & Wilson (2011).

CHARACTERS

The data matrix includes 119 characters (Appendix 2), six of which are multistate (characters 14, 18, 32, 69, 81, 88; three character states each) and all of which were ordered. These characters were ordered because state 1 is structurally intermediate between state 0 and state 2. The analysis was also run with all characters unordered, which had little effect on the topology (see below). The distribution of characters throughout the skeleton was uneven, with more characters representing the axial and appendicular skeleton than the cranium, perhaps reflecting the paucity of skull data in the group (Fig. 4). Previously formulated characters were selected and modified from the studies of Salgado *et al*. (1997), Wilson (2002), Upchurch *et al*. (2004), Curry Rogers (2005), González Riga *et al*. (2009), Royo-Torres (2009), Chure *et al*. (2010), Mannion (2011), and Mannion & Calvo (2011). Scoring changes to some characters outlined in Wilson (2005) and Wilson & Upchurch (2009) were implemented where appropriate. Other characters were formulated from personal observation, published diagnoses, autapomorphy lists (e.g. Wilson, 2002), and descriptions. Character states were modified for most previously formulated characters to reflect the taxonomic scope of this analysis. For example, Wilson (2002: character 80) coded the number of cervical vertebrae into five states (nine or fewer, 10, 12, 13, 15 or greater) in a cladistic analysis of Sauropoda. Because of the narrower taxonomic scope of the analysis presented herein, the number of states was reduced to two (14 or fewer, 15 or more).

Character state scorings were examined manually for errors in the data matrix; errors were also checked for as synapomorphy optimizations were listed. Characters were worded according to standardized cladistic 'grammar' in order to facilitate comparisons with other studies (Sereno, 2007).

Some characters that have previously been recovered as synapomorphies of clades relevant to this analysis (e.g. Titanosauria) were excluded because they either displayed too much individual or ontogenetic variation to confidently score or were invariant amongst the ingroup or outgroup.

Many other characters purported to be relevant to basal titanosauriform phylogeny by several authors were not included in this analysis because character states could not confidently be scored. For example, several characters presented by Royo-Torres (2009) are substantially variable along a single vertebral column (e.g. characters C30, C41, C42, C84, C89, C90, C104 in that analysis). For such characters, scorings for vertebrae just a few positions away from one another in the column are often different. Character C30 (mislabelled as character C39 in Royo-Torres, 2009: 426, translated from the Spanish) is an example of this type of character: 'dorsal surface of the neural spine in dorsal vertebrae: flat or flat-convex (0), concave (1)'. This character was scored as derived only for *Camarasaurus* and *Tastavinsaurus*. However, the concavity or convexity of the top of the neural spine varies substantially along the dorsal vertebral column in *Camarasaurus* (Osborn & Mook, 1921; compare Royo-Torres, 2009: fig. 4.20 with fig. 4.28). When available character data are anatomically disjunct (e.g. only dorsal vertebrae 1–3 are preserved in one species versus 4–6 in another species), serial variation may be spuriously cast as phylogenetically meaningful. Other characters have states that are indistinguishable when small amounts of individual variation or taphonomic deformation are taken into account (e.g. characters 154, 162, 172, 184, 213 of Royo-Torres, 2009; see figs 4.162, 4.170, 4.203 in that publication). Still other characters are linked (characters 192, 194 in Royo-Torres, 2009).

MISSING DATA

The amount of missing data for each terminal taxon is given in Table 4. The average amount of missing data per taxon was 42%; this ranged from 0% (*Camarasaurus*, Diplodocoidea) to 86% (*Qiaowanlong*). In addition, *Omeisaurus*, *Giraffatitan*, *Phuwiangosaurus*, 'Saltasaurini', and *Alamosaurus* had less than 20% missing data; *Atlasaurus*, *Erketu*, and *Venenosaurus* had more than 70% missing data. Missing data were usually a result of incompleteness of specimens, although in a few cases some data are preserved but were undescribed and could not be observed first-hand as part of this study (e.g. *Atlasaurus*).

TOPOLOGY

Twenty-five ingroup taxa and three outgroup taxa were scored for 119 characters (Appendix 1) in MacClade (Maddison & Maddison, 1992) and MESQUITE (Maddison & Maddison, 2009) and analysed in PAUP* (Swofford, 2002). The branch-and-bound search algorithm was used with stepwise addition and random branch swapping via the tree-bisection-

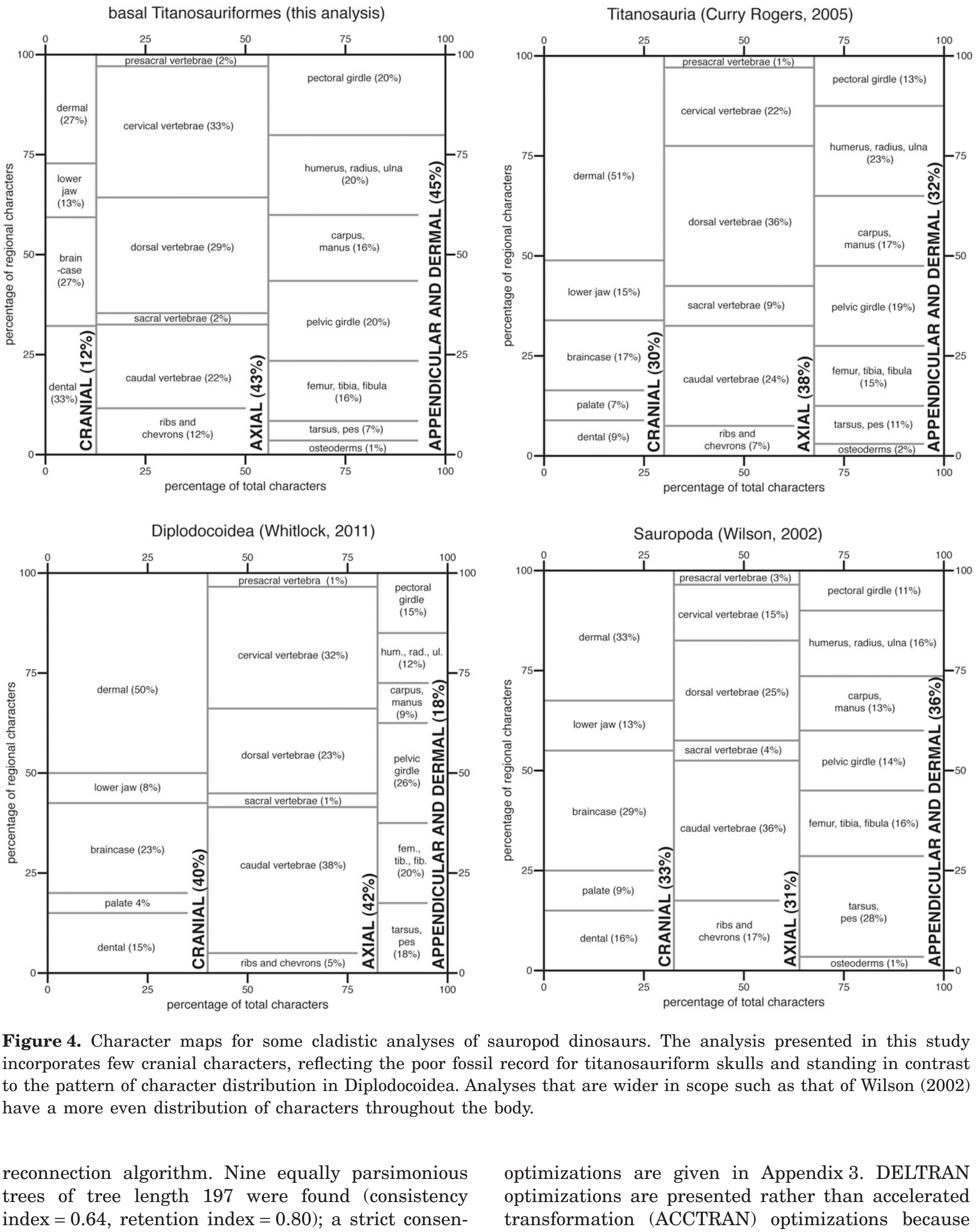

Figure 4. Character maps for some cladistic analyses of sauropod dinosaurs. The analysis presented in this study incorporates few cranial characters, reflecting the poor fossil record for titanosauriform skulls and standing in contrast to the pattern of character distribution in Diplodocoidea. Analyses that are wider in scope such as that of Wilson (2002) have a more even distribution of characters throughout the body.

reconnection algorithm. Nine equally parsimonious trees of tree length 197 were found (consistency index = 0.64, retention index = 0.80); a strict consensus of these trees is given in Figure 5. Synapomorphies supporting a strict consensus of these nine topologies under delayed transformation (DELTRAN) optimizations are given in Appendix 3. DELTRAN optimizations are presented rather than accelerated transformation (ACCTRAN) optimizations because DELTRAN minimizes the distribution of ambiguous synapomorphies owing to missing data (Table 4), and thus results in more phylogenetically restricted infer-

Table 4. Missing data in the outgroups and terminal taxa analysed, broken down by anatomical region

Taxon	Cranial	Axial	Appendicular/dermal	Total
Shunosaurus lii	0	8	15	10
Omeisaurus	0	10	10	8
Jobaria tiguidensis	6	0	2	2
Atlasaurus imelaki	56	75	87	77
Diplodocoidea	0	0	0	0
Camarasaurus	0	0	0	0
Tehuelchesaurus benitezii	100	55	48	58
Europasaurus holgeri	13	35	50	39
Giraffatitan brancai	0	10	2	5
Brachiosaurus altithorax	100	51	65	64
Cedarosaurus weiskopfae	100	47	48	55
Venenosaurus dicrocei	100	73	62	71
Abydosaurus mcintoshi	0	73	79	66
Ligabuesaurus leanzi	94	67	46	61
Sauroposeidon proteles	88	14	17	25
Chubutisaurus insignis	100	57	46	58
Tastavinsaurus sanzi	100	39	58	55
Qiaowanlong kangxii	100	84	83	86
Erketu ellisoni	100	76	85	83
Daxiatitan binglingi	100	51	81	71
Euhelopus zdanskyi	44	31	31	33
Phuwiangosaurus sirindhornae	50	0	25	18
Tangvayosaurus hoffeti	100	59	62	67
Andesaurus delgadoi	100	49	75	67
Malawisaurus dixeyi	38	8	40	26
Opisthocoelicaudia skarzynskii	100	31	12	32
Alamosaurus sanjuanensis	88	10	6	18
'Saltasaurini' *(Saltasaurus, Neuquensaurus, Rocasaurus)*	75	8	16	20
Average	63	36	41	42

ences of character distribution when missing data are substantial. Ambiguously optimized synapomorphies because of missing data and/or character conflict are given in Tables 5 and 6. All nodes within the ingroup are resolved with the exception of two polytomies, each involving three taxa. Pertinent phylogenetic nomenclature is listed in Table 1.

This analysis recovered three main titanosauriform clades: Brachiosauridae, Euhelopodidae, and Titanosauria (Fig. 5). *Atlasaurus* is recovered as the sister taxon to Neosauropoda, with Diplodocoidea, *Camarasaurus*, and *Tehuelchesaurus* as successive outgroups to Titanosauriformes. Titanosauriformes is composed of two sister clades, Brachiosauridae and Somphospondyli. Brachiosauridae contains a mix of Late Jurassic and Early Cretaceous Laurasian and Gondwanan taxa. Basal members of Somphospondyli include *Ligabuesaurus*, *Sauroposeidon*, and *Tastavinsaurus*. More derived somphospondylans are composed of two major clades, Euhelopodidae and the Titanosauria, with *Chubutisaurus* as outgroup to the latter. Euhelopodidae is comprised exclusively of East Asian Cretaceous genera. Two nested clades were recovered within Titanosauria: Lithostrotia and Saltasauridae. *Alamosaurus* and *Opisthocoelicaudia* were recovered as successive sister taxa of 'Saltasaurini'.

Basal (non-titanosaur) titanosauriforms were found to be diverse in this study (16 genera), in contrast to previous studies, which recovered at most six genera in this part of the cladogram (Table 2). The topology shows general congruence with geological age (Fig. 6), with basal titanosauriforms and their outgroups found in the Jurassic, basal somphospondylans in the Early and 'middle' Cretaceous, and titanosaurs mostly in the Late Cretaceous. Treating the ordered characters as unordered led to loss of all resolution within Euhelopodidae; all other relationships were identical to those recovered in the strict consensus of the nine most parsimonious trees found with ordered characters. When character transformations were unordered, the decay index of Brachiosauridae dropped from 3 to 2; all other decay indices were unaffected.

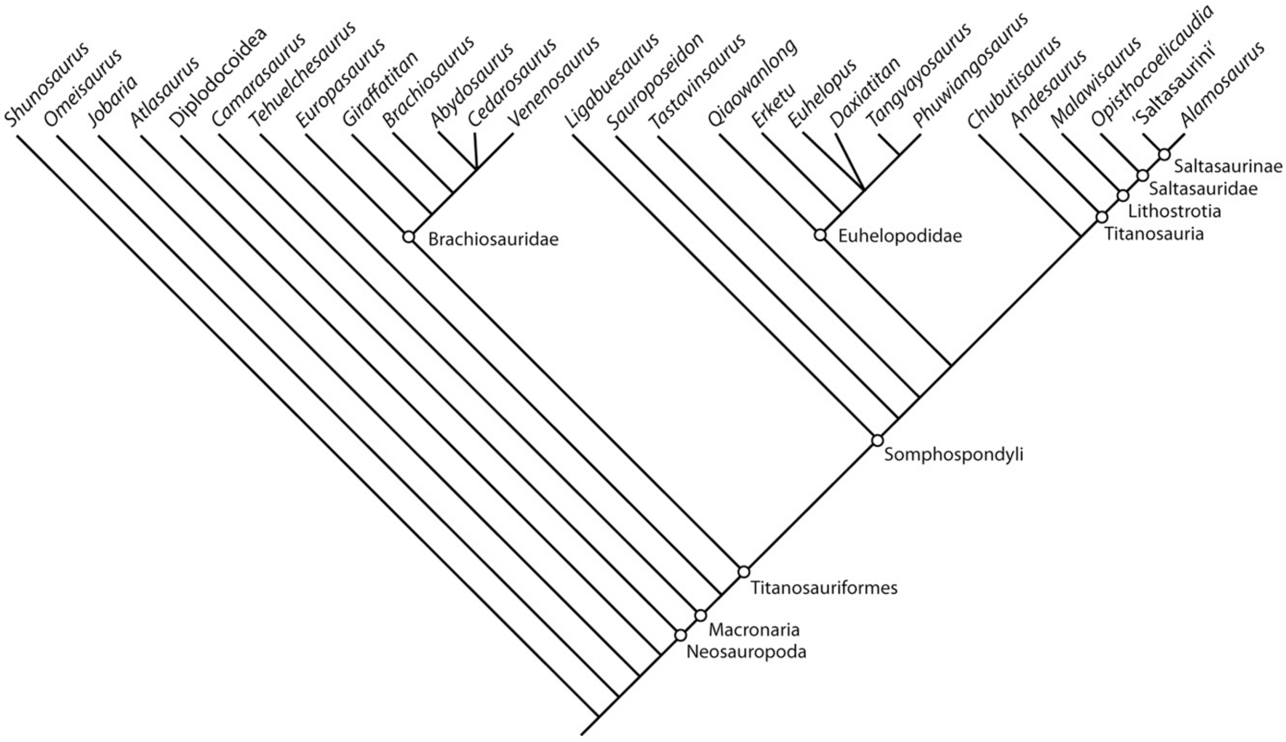

Figure 5. Cladistic hypothesis presented in this study. The cladogram is a strict consensus of nine equally parsimonious trees. Clade names as defined by phylogenetic taxonomy (Table 1; Wilson & Upchurch, 2003) are listed beside each node.

ROBUSTNESS OF RESULTS

The robustness of the most parsimonious trees was evaluated in terms of Bremer support, also known as the decay index (the number of additional steps required for a given node to disappear from a cladogram; Bremer, 1994). Decay indices for the topology presented in Figure 5 are given in Table 7. Decay indices were calculated in MacClade (Maddison & Maddison, 1992) by writing a 'Decay Index to PAUP' file, which was executed in PAUP* (Swofford, 2002). Almost half of the nodes (ten of 22) had a decay index equal to 1; most of these weaker nodes were within Brachiosauridae and the Euhelopodidae. Somphospondyli and Brachiosauridae are moderately supported (decay index = 3).

COMPARISONS WITH PREVIOUS ANALYSES

Below, I explore the topology presented in Figure 5 in detail, focusing on novel hypotheses of relationship presented in this analysis. Metrics and data supporting these relationships (number of additional steps required to support a given hypothesis, Templeton test statistics, synapomorphies) are given when relevant. See Templeton (1983) and Wilson (2002) for details regarding the Templeton test.

TITANOSAURIFORM OUTGROUPS

Atlasaurus is recovered as the sister taxon to Neosauropoda rather than as a brachiosaur relative as originally described (Monbaron, Russell & Taquet, 1999). Eight additional steps are required to position *Atlasaurus* within Brachiosauridae, a position rejected by a Templeton test ($N = 14$; $P = 0.0003$). *Atlasaurus* lacks several expected features of neosauropods and clades therein, such as mid-dorsal vertebrae with opisthocoelous centra, horizontally directed dorsal vertebral transverse processes, a ventrally expanded posterior centrodiapophyseal lamina, a process at the ventral base of the scapular blade, a single carpal, and a metacarpal I that is longer than metacarpal IV. Although brachiosaurid affinities for *Atlasaurus* can be ruled out, the precise phylogenetic position of *Atlasaurus* presented in Figure 5 should be considered preliminary, because most characters were unscored in this analysis (Table 4). Its completeness and Middle Jurassic age make *Atlasaurus* an important genus for understanding the origins of Neosauropoda.

Camarasaurus and Titanosauriformes are found to be more closely related to one another than either is to Diplodocoidea, as in taxonomically broader analyses of sauropod relationships (e.g. Wilson, 2002;

Table 5. Ambiguous character state optimizations attributable to missing data based on two optimization strategies in PAUP* (Swofford, 2002). Delayed transformations (DELTRAN) favour parallelism over reversals; accelerated transformations (ACCTRAN) favour reversals over parallelisms

Character number	ACCTRAN	DELTRAN
44, 65, 115	*Atlasaurus* + Neosauropoda	Neosauropoda
39, 41	Neosauropoda	Macronaria
23, 53, 58, 59, 66, 68, 91–93, 97–99, 101, 113	*Tehuelchesaurus* + Titanosauriformes	Titanosauriformes
31, *118*	*Tehuelchesaurus* + Titanosauriformes	Somphospondyli
33, 35	Titanosauriformes, Euhelopodidae	Somphospondyli, *Euhelopus* + mde
4, 10, 56, 82, 118	Brachiosauridae	*Giraffatitan* + mdb
57	Brachiosauridae	*Giraffatitan*
95	*Giraffatitan* + mdb	*Abydosaurus* + mdb
100	*Giraffatitan* + mdb, (*Chubutisaurus* + Titanosauria)	*Giraffatitan*, Saltasaurinae
11	*Brachiosaurus* + mdb	*Abydosaurus*
14	*Brachiosaurus* + mdb; Somphospondyli	*Abydosaurus* + mdb; (*Chubutisaurus* + Titanosauria) + Euhelopodidae
6, 15	Somphospondyli	Euhelopodidae + (*Chubutisaurus* + Titanosauria)
103	Somphospondyli	*Sauroposeidon* + mdso
19	Somphospondyli	*Euhelopus* + mde
90	Somphospondyli	Saltasauridae
75	*Tastavinsaurus* + mdso	Euhelopodidae + (*Chubutisaurus* + Titanosauria)
77	*Tastavinsaurus* + mdso	Lithostrotia
26	Euhelopodidae	*Erketu* + mde
31, 32, 33, 34, 49	Euhelopodidae	*Euhelopus* + mde
117	Euhelopodidae	*Euhelopus*
57, 66	Euhelopodidae	*Phuwiangosaurus* + *Tangvayosaurus*
97	*Erketu* + mde	*Euhelopus* + mde
70, *78*	*Phuwiangosaurus* + *Tangvayosaurus*	*Phuwiangosaurus*
7, 8, 28, 73, 119	*Chubutisaurus* + Titanosauria	Lithostrotia
20, 27	*Chubutisaurus* + Titanosauria	Saltasaurinae
72, 115	*Chubutisaurus* + Titanosauria	Saltasauridae
76	(Chubutisaurus + Titanosauria), – *Opisthocoelicaudia*	*Malawisaurus*, *Alamosaurus*
81, 110	Titanosauria	Saltasauridae

mdb, more derived brachiosaurids; mde, more derived euhelopodids; mdso, more derived somphospondylans.
Italicization indicates characters that have ambiguous changes in other parts of the cladogram that are instead because of character conflict (Table 6). Plus signs indicate gains, minus signs indicate losses.

Upchurch *et al*., 2004). *Tehuelchesaurus* is resolved as the sister taxon of Titanosauriformes rather than closely related to *Omeisaurus* as previously suggested (Rich *et al*., 1999; Upchurch *et al*., 2004). Two additional steps are required to position *Tehuelchesaurus* as the sister taxon of *Omeisaurus* and a Templeton test does not reject such a position ($N = 6$; $P = 0.41$). Several features recovered as titanosauriform synapomorphies in previous analyses such as a lateral bulge on the femur or plank-like anterior dorsal ribs (e.g. Wilson, 2002; Upchurch *et al*., 2004) are instead recovered as synapomorphies of *Tehuelchesaurus* + Titanosauriformes.

BRACHIOSAURIDAE

This analysis recovered six taxa as brachiosaurids, more than any other analysis to date. The fragmentary and often non-overlapping anatomy of putative brachiosaurids (e.g. *Cedarosaurus*) has yielded limited taxonomic breadth and/or resolution for this clade in previous analyses (e.g. Upchurch *et al*., 2004; Rose, 2007; Ksepka & Norell, 2010), although many taxa were suggested to be brachiosaurids without a cladistic analysis. In particular, cranial data are known for only three brachiosaurids (*Abydosaurus*, *Europasaurus*, *Giraffatitan*), and the only brachiosaurid for which

Table 6. Ambiguous character optimizations attributable to character conflict, based on two optimization strategies in PAUP* (Swofford, 2002)

Character number	ACCTRAN	DELTRAN
13	(*Atlasaurus* + Neosauropoda), – *Camarasaurus*	Diplodocoidea, Titanosauriformes
95	Macronaria, – Brachiosauridae	*Camarasaurus*, Saltasauridae
117	– *Giraffatitan*	*Venenosaurus*
71	– (*Tehuelchesaurus* + Titanosauriformes), Brachiosauridae	– *Tehuelchesaurus*, – Somphospondyli
78	– *Europasaurus*, Titanosauriformes, –*Tastavinsaurus* + mdso	*Giraffatitan* + mdb, *Ligabuesaurus*, *Sauroposeidon*
30	*Tastavinsaurus* + mdso, Saltasauridae	*Malawisaurus, Euhelopus* + mde
16	*Tastavinsaurus* + mdso, –*Euhelopus*	Lithostrotia, *Phuwiangosaurus*
69	Titanosauria, – 'Saltasaurini'	*Opisthocoelicaudia*, *Alamosaurus*
21	– (*Chubutisaurus* + Titanosauria), 'Saltasaurini'	*Malawisaurus*, *Alamosaurus*

ACCTRAN, accelerated transformation; DELTRAN, delayed transformation; mdb, more derived brachiosaurids; mde, more derived euhelopodids; mdso, more derived somphospondylans.
Italicization indicates characters that have ambiguous changes in other parts of the cladogram that are instead because of missing data (Table 5). Plus signs indicate gains, minus signs indicate losses.

substantial cranial and postcranial data are available is *Giraffatitan*.

The traditional (noncladistic) content of the Brachiosauridae was maintained by this analysis (i.e. *Brachiosaurus*, *Giraffatitan*). In addition, the affinities of several putative brachiosaurids were confirmed by this analysis, including *Cedarosaurus*, *Venenosaurus*, and *Abydosaurus*. In contrast, some putative brachiosaurids [*Atlasaurus*, *Sauroposeidon* (including '*Paluxysaurus*'), *Qiaowanlong*] were recovered outside the clade, and some likely brachiosaurids ('French' *Bothriospondylus*, *Sonorasaurus*) were not included in this analysis (but see 'Fragmentarily represented taxa' below). Five unambiguous brachiosaurid synapomorphies were recovered (wide supratemporal fenestrae, ventral triangular projection on anterior ramus of quadratojugal, maxillary teeth twisted axially, dorsal vertebrae with 'rod-like' transverse processes, ischium with abbreviate pubic peduncle) as well as eight more under ACCTRAN (Tables 5, 6). Under DELTRAN, these eight synapomorphies optimize either as synapomorphies of *Giraffatitan* plus more derived brachiosaurids, an autapomorphy of *Giraffatitan*, or as multiple gains and losses amongst various titanosauriforms.

Europasaurus was recovered as the basal-most brachiosaurid, in contrast to previous hypotheses that suggested that it was a basal macronarian (Sander *et al*., 2006). Although strongly supported as a brachiosaurid, the affinities of *Europasaurus* within that clade are labile given the data at hand. The basal position of *Europasaurus* within the Brachiosauridae may be strongly influenced by missing data, because many of the synapomorphies that unite more derived brachiosaurids could not be scored for *Europasaurus* given that those aspects of its anatomy are unknown or undescribed (e.g. lacrimal, metatarsal IV, caudal vertebrae).

Giraffatitan and *Brachiosaurus*, once considered congeneric (e.g. Janensch, 1950), are recovered as successively more derived brachiosaurids in this analysis (Fig. 5). Only a few steps are required to move *Brachiosaurus* into a more or less derived position within Brachiosauridae or as the sister taxon of *Giraffatitan* as traditionally hypothesized (Janensch, 1950; Taylor, 2009). Future, confident referrals of material to *Brachiosaurus altithorax* are needed to understand better its phylogenetic position. *Cedarosaurus*, *Venenosaurus*, and *Abydosaurus*, all known from the Early Cretaceous of North America, are recovered in a polytomy as the most derived brachiosaurids. This result is in keeping with the original descriptions and other cladistic analyses dealing with these taxa (Tidwell *et al*., 1999; Upchurch *et al*., 2004; Rose, 2007; Chure *et al*., 2010).

BASAL SOMPHOSPONDYLI

Three Early-middle Cretaceous sauropods make up a 'grade' of basal somphospondylans: *Ligabuesaurus*, *Sauroposeidon*, and *Tastavinsaurus*. Several features support the monophyly of Somphospondyli, for example: subcentimetre-scale pneumatic chambers permeating the presacral vertebrae, a prespinal lamina in posterior cervical and dorsal vertebrae, anterior dorsal vertebrae with 'paddle-shaped' neural spines (anteroposteriorly flat neural spines that widen distally before tapering to a blunt or rounded

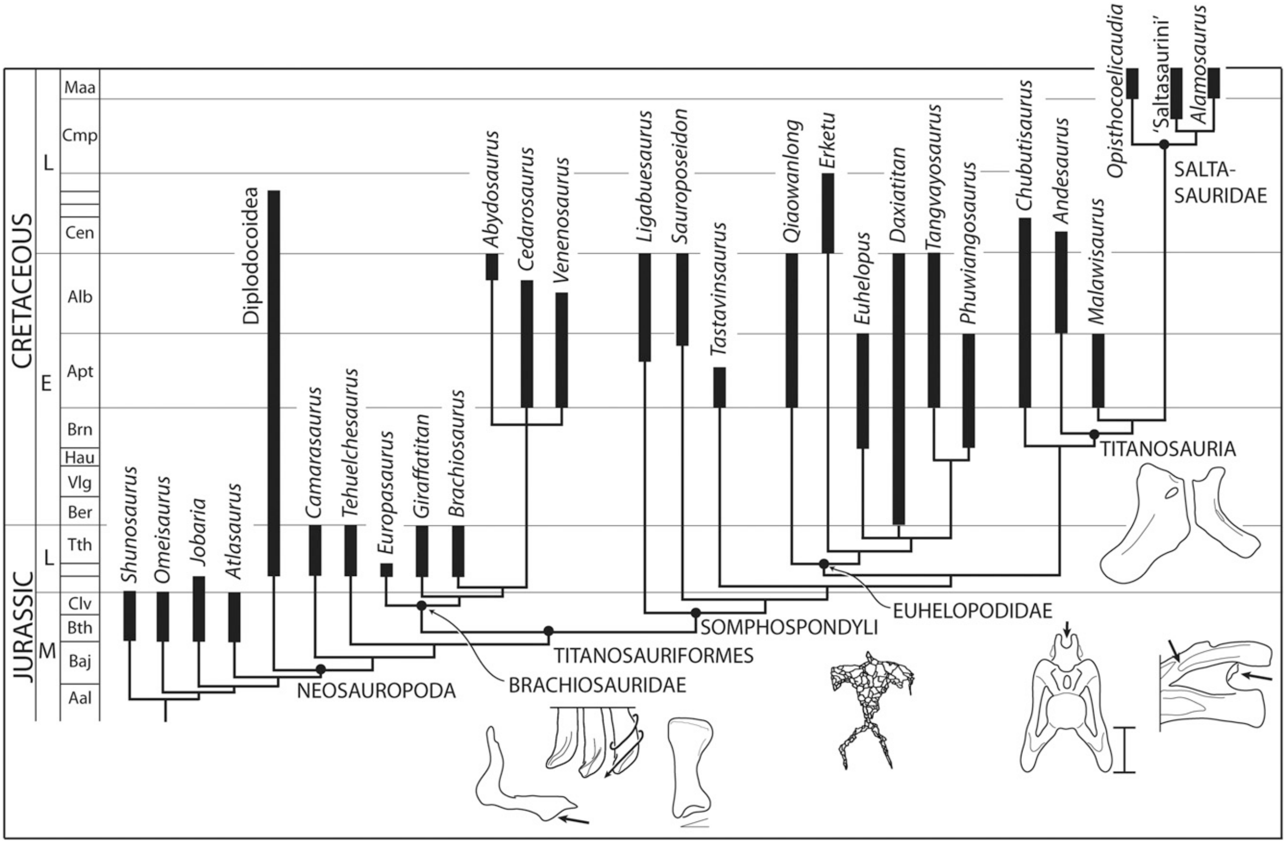

Figure 6. Phylogenetic hypothesis presented in this study plotted on a geological timescale (Gradstein, Ogg & Smith, 2004), with relevant clade names (Table 1) labelled. Selected synapomorphies highlighting some nodes are shown. Brachiosauridae: quadratojugal with triangular ventral prong (shown here in *Europasaurus*), twisted maxillary teeth (shown here in *Giraffatitan*), bevelled distal end of metatarsal IV (shown here in *Sonorasaurus*). Somphospondyli: somphospondylus vertebral pneumaticity, consisting of subcentimetre and submillimetre cells and walls, respectively, that permeate the vertebra (shown here in *Saruoposeidon*). Euhelopodidae: cervical vertebrae with bifid neural spines, pendant cervical ribs, a thick, vertically orientated epipophyseal–prezygapophyseal lamina, a 'kinked' intrapostzygapophyseal lamina (shown here in *Erketu*). Titanosauria: plate-like ischium (shown here in *Andesaurus*). Also shown here are a short ischium (a synapomorphy of *Sauroposeidon* plus more derived somphospondyls) and a raised tubercle on the lateral ischium (a titanosauriform synapomorphy).

distal end), a medially bevelled scapular glenoid, and an embayed medial face of the proximal end of metatarsal IV. Some studies have recovered *Ligabuesaurus* and *Tastavinsaurus* as basal somphospondylans (Gomani, Jacobs & Winkler, 1999; Bonaparte *et al*., 2006; Canudo *et al*., 2008; Royo-Torres, 2009; Carballido *et al*., 2011a), but their precise relationships vary by study. This region of the cladogram presented in this study (Fig. 5) is likewise weakly supported, with low decay indices (Table 7).

A recent revision substantially augmented the hypodigm of *Sauroposeidon proteles* with material from Texas previously referred to '*Paluxysaurus jonesi*' (Rose, 2007) and material from Wyoming (D'Emic, in press; D'Emic & Foreman, 2012). Both *Sauroposeidon* and '*Paluxysaurus*' were originally described as brachiosaurids. A comparative study suggested that '*Paluxysaurus*' possibly represented a basal somphospondylan (Gomani *et al*., 1999), whereas a later a cladistic analysis recovered it as a brachiosaurid (Rose, 2007). Synapomorphies supporting brachiosaurid affinities for *Sauroposeidon* and '*Paluxysaurus*' in the analysis of Rose (2007) (e.g. elongate cervical vertebrae) are inclusive of larger clades than Brachiosauridae according to the analysis presented herein. As well as possessing the somphospondylan features mentioned above, several synapomorphies support the position of *Sauroposeidon* as a somphospondylan more derived than *Ligabuesaurus* (Appendix 3). *Sauroposeidon* lacks several features including 'rod-like' dorsal vertebral diapophyses, fossae variably present in anterior and middle caudal

Table 7. Decay indices (Bremer, 1994) for the nodes in the topology presented in this study (Fig. 5), calculated using MacClade (Maddison & Maddison, 1992) and PAUP* (Swofford, 2002)

Node	Decay index	Rank
Neosauropoda	2	4
Macronaria	2	4
Tehuelchesaurus + Titanosauriformes	2	4
Titanosauriformes	4	2
Brachiosauridae	3	3
Somphospondyli	3	3
Sauroposeidon + more derived somphospondyls	2	4
Tastavinsaurus + more derived somphospondyls	2	4
Euhelopodidae	2	4
Lithostrotia	5	1
Saltasauridae	5	1
Saltasaurinae	3	3

If no decay index is listed for a node shown in Figure 5, decay index = 1.

vertebral centra, and a rounded proximolateral corner of the humerus, which would be expected in a brachiosaurid. Seven and two steps are required to position *Sauroposeidon* within Brachiosauridae or Titanosauria, respectively, and a Templeton test rejects both hypotheses ($N = 13$, $P = 0.006$; $N = 37$; $P = < 0.001$). *Tastavinsaurus* is recovered as slightly more derived than *Sauroposeidon* at a node with a decay index of 2 (Table 7). No support for a clade of Laurasian sauropods allied with *Tastavinsaurus* is found (see 'Laurasiformes' below).

EUHELOPODIDAE

The name 'Euhelopodidae' was originally employed to describe a clade containing *Euhelopus* and some Jurassic East Asian forms (Romer, 1956; Upchurch, 1995). Although the name 'Euhelopodidae' has been applied to clades in some studies (e.g. Upchurch, 1995; Upchurch, 1998), it has never received a definition using phylogenetic nomenclature; only its content has been described or pointed to by labelling a cladogram. This content varies by phylogenetic analysis; *Mamenchisaurus*, *Omeisaurus*, *Shunosaurus*, and *Euhelopus* have all been considered members (see review in Wilson, 2002). The name 'Euhelopodidae' is not currently in use (Wilson & Upchurch, 2009). Most of the fluidity in euhelopodid membership is because of the conflicting placement of *Euhelopus* in different phylogenies. For example, Wilson & Sereno (1998) and Wilson (2002) recovered it as the sister taxon of Titanosauria, whereas Upchurch (1998) and Upchurch *et al*. (2004) recovered it as a non-neosauropod. Recent restudy and rescoring of the data matrices of Wilson (2002) and Upchurch *et al*. (2004) favoured the conclusions of the former study, that *Euhelopus* is closely related to titanosaurs (Wilson & Upchurch, 2009).

Herein Euhelopodidae is defined using phylogenetic nomenclature as a stem-based taxon comprising all sauropods more closely related to *Euhelopus zdanskyi* than *Neuquensaurus australis* (see Table 1 for phylogenetic nomenclature). I have chosen to define and employ Euhelopodidae herein (rather than coin and define a novel name) because (1) the name with its old definition has been in disuse for a decade; (2) coining new names instead of using old ones proliferates nomenclature, which should be avoided if possible; (3) the name does carry some of the original intended meaning with its new definition (i.e. *Euhelopus*-like, Asian sauropods). Regarding the last point, in this analysis, a previously unrecognized group of six Early-middle Cretaceous East Asian taxa is recovered: *Qiaowanlong*, *Erketu*, *Daxiatitan*, *Euhelopus*, *Phuwiangosaurus*, and *Tangvayosaurus*. Likewise, several fragmentarily represented taxa that were not included in this analysis seem to have affinities with these taxa based on the presence of synapomorphies recovered in this analysis (see 'Fragmentarily represented taxa' below).

Usually the six taxa recovered as euhelopodids in this analysis have been recovered as basal somphospondylans or basal titanosaurs when considered in cladistic analyses previously (e.g. You *et al*., 2008; Ksepka & Norell, 2010; Suteethorn *et al*., 2010), but features novel to this study suggest their monophyly (see Appendices 2, 3). Excluding these fragmentarily represented, basal taxa (e.g. *Erketu*, *Qiaowanlong*) from the analysis tends to increase Bremer support for more derived euhelopodid clades. New discoveries or more complete descriptions may provide character scores that support a more derived position for basal forms such as *Qiaowanlong* or *Erketu*. Euhelopodid monophyly is supported by two unambiguous synapomorphies: (1) bifid cervical vertebrae and (2) cervical vertebrae with thick, subhorizontal epipophyseal–prezygapophyseal lamina. Nine additional synapomorphies support Euhelopodidae under ACCTRAN (Tables 5, 6).

Qiaowanlong was originally described as a brachiosaurid, a position refuted by Ksepka & Norell (2010), Mannion & Calvo (2011), and this analysis. The early identification of *Sauroposeidon* as a brachiosaurid is likely to have contributed to the original description of *Qiaowanlong* as such, because most comparisons in its original description were focused on *Sauroposeidon* (You & Li, 2009). Three steps are required to position *Qiaowanlong* within Brachiosauridae according to this analysis, and a Templeton test rejects such a position ($N = 9$, $P = 0.004$). The position of *Erketu* is likewise supported by two synapomorphies, and the position of more derived euhelopodids is supported by a suite of nine features, including prong-like epipophyses, 'trifid' posterior cervical and anterior dorsal neural spines, and a low, pointed preacetabular process of the ilium.

Tangvayosaurus and *Phuwiangosaurus* are sister taxa within derived Euhelopodidae, in contrast to various studies that have suggested that these taxa are basal titanosaurs (Allain *et al.*, 1999; Upchurch *et al.*, 2004; Canudo *et al.*, 2008; Carballido *et al.*, 2011a). Ten and three steps are required to place *Phuwiangosaurus* and *Tangvayosaurus* within the Titanosauria, respectively. Templeton tests reject the titanosaur affinities of both genera (*Phuwiangosaurus*: $N = 47$, $P = 0.0001$; *Tangvayosaurus*: $N = 23$, $P < 0.0001$).

TITANOSAURIA

The inter-relationships of Titanosauria were not the focus of this analysis, so only a small portion of its diversity (more than 65 genera; Curry Rogers, 2005; Mannion & Calvo, 2011) was sampled. More derived nodes (Lithostrotia, Saltasauridae, Saltasaurinae) are very well supported. *Alamosaurus* was recovered as a member of the Saltasaurinae rather than the sister taxon of *Opisthocoelicaudia* as in Wilson (2002) and González Riga *et al.* (2009), or the outgroup to Saltasauridae as in Upchurch *et al.* (2004) and Carballido *et al.* (2011a).

'LAURASIFORMES'

Several authors have found support for a clade of mostly Early Cretaceous Laurasian sauropods, termed 'Laurasiformes' (Canudo *et al.*, 2008; Barco, 2009; Royo-Torres, 2009; Royo-Torres *et al.*, 2012). 'Laurasiformes' was defined by Royo-Torres (2009) as a stem-based clade containing sauropods more closely related to *Tastavinsaurus* than *Saltasaurus*, and has been found to include Laurasian taxa such as *Galvesaurus*, *Aragosaurus*, *Tastavinsaurus*, *Phuwiangosaurus*, *Cedarosaurus*, *Sonorasaurus*, *Venenosaurus*, and a single Gondwanan genus, *Tehuelchesaurus* (Carballido *et al.*, 2011b). The results presented herein do not support such a grouping; instead *Tehuelchesaurus* is considered a non-titanosauriform, *Venenosaurus*, *Cedarosaurus*, and *Sonorasaurus* brachiosaurids, and *Phuwiangosaurus* a euhelopodid (Fig. 5). *Aragosaurus* and *Galvesaurus* were not included in this analysis because their validity and constituency were uncertain given the data at hand (see 'Relationships of fragmentarily represented taxa' below).

The features supporting the monophyly of 'Laurasiformes' in each analysis are listed in Table 8. These features are mostly problematic in terms of definition or scoring, and revision of them erodes support for 'Laurasiformes' (Table 8). For example, the cited 'wrinkle' on the lateral face of middle and posterior caudal vertebrae (Royo-Torres, 2009) represents a remnant of the neurocentral suture, and is present in many sauropods (e.g. *Camarasaurus*, Osborn & Mook, 1921; *Andesaurus*, Mannion & Calvo, 2011). Likewise, a hyposphene-hypantrum in the middle and posterior dorsal vertebrae is present in most non-titanosaur sauropods (Wilson & Sereno, 1998). Other 'laurasiform' synapomorphies are problematic because they are not preserved in most or all 'laurasiforms', such as a six-degree bevel on the distal femur or a narrow sacrum (Royo-Torres, 2009). Still other features do not characterize any sauropod, such as metatarsal III equal to 30% the length of the tibia. A constraint tree containing the 'laurasiform' taxa in this analysis (*Tastavinsaurus*, *Cedarosaurus*, *Venenosaurus*, *Phuwiangosaurus* in a polytomy) was evaluated against the tree presented in Figure 5 via a Templeton test, which rejected the existence of 'Laurasiformes' ($N = 34$, $P < 0.0001$). Thirty-four additional steps were required to accommodate the monophyly of 'Laurasiformes'.

RELATIONSHIPS OF FRAGMENTARILY REPRESENTED TAXA

Missing data are especially problematic in some members of Titanosauriformes such as Brachiosauridae or basal Titanosauria, because in those cases the missing data often occur in non-overlapping anatomical regions amongst purportedly closely related taxa. For example, only a few preserved skulls of brachiosaurids have been found, and in other cases appendicular material has not been preserved. In this case, the disjunct distribution of missing data could support the monophyly of species with skulls on the one hand, and the monophyly of species with appendicular material on the other. As the synapomorphies supporting these clades are ambiguous because of missing data, the robustness of nodes (e.g. their decay index) is low. Furthermore, the few mostly complete taxa (e.g. *Giraffatitan* in the brachiosaurid case) may be simultaneously pulled towards phylogenetic relationships with several taxa by character data from different anatomical regions, depending on the data available in fragmentarily represented taxa. This 'monophyly of the preserved' at best leads to loss of robustness or resolution, and at worst can lead to spurious results.

Table 8. Synapomorphies published in support of the monophyly of Laurasiformes (*Galvesaurus*, *Phuwiangosaurus*, *Aragosaurus*, *Tastavinsaurus*, *Venenosaurus*), with supporting references. Problematic features of each character are given in the Comments column

Character state	Analysis	Comments
'Lateral' pneumatic fossae of anterior cervical vertebrae undivided; those of posterior cervical vertebrae subdivided	Barco (2009)	Serial variability in the subdivision of vertebral fossae is present in several neosauropods (Wilson *et al*., 2011)
Hyposphene–hypantrum articulations only present in middle and posterior dorsal vertebrae	Barco (2009)	Characterizes most saurischians; absent in derived titanosaurs
Anterior caudal vertebrae (excluding the first) weakly procoelous	Barco (2009)	Feature common to most non-lithostrotian sauropods, e.g. *Patagosaurus*, *Giraffatitan*, *Chubutisaurus*; subtlety is serially variable
Anterior caudal haemal canals bridged; middle haemal canals open	Barco (2009)	Also present in some diplodocoids, *Jobaria*, and some specimens of *Camarsaurus* (Wilson & Sereno, 1998)
Spinopostzygapophyseal lamina separated from spinodiapophyseal lamina in dorsal vertebrae	Royo-Torres (2009)	Contact between these laminae varies along the vertebral series in most eusauropods
Sacrum narrow (width 50–70% length)	Royo-Torres (2009)	Only *Tastavinsaurus* has this feature amongst neosauropods
Anterior caudal vertebral centra concave anteriorly, flat posteriorly	Royo-Torres (2009)	Feature common to most non-lithostrotian sauropods, e.g. *Patagosaurus*, *Giraffatitan*, *Chubutisaurus*; subtlety is serially variable
'Wrinkle' on lateral face of neural arch of middle–posterior caudal vertebrae	Royo-Torres (2009)	Remnant of neurocentral suture; present in all sauropods at some ontogenetic stage
Neural spines of anterior caudal vertebrae bulbous	Royo-Torres (2009)	Displays variation within some genera (e.g. *Camarasaurus*); also present in some brachiosaurids
Anterior caudal neural spines straight, directed posteriorly, vertically, or anteriorly, with anterodorsal edge anterior of postzygapophyses	Royo-Torres (2009)	Uninformative; character states span known morphologies for sauropods
Angle between distal condyles and shaft of femur 6°	Royo-Torres (2009)	Angle not preserved in *Tastavinsaurus*, *Cedarosaurus*, *Venenosaurus*, *Sonorasaurus*, similar angle found amongst many titanosauriforms
Metatarsal III more than 30% tibia length	Royo-Torres (2009)	Not found in any sauropod

The ways to combat the 'monophyly of the preserved' are to build larger operational taxonomic units with new discoveries or taxonomic referrals (e.g. Carballido *et al.*, 2011a; D'Emic, Wilson & Williamson, 2011), or to collapse genera into higher-level clades before scoring (e.g. see 'Saltasaurini' above).

Numerous fragmentary taxa could not be included within the cladistic analysis presented above because their validity and constituency remain to be established or verified, and/or their remains do not bear enough relevant synapomorphies to nest them in lower-level clades. Discovery of synapomorphies using more informative taxa in the cladistic analysis above allows general phylogenetic statements to be made for most fragmentarily represented taxa, as shown in Table 9. However, some basal titanosauriforms warrant further explication because of their interesting geographical location or age, their complex taxonomy, or differences between results of previous studies and those presented here.

AMARGATITANIS MACNI (APESTEGUÍA, 2007)

Apesteguía (2007) named *Amargatitanis* on the basis of fragmentary material (caudal vertebrae, scapula, femur, astragalus; MACN PV N52, 53, 34) from Neuquén, Argentina. Material referred to *Amargatitanis* was thought to come from the Kimmeridgian Pichi Pecún Leufú Formation when it was discovered, but the preservational style suggests that it is from the Barremian La Amarga Formation (Apesteguía, 2007). *Amargatitanis* was described as a derived titanosaur, and would constitute one of the oldest known members of that clade. However, although Apesteguía (2007) reported that the material was associated, field notebooks of J. Bonaparte indicate that the material was collected over several hundred metres of outcrop – for example, the femur and astragalus were collected over 400 m from the caudal vertebrae (pers. observ., 2009; S. Apesteguía, pers. comm.).

Although presented as a titanosaur (Apesteguía, 2007), none of the material referred to *Amargatitanis* bears synapomorphies of Titanosauria according to the analysis presented herein. Several of the features cited in support of somphospondylan or titanosaur affinities by Apesteguía (2007) are instead the result of breakage. These include the medially bevelled scapular glenoid, straight scapular blade, and bevelled femoral condyles (i.e. these features are all broken; M. D. D'Emic, pers. observ., 2009). Likewise, fragmentary teeth from the La Amarga region cannot be ascribed to titanosaurs. A 'dendritical enamel pattern' and 'homogenous slenderness' were features used to refer these teeth to titanosaurs (Apesteguía, 2007: 539), but titanosaur enamel is not diagnostic (Upchurch *et al.*, 2004), and diplodocoids and some basal titanosauriforms also have similarly slender and similarly shaped teeth (Chure *et al.*, 2010). The purported titanosaur teeth could pertain to non-titanosaurs similar to *Abdyosaurus* or *Ligabuesaurus* based on their shape (Apesteguía, 2007: fig. 4). Some of the other material referred to *Amargatitanis* may pertain to diplodocoids on the basis of complex neural arch lamination in the anterior caudal vertebrae (pers. observ., 2009). The titanosaur affinities of material referred to *Amargatitanis* cannot be substantiated at present, and its validity is questionable.

BRONTOMERUS MCINTOSHI
(TAYLOR, WEDEL & CIFELLI, 2011)

Brontomerus was named on the basis of dissociated material consisting of an ilium, scapula, distal caudal vertebra, ribs, and other fragmentary bones (Taylor *et al.*, 2011: table 3) from the Early Cretaceous Burro Canyon Formation (equivalent to the Ruby Ranch Member of the Cedar Mountain Formation) of Utah. As (1) the material is disarticulated, (2) there is substantial size variation amongst the known elements in the quarry, and (3) no elements from the quarry overlap with the holotype (an ilium), referral of material from the holotypic quarry to *Brontomerus* is weak. Thus, the diagnosis of the species rests on the holotypic ilium (Taylor *et al.*, 2011). Five autapomorphies were presented for the holotype of *Brontomerus*: (1) ischial peduncle reduced to very low bulge; (2) preacetabular lobe directed anterolaterally but not curved; (3) ilium height 52% of total length; (4) preacetabular lobe 55% of total ilium length; (5) postacetabular lobe reduced to near absence. The first two characters are present in a variety of taxa (e.g. *Tastavinsaurus*, Royo-Torres, 2009; *Giraffatitan*, Janensch, 1961).

The latter three characters cannot be evaluated in *Brontomerus* because the postacetabular process is broken – although Taylor *et al.* (2011: 81) described this as a 'genuine osteological feature not related to damage', it is clear that this margin is not complete, and the reconstruction of the posterior curvature of the ilium is arbitrary. When reconstructed with a postacetabular process similar to that in other sauropods, the ilium of *Brontomerus* is similar to those of brachiosaurids (e.g. *Giraffatitan*, Janensch, 1961: pl. E). Because of its problematic diagnosis, *Brontomerus mcintoshi* represents a nomen dubium. Some of the material referred to *Brontomerus* by Taylor *et al.* (2011) appears to pertain to Titanosauriformes based on the presence of pneumatic dorsal ribs or coarse camellate vertebral pneumaticity.

Table 9. Age, provenance, and taxonomic assignment of 40 fragmentary basal titanosauriform–basal titanosaur sauropods. Numbers refer to characters (Appendix 2) supporting and refuting higher-level assignments (Appendix 4) that were recovered as synapomorphies under delayed transformation. An exclamation mark before a clade name means that the genus probably does not belong to that clade based on the absence of some synapomorphies; those characters are also preceded by an exclamation mark. When affinities with more than one clade are suggested, the largest encompassing clade is listed

Taxon	Age	Area	Clade/validity	Characters
Agustinia ligabuei	EK	SA	nd	–
Amargatitanis macni	EK	SA	nd	–
Angolotitan adamastor	LK	AF	Lithostrotia	83
Aragosaurus ischiaticus	LJ–EK	EU	TSF; !Titanosauria	106; !103
Argentinosaurus hunculensis	LK	SA	*Tastavinsaurus* + mdso; !Euhelopodidae; !Lithostrotia	36; !22; !48
Australodocus bohetii	LJ	AF	TSF	18, 23
Baotianmansaurus henanensis	LK	AS	*Euhelopus* + mde	30
Brontomerus mcintoshi	EK	NA	nd	–
Daanosaurus zhangi	LJ	AS	Macronaria	39
Diamantinasaurus matildae	EK	AU	Saltasauridae	110
Dongbeititan dongi	EK	AS	Somphospondyli	68
Dongyangosaurus sinensis	LK	AS	*Euhelopus* + mde	30, 97
Fukuititan nipponensis	EK	AS	Macronaria	89
Fusuisaurus zhaoi	EK	AS	*Tehuelchesaurus* + Titanosauriformes	64
‘French *Bothiospondylus*’/ *Damparis sauropod*	LJ	EU	*Giraffatitan* + mdb	78, 79, 81, 93
Galvesaurus herreroi	LJ–EK	EU	TSF; !Titanosauria	23, 58, 106; !103
Gobititan shenzhouensis	EK	AS	*Sauroposeidon* + mdso	111
Huabeisaurus allocotus	LK	AS	*Euhelopus* + mde	97
Huanghetitan liujiaxiaensis	EK	AS	Somphospondyli	69
‘Huanghetitan’ ruyangensis	LK	AS	Euhelopodidae + (*Chubutisaurus* + Titanosauria)	50
Janenschia robusta	LJ	AF	TSF; !TSF; !(*Sauroposeidon* + mdso); !(Euhelopodidae + (*Chubutisaurus* + Titanosauria))	112; !86; !111; !116
Jiangshanosaurus lixianensis	EK	AS	Saltasauridae	72, 74
Jiutaisaurus xidiensis	EK	AS	TSF	67
Lusotitan atalaiensis	LJ	EU	*Brachiosaurus* + mdb	79
Malarguesaurus florenciae	LK	SA	*Tehuelchesaurus* + TSF; !Lithostrotia	107; !55
Mongolosaurus haplodon	EK	AS	Euhelopodidae + (*Chubutisaurus* + Titanosauria)	7, 22
MPEF PV 3098 (partial skeleton)	LJ	SA	*Brachiosaurus* + mdb	79
NHMUK R5333 (isolated caudal vertebrae)	EK	EU	Lithostrotia	55
NSM 60104403-20554450 (embryo)	EK	AS	*Tehuelchesaurus* + TSF	107
‘Pelorosaurus’ becklesii	EK	EU	TSF; !(*Chubutisaurus* + Titanosauria)	85, !83
Pukyongosaurus milleniumi	EK	AS	Somphospondyli	18
Qingxiusaurus youjiangensis	LK	AS	Lithostrotia	83*
Rugocaudia cooneyi	EK	NA	nd	–
Ruyangosaurus giganteus	LK	AS	Somphospondyli	18
SMU 61732 (partial skeleton)	EK	NA	*Sauroposeidon* + msdo; !Titanosauria	70, !103
Sonidosaurus saihangaobiensis	LK	AS	Euhelopodidae + (*Chubutisaurus* + Titanosauria)	30, 48
Sonorasaurus thompsoni	EK/LK	NA	*Giraffatitan* + mdb	78, 118
Wintonotitan wattsi	EK	AU	TSF; !(*Abydosaurus* + mdb); !Titanosauria	96; !93; !54
Xenoposeidon proneneukos	EK	EU	nd	–
Xianshanosaurus shijiagouensis	LK	AS	Lithostrotia	55

**Qingxiusaurus* also shares the presence of a posteriorly expanded sternal plate (character 76) with *Alamosaurus* and *Malawisaurus*. This is recovered as a lithostrotian synapomorphy under accelerated transformation.

Age abbreviations: EK, Early Cretaceous; LJ, Late Jurassic; LK, Late Cretaceous.

Area abbreviations: AF, Africa; AS, Asia; AU, Australia; EU, Europe; NA, North America; SA, South America.

Clade/validity abbreviations: mdb, more derived brachiosaurids; mde, more derived euhelopodids; mdso, more derived somphospondylans, nd, nomen dubium; TSF, titanosauriform.

Galvesaurus herreroi (Barco *et al.*, 2005)

Galvesaurus herreroi was named by Barco *et al.* (2005) on the basis of a holotypic middle dorsal vertebra and several referred bones from the Villar del Arzobispo Formation of Spain. These bones are thought to belong to a single individual based on their close association (Sánchez-Hernández, 2005), but the supposed left and right humeri are too disparate in size and shape to belong to a single animal or even species (see Barco *et al.*, 2005: fig. 4). Explaining these differences taphonomically is not feasible, because the longer humerus is shorter transversely, unlike what would be expected with flattening or shearing. Further discoveries in the Villar del Arzobispo Formation would corroborate or refute referrals to *Galvesaurus*. Provisionally considering this material to represent a single genus, *Galvesaurus* was recently suggested to be a laurasiform macronarian outside of Titanosauriformes (Barco, 2009). Barco (2009) refuted earlier suggestions that *Galvesaurus* represented a diplodocoid (Barco *et al.*, 2005) or non-neosauropod (Royo-Torres *et al.*, 2006).

The lower-level phylogenetic relationships of *Galvesaurus* were sensitive to taxon sampling in the cladistic analyses of Barco (2009). The constituency and a consensus on the phylogenetic affinities of *Galvesaurus* await further discoveries, but the material from Villar del Arzobispo appears to pertain to Titanosauriformes based on a few features such as elongate cervical vertebrae and middle caudal vertebrae with anteriorly set neural arches (Appendix 3). The gracility and rounded proximolateral corner of the humeri suggest possible brachiosaurid affinities for those bones.

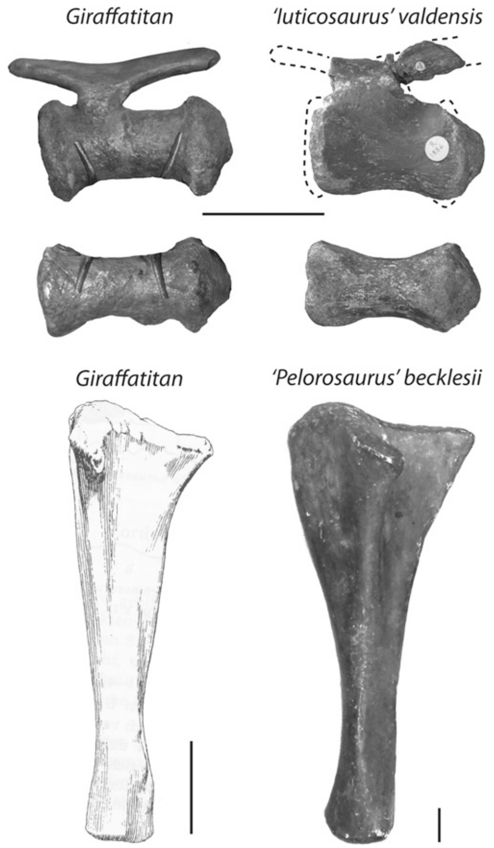

Figure 7. Purported early 'titanosaur' species in comparison with a basal titanosauriform (*Giraffatitan*). The caudal vertebral procoely of '*Iuticosaurus*' and curved/raised ulnar olecranon of '*Pelorosaurus*' *becklesii* are indistinguishable from the situation in *Giraffatitan*. Scale bars: *Giraffatitan* vertebra = 5 cm; '*Iuticosaurus*', *Giraffatitan* ulna, and '*Pelotosaurus*' *becklesii* = 10 cm.

'*Iuticosaurus*' *valdensis* (Le Loeuff, 1993)

Iuticosaurus was named on the basis of two procoelous caudal vertebrae (NHMUK R151, lectotype and R146a, paralectotype; Upchurch, Mannion & Barrett, 2011) and a third specimen (NHMUK R1886) that was later referred (Le Loeuff, 1993). These specimens probably come from the Barremian Wessex Formation (Upchurch *et al.*, 2011). Although '*Iuticosaurus*' is regarded as a nomen dubium, its phylogenetic status is still of importance because of its early age and purported titanosaur affinities. However, the titanosaur affinities of '*Iuticosaurus*' are problematic. Le Loeuff (1993) interpreted the holotype of *Iuticosaurus* to represent a middle caudal vertebra with autapomorphically long postzygapophyses. Reinterpreted as a more distal caudal vertebra based on its elongation, the postzygapophyses of *Iuticosaurus* (NHMUK R151) are normal and its procoely is shared with some non-titanosaurs (e.g. *Giraffatitan* HMN MB.R.5000, Janensch, 1950: pl. IV; *Malarguesaurus*, González Riga *et al.*, 2009; Fig. 7). The titanosaur affinities of '*Iuticosaurus*' cannot be substantiated at present.

Janenschia robusta (Wild, 1991)

Janenschia is an important taxon because of its proposed titanosaur affinities (e.g. McIntosh, 1990; Upchurch, 1995; Bonaparte, Heinrich & Wild, 2000; Wilson, 2002; Upchurch *et al.*, 2004) and Late Jurassic age. *Janenschia* appears to be a titanosauriform based on the absence of a proximomedial triangular scar on the fibula (Appendix 3). Bonaparte *et al.* (2000) pointed out that the procoelous anterior caudal vertebrae possibly referable to *Janenschia* could not strongly attest to titanosaur affinities because this feature is also present in some diplodocoids and non-neosauropods (see also Whitlock *et al.*, 2011). Upchurch (1995), Wilson (2002), and Upchurch *et al.* (2004) suggested titanosaur affinities for *Janenschia* on the basis of its robust forelimb bones and a raised ulnar olecranon process. However, similarly robust bones and a raised olecranon are found in some non-titanosaurs or non-titanosauriforms such as *Tehuelchesaurus* according to this analysis, and these features were not found to be titanosaur synapomorphies in this study.

Likewise, Royo-Torres & Cobos (2009) presented evidence that some material referred to *Janenschia* pertains to non-neosauropods. Furthermore, several features of *Janenschia* are inconsistent with its placement within Titanosauria, Somphospondyli, or even Titanosauriformes: ulnar proximal arms subequally developed, the lack of an embracing proximal tibia and fibula, and a divided posterior fossa on the astragalus (Appendix 3). Curry Rogers (2005) included *Janenschia* in a cladistic analysis of titanosaurs, but a strict consensus of those results did not resolve its relationships amongst titanosauriforms. The only other cladistic analysis that included *Janenschia* recovered it as a non-titanosaur (Carballido *et al*., 2011b). The titanosaur affinities of *Janenschia* cannot be substantiated at present.

MONGOLOSAURUS HAPLODON (GILMORE, 1933)

Mongolosaurus was collected from the Early Cretaceous of China and is based on fragmentary teeth, part of a basicranium, and three vertebrae. Wilson (2005) and Mannion (2011) established the validity of *Mongolosaurus* on the basis of several features, and both studies suggested that it was a titanosaur. In contrast, as noted by Wilson & Upchurch (2009), *Mongolosaurus* shares some features with *Erketu*, a Cretaceous East Asian sauropod outside of Titanosauria: tall, pillar-like epipophyses and an elongate axis with a tall ventral keel. *Mongolosaurus* possesses bifid neural spines as in all East Asian Cretaceous titanosauriforms (see below). These three features suggest euhelopodid affinities for *Mongolosaurus*, in contrast to the 11 features suggesting titanosaur affinities proposed by Mannion (2011). However, many of the 11 characters proposed by Mannion (2011) deal with parts of the skull that are unknown in almost all euhelopodids, making these comparisons equivocal. Furthermore, some cranial 'titanosaur' features proposed by Mannion (2011) have a broader distribution amongst sauropods. For example, mesial and distal tooth carinae and D-shaped cross-sections are features of the teeth of the non-titanosaur *Phuwiangosaurus* (pers. observ.), and variability in tooth shape between upper and lower jaws is also present in the brachiosaurid *Abydosaurus* (Chure *et al*., 2010). In sum, *Mongolosaurus* displays a mix of features that suggest titanosaur or euhelopodid affinities.

OTHER EAST ASIAN CRETACEOUS SAUROPODS

In the last decade, reports of new species in the Cretaceous of East Asia are on a par with those of the rest of the world combined (Mannion, 2011). Few of these new genera have been placed into a phylogenetic context via cladistic analysis, obfuscating their significance in overall sauropod evolution. Suggestions that some of these species form a clade have been made (Xu *et al*., 2006; Wilson & Upchurch, 2009) but no cladistic analysis has found support for a large clade of East Asian Cretaceous sauropods prior to the results presented herein. In addition to the six East Asian Cretaceous taxa recovered as a clade in this analysis (Fig. 5), several taxa bear features recovered as euhelopodid synapomorphies in the analysis presented herein (*Baotianmansaurus*, *Dongyangosaurus*, *Huabeisaurus*, *Mongolosaurus*; Table 9). Other genera may belong to Euhelopodidae, but euhelopodid synapomorphies are not evident in them given the data at hand (*Fukuititan*, *Gobititan*, *Huanghetitan liujiaxiaensis*, *'Huanghetitan' ruyangensis*, *Jiutaisaurus*, *Pukyongosaurus*, *Ruyangosaurus*; Table 9).

Still other Cretaceous East Asian genera appear to lie outside Euhelopodidae because they lack euhelopodid synapomorphies and possess synapomorphies of Titanosauria and clades therein. These genera include *Opisthocoelicaudia*, *Nemegtosaurus*, *Jiangshanosaurus*, *Sonidosaurus*, *Qingxiusaurus*, and *Xianshanosaurus* (Table 9). Importantly, all Cretaceous East Asian sauropods with preserved cervical vertebrae have bifid cervical neural spines. East Asia is an important area of future study for early titanosauriform evolution. Future research into the many fragmentarily represented Cretaceous genera will be likely to yield a core of euhelopodid taxa as well as an assemblage of more derived forms. Key to resolving the place of East Asian titanosauriforms in sauropod evolution will be taxonomic revision of several fragmentarily represented genera as well as the establishment of more precise geological ages in various basins.

Grellet-Tinner *et al*. (2011) reported a sauropod egg from the Aptian-Albian-aged Algui Ulaan Tsav site of Mongolia (NSM 60104403-20554450). They reported in-ovo remains of NSM 60104403-20554450 as an embryonic lithostrotian titanosaur, and on this basis inferred an Aptian-Albian palaeobiogeographical connection between Gondwana and Laurasia. No lithostrotian synapomorphies were identified in NSM 60104403-20554450 by Grellet-Tinner *et al*. (2011), but a series of general similarities shared with *Diamantinasaurus*, *Opisthocoelicaudia*, *Phuwiangosaurus*, and *Rapetosaurus* were used to refer the embryo to Lithostrotia. These similarities were: (1) proximal and distal ends of humerus subequal in size (citied as a similarity to *Diamantinasaurus*); (2) prominent deltopectoral crest 'merges mid-shaft at its narrowest level' (cited as a similarity to *Phuwiangosaurus*), (3) deltopectoral crest 'reduced to a low rounded ridge' (cited as a similarity to *Rapetosaurus* and to Saltasaurinae), (4) head of humerus projects above deltopectoral crest margin (citied as a similarity to *Diamantinasaurus*), and (5) two longitudinal fossae on the posterior face of the femur, one around midlength and one near the distal condyles (cited as a similarity to *Diamantinasaurus*) (Grellet-Tinner *et al*., 2011: 625–626). Re-examination of these similarities indicates that none of them can be used to refer the embryo to Lithostrotia – these features are found in an array of more basal titanosauriforms. Features 1–4 are found in the non-titanosaurs *Chubutisaurus* (Carballido *et al*., 2011a) and *Sauroposeidon* (Rose, 2007), and feature 5 is an artefact of crushing in *Diamantinasaurus* (Hocknull *et al*., 2009: 11), and is present (weakly) in many non-titanosaurs (e.g. *Camarasaurus*, Ostrom & McIntosh, 1966: pl. 72). The presence of a lateral bulge on the proximal femur suggests that NSM 60104403-20554450 is referable to the clade (*Tehuelchesaurus* + Titanosauriformes), but a more precise determination of its affinities is not possible at present. NSM 60104403-20554450 does not represent evidence for a middle Cretaceous Gondwana–Laurasia palaeobiogeographical connection.

'*PELOROSAURUS*' *BECKLESII* (MANTELL, 1852)

The complex history of the genus '*Pelorosaurus*' is discussed elsewhere (Naish & Martill, 2001; Upchurch *et al*., 2004). '*Pelorosaurus*' *becklesii* comes from the Barremian Wessex Formation, UK, and consists of a humerus, radius, ulna, and some skin impressions. Upchurch (1995) suggested that '*Pelorosaurus*' *becklesii* was an early titanosaur on the basis of its proximally curved anteromedial process of the ulna and the presence of polygonal plates similar to those of the titanosaur *Saltasaurus* in its skin. However, a similarly curved anteromedial process of the ulna and raised olecranon process are also found in non-titanosaurs (e.g. *Giraffatitan*, *Sauroposeidon*; pers. observ. of YPM 326, a cast of '*Pelorosaurus*' *becklesii*; Fig. 7) and should not be treated as a titanosaur synapomorphy in the absence of a cladistic analysis. Since the assessment of Upchurch (1995), similar polygonal dermal patterns have been reported in non-titanosaurs (e.g. *Tehuelchesaurus*, Giménez, 2007). Furthermore, '*Pelorosaurus*' *becklesii* lacks one unambiguous synapomorphy of the clade uniting *Chubutisaurus* + Titanosaura: an undivided notch on the humeral radial condyle. '*Pelorosaurus*' *becklesii* probably represents a titanosauriform on the basis of the anteromedial arm of the ulna being much longer than its anterolateral arm, but its titanosaur affinities cannot be substantiated at present.

SONORASAURUS THOMPSONI (RATKEVITCH, 1998)

Sonorasaurus was originally described as a brachiosaurid and is important because of its Albian–?Cenomanian age, which would be on a par with the youngest known North American sauropods before the start of the 'sauropod hiatus' (Lucas & Hunt, 1989; Ratkevitch, 1998). *Sonorasaurus* is represented by a somewhat fragmentary partial skeleton, which includes presacral and caudal vertebrae and some limb elements. *Sonorasaurus* is a titanosauriform on the basis of semicamellate presacral vertebral pneumaticity, middle caudal vertebrae with neural arches set on the anterior half of the centrum, anterior–middle caudal vertebrae with posteriorly projecting transverse processes, metacarpal I with an undivided distal condyle that is perpendicular to the shaft, metacarpals with reduced or absent distal articular facets, and a fibula that lacks a corrugated subtriangular proximal scar (Appendix 3).

Brachiosaurid affinities are supported for *Sonorasaurus* on the basis of metatarsal IV bevelled distally and metatarsal IV with a medial embayment on proximal end (Appendix 3). Previous hypotheses for brachiosaurid affinities for *Sonorasaurus* were based on its elongate forelimb bones (Ratkevitch, 1998), but more recent discoveries have shown that similarly elongate limb bones are present in taxa that are here resolved as basal somphospondylans (e.g. *Ligabuesaurus*, *Sauroposeidon*) and basal titanosaurs (e.g. *Andesaurus*, *Malawisaurus*). Further data are needed to firmly establish the affinities of *Sonorasaurus*.

WINTONOTITAN WATTSI (HOCKNULL *ET AL*., 2009)

Longman (1933) named *Austrosaurus mckillopi* on the basis of several fragmentary dorsal vertebrae (QMF 2316) from the Early Cretaceous Allaru Mudstone of Australia. Hocknull *et al*. (2009) regarded *Austrosaurus* as a nomen dubium and named a new genus – *Wintonotitan* – from the slightly younger Winton Formation based on materials that had previously been referred to *Austrosaurus* sp. (QMF 7292). *Wintonotitan* was diagnosed by a combination of many characters (see Hocknull *et al*., 2009: 16). Two features were cited as autapomorphies: dorsal vertebrae with 'incipient' spinoprezygapophyseal lamina, and cylindrical, incipiently biconvex distal caudal vertebrae. Both of these features characterize a wider array of basal titanosauriforms, however. An 'incipient' (subtle or small) spinoprezygapophyseal lamina (i.e. anterior spinodiapophyseal lamina) is found in several titanosauriforms (e.g. *Ligabuesaurus*, *Sauroposeidon*, *Giraffatitan*, *Argentinosaurus*, pers. observ.). Likewise, weakly biconvex, cylindrical distal caudal vertebrae are found in *Giraffatitan* and *Rinconsaurus* (pers. observ.). These features may be local autapomorphies, but this awaits determination via cladistic analysis. However, the validity of *Wintonotitan* is supported by one unique feature recognized herein, distal caudal vertebrae with strongly arched ventral surfaces (see Hocknull *et al*., 2009: fig. 14).

Hocknull *et al*. (2009) recovered *Wintonotitan* as a member of Laurasiformes or the sister taxon of *Malarguesaurus* in modified versions of the matrices of Canudo *et al*. (2008) and González Riga *et al*. (2009), respectively, but did not rule out titanosaur affinities for the genus. These results were supported by low bootstrap values (Hocknull *et al*., 2009: fig. 38) and the node supporting *Wintonotitan* and other titanosauriforms had a decay index of 2 in each analysis. The results of the present analysis suggest that *Wintonotitan* is a titanosauriform on the basis of reduced metacarpal phalangeal articular facets (Appendix 3), but more precise knowledge of its affinities await future discoveries and studies.

XENOPOSEIDON PRONENEUKOS
(TAYLOR & NAISH, 2007)

Xenoposeidon was named on the basis of a single partial middle-posterior dorsal vertebra (NHMUK R2095) from the Early Cretaceous Hastings Beds, UK. Six features were presented as diagnostic for *Xenoposeidon* by Taylor & Naish (2007: 1549): '(1) neural arch covers dorsal surface of centrum, with its posterior margin continuous with that of the cotyle; (2) neural arch slopes anteriorly 35 degrees relative to the vertical; (3) broad, flat area of featureless bone on lateral face of neural arch; (4) accessory infraparapophyseal and postzygapophyseal laminae meeting ventrally to form a V; (5) neural canal is asymmetric: small and circular posteriorly but tall and teardrop-shaped anteriorly; (6) supporting laminae form vaulted arch over anterior neural canal'. Instead of representing autapomorphies, these features are the result of damage or are actually more widespread amongst sauropods. For example, interpreting the flush posterior neural arch-centrum as an autapomorphy (1) does not account for missing bone in the posterior centrum. The forward lean of the neural arch relative to the centrum (2) characterizes dorsal vertebrae of some other sauropods (e.g. *Camarasaurus*, Osborn & Mook, 1921: pls 69, 72). Likewise, the laminar pattern characters (3, 4, 6) are observed in a variety of sauropods when individual or serial variation are explored (e.g. *Camarasaurus*, Osborn & Mook, 1921; *Brachiosaurus*, Riggs, 1903; *Tehuelchesaurus*, Carballido *et al*., 2011b. The 'asymmetrical neural canal' (5) cited by Taylor & Naish (2007) misrepresents the large centroprezygapophyseal fossae as the entire anterior neural canal, which is a feature observed in many neosauropods (e.g. *Camarasaurus*, Osborn & Mook, 1921). The absence of diagnostic features renders *Xenoposeidon* a nomen dubium (as also suggested by Mannion & Calvo, 2011). The presence of coarse camellate pneumaticity suggests that NHMUK R2095 pertains to a titanosauriform.

TIMING OF THE ORIGIN OF TITANOSAURIA

As shown above, previous reports of Late Jurassic and earliest Cretaceous titanosaurs (*Janenschia*, *Amargatitanis*, *Iuticosaurus*, '*Pelorosaurus*' *becklesii*) do not pertain to Titanosauria. Thus, the oldest known titanosaurs are Barremian–Albian in age (e.g., *Malawisaurus*, *Jiangshanosaurus*, NHMUK R5333; Fig. 6; Table 8). These taxa appear to be lithostrotians, yet they pre-date or are the same age as the relatively more basal Albian–Cenomanian titanosaur *Andesaurus*, which suggests an earlier origin for Titanosauria.

Furthermore, the Barremian–Aptian (*c*. 128–112 Mya) age for these oldest titanosaurs is far younger than the Middle Jurassic (Bathonian, *c*. 163 Mya) age of origin for Titanosauria inferred from wide-gauge track-ways in Oxfordshire, UK (Day *et al*., 2002, 2004). That inference was based on the proposal by Wilson & Carrano (1999) that wide-gauge track-ways were produced by titanosaurs. In turn, wide-gauge track-ways are thought to have been produced by titanosaurs because those clades bear synapomorphies in the limbs inferred to produce such a track-way, including a proximomedially deflected femur with a proximolateral bulge, an eccentric femoral cross-section, and a distally bevelled femoral condyles (Wilson & Carrano, 1999). Wilson & Carrano (1999) noted that several wide-gauge track-ways pre-dated the titanosaur body fossil record, and tentatively suggested that titanosaurs may have a ghost lineage leading back to the Middle Jurassic. Wide-gauge track-ways are known from the Middle (Santos *et al*., 1994) and Late (Lockley *et al*., 1994) Jurassic of Portugal and the Late Jurassic of Switzerland (Lockley *et al*., 1994), as well as the Middle Jurassic of Oxfordshire as mentioned above (Day *et al*., 2002, 2004).

An alternative explanation to the inference of a ghost lineage for Titanosauria into the Middle Jurassic would be that the anatomical features required to produce a wide-gauge track-way were present in non-titanosaurs as well. Wilson & Carrano (1999) noted that one of the features hypothesized to be related to wide-gauge track-making – a proximolateral femoral

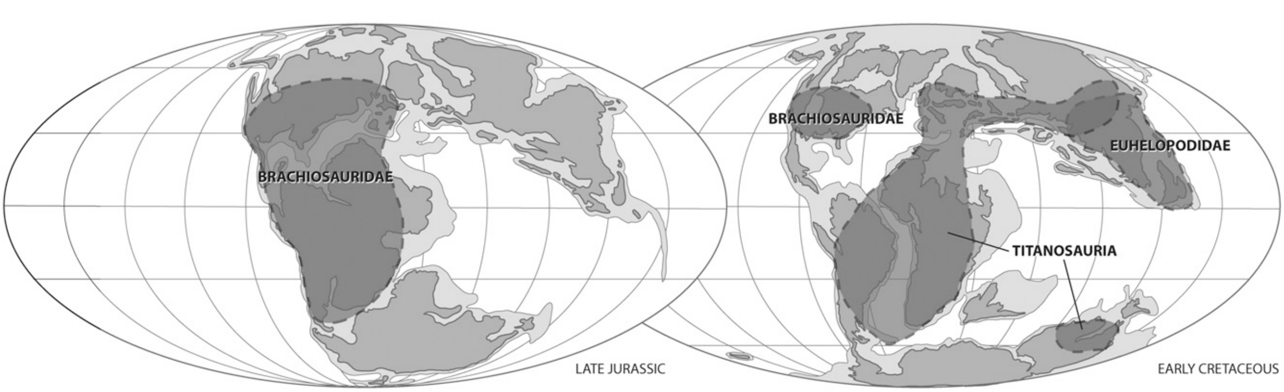

Figure 8. Titanosauriform palaeobiogeography. The Early Cretaceous is characterized by some endemism, with mostly brachiosaurids in North America, mostly euhelopodids in Asia, and mostly titanosaurs in South America. Palaeogeographical reconstructions modified from Blakey (2006).

bulge – is present in Late Jurassic non-titanosaur titanosauriforms such as *Brachiosaurus*. The study presented herein recovers that feature as a synapomorphy of *Tehuelchesaurus* + Titanosauriformes, a clade whose earliest members are Late Jurassic in age (Fig. 6). In addition, although titanosaurs have more eccentric femoral cross-sections on average than other sauropods (Wilson & Carrano, 1999: table 2), some Late Jurassic non-titanosaurs have femoral cross-sections similar to those of titanosaurs (e.g. *Giraffatitan* and *Neuquensaurus*, ratio of transverse width/anteroposterior breadth of midshaft > 2; Janensch, 1961; pers. observ.). The exact morphology required to produce a wide-gauge track-way (e.g. how prominent a proximolateral femoral bulge or eccentric a femoral shaft needs to be) is ambiguous at present. Therefore, wide-gauge track-ways should not necessarily be ascribed to titanosaurs – they may pertain to members of a more inclusive clade such as Titanosauriformes.

One other feature has been used to link the Oxfordshire track-ways to titanosaurs. Day *et al*. (2002, 2004) suggested that the absence of a pollex claw impression in Middle Jurassic wide-gauge track-ways from Oxfordshire, UK, indicated that the track-maker was a titanosaur in that case. In contrast, other Jurassic wide-gauge track-ways (Lockley *et al*., 1994; Santos *et al*., 1994) do possess a prominent pollex claw impression. Narrow-gauge track-ways from Oxfordshire, probably made close to the same time as the wide-gauge track-ways (Day *et al*., 2002; 2004), do possess prominent pollex claw impressions, suggesting that these features were preservable by the substrate. However, even narrow-gauge sauropod track-ways commonly do not possess a pollex claw impression for taphonomic or perhaps behavioural reasons (Santos *et al*., 1994; Wilson & Carrano, 1999). Such preservational problems could explain the absence of a pollex claw impression in the Oxfordshire wide-gauge track-ways. Indeed, the Oxfordshire wide-gauge track-way lacks the pronounced heteropody and pedal claw impressions generally observed in sauropod track-ways (compare Day *et al*., 2002: fig. 1 with Lockley *et al*., 1994: fig. 2). The lack of heteropody is either the result of a true, aberrant morphology for the Oxfordshire wide-gauge track-maker or a preservational problem. If nonpreservation is indeed responsible for the absence of half of the pes impression, then the absence of a pollex claw impression might equally be explainable by nonpreservation. Another possibility is that the wide-gauge, pollux-less track-ways in Oxfordshire represent a currently unknown type of Middle Jurassic sauropod that lost manual phalanges independently of titanosaurs. As the absence of a pollex claw on the Oxfordshire track-ways is ambiguous, they do not demonstrably represent Middle Jurassic titanosaurs. Based on the evidence at hand, the earliest titanosaurs are known from the Early Cretaceous.

PALAEOBIOGEOGRAPHICAL IMPLICATIONS

During the Early Cretaceous, different titanosauriform clades became predominant on different continents – brachiosaurids in North America, euhelopodids in Asia, and titanosaurs in Gondwana and Eurasia (Fig. 8). The appearance of these three clades outside of their main geographical areas probably represents cases of dispersal, such as for somphospondylans in North America (*Sauroposeidon*, D'Emic, in press) or titanosaurs in Laurasia (e.g. *Alamosaurus*; Lucas & Hunt, 1989; D'Emic, Wilson & Thompson, 2010). At the moment, more precise ages for many genera are necessary to resolve such lower-level biogeographical patterns, because the ages of many 'middle' Cretaceous taxa overlap given their current age uncertainty (Fig. 6).

The revised picture of titanosaur origins presented in this study prompts reappraisal of their possible vicariant origins related to the break-up of Pangaea. Vicariance has been called upon to explain titanosaur origins by several authors (e.g. Lydekker, 1895; Bonaparte, 1999), but more recently, several authors have challenged vicariant origins for Titanosauria (Sereno, 1999; Wilson & Upchurch, 2003, 2009). Instead, it has been argued that most sauropod groups were present across Pangaea in the Middle and Late Jurassic, and that later geographical differences in sauropod faunas reflect differential extinction (e.g. Wilson & Sereno, 1998). This seems to be the case for Brachiosauridae, whose basal, Jurassic members are found on several continents (Figs 6, 8; see also Rauhut, 2006), whereas Cretaceous brachiosaurids are only found in North America.

In light of the new data presented in this paper, a vicariant origin for Titanosauria remains problematic, albeit for somewhat different reasons than previously proposed. Wilson & Upchurch (2003) rejected such a vicariant scenario for two reasons: (1) the proposed Middle Jurassic origin of Titanosauria predated the break-up of Pangaea; (2) the existence of several Laurasian titanosaurs. The first objection is resolved by this study, because the revised picture of titanosaur evolution presented herein suggests that titanosaurs originated in the Early Cretaceous, during the break-up of Pangaea. The second objection is ameliorated by the data presented herein, but requires further study. Some of the Laurasian taxa cited as titanosaurs by Wilson & Upchurch (2003) have been shown above to be either non-titanosaurs (*Phuwiangosaurus*, *Tangvayosaurus*, D'Emic and Foreman, 2012; Table 9). Other Laurasian titanosaurs are latest Cretaceous in age and seem to have dispersed from Gondwana, as they are nested within Gondwanan clades (e.g. *Opisthocoelicaudia* and *Alamosaurus*). Confirmation of a dispersal origin for these and other Late Cretaceous Laurasian titanosaurs awaits a cladistic analysis that incorporates more titanosaurs and more precise age dates. Basal titanosaurs (*Andesaurus*, *Malawisaurus*) and their closest outgroup (*Chubutisaurus*) appear in the Early Cretaceous of Gondwana, suggesting a Gondwanan origin for the group (Fig. 6; Table 9). However, the geologically oldest known titanosaurs are Barremian–Aptian forms: *Jiangshanosaurus* from China, NHMUK 5333 (middle caudal vertebrae) from the UK, *Malawisaurus* from Malawi, and *Tapuiasaurus* from Brazil (Table 9). These genera all appear to be derived members within Titanosauria (i.e. lithostrotians), suggesting that the clade had achieved a wide geographical distribution well before the Aptian. Vicariance in titanosauriform evolution may have played a role at lower taxonomic levels (Upchurch *et al*., 2002; Wilson & Upchurch, 2009), a possibility that awaits further taxon sampling and analysis within Titanosauria. In sum, understanding the precise origins of Titanosauria requires new Jurassic or earliest Cretaceous (pre-Aptian) discoveries.

CONCLUSIONS

This study has presented a cladistic analysis focusing on the early members of the Titanosauriformes, a widespread and long-lived clade of sauropod dinosaurs. The analysis yielded a nearly fully resolved cladogram for 25 ingroup taxa; many of the relationships hypothesized herein are novel. Titanosauriformes is composed of three main clades: Brachiosauridae, Euhelopodidae, and Titanosauria. The Jurassic members of Titanosauriformes, Brachiosauridae, and outgroups to Titanosauria are found on various continents. In contrast, Cretaceous brachiosaurids were restricted to North America and euhelopodids predominated in Asia. Brachiosauridae and Euhelopodidae are currently known from about ten genera each, whereas Titanosauria is several times more diverse. Previous claims for a Middle or Late Jurassic origin for Titanosauria have been refuted by new data and this analysis. The earliest known titanosaurs are Barremian–Aptian-aged genera and are found on several continents, and these represent derived forms (lithostrotians), highlighting the need for new earliest Cretaceous discoveries for understanding the enigmatic origin of Titanosauria.

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REFERENCES

Allain R, Taquet P, Battail B, Dejax J, Richir P, Véran M, Limon-Duparcmeur F, Vacant R, Mateus O, Sayarath P, Khenthavong B, Phouyavong S. 1999. Un nouveau genre de dinosaure sauropode de la formation de Grès supérieurs (Aptien-Albien) du Laos. *Comptes Rendus De l'Academie Des Sciences De Paris, Sciences De La Terres Et Des Planètes* **329:** 609–616.

Antunes MT, Mateus O. 2003. Dinosaurs of Portugal. *Comptes Rendus Palevol* **2:** 77–95.

Apesteguía S. 2007. The sauropod diversity of the La Amarga Formation (Barremian), Neuquén (Argentina). *Gondwana Research* **12:** 533–546.

Barco JL. 2009. Sistemátic e implicaciones filogenéticas y paleobiogeográficas del saurópodo *Galvesaurus herreroi* (Formación Villar del Arzobispo, Galve, España). Unpublished D. Phil. Thesis, Universidad de Zaragoza.

Barco JL, Canudo JI, Cuenca-Bescos G, Ruiz-Omeñaca JI. 2005. Un nuevo dinosaurio saurópodo *Galvesaurus herreroi* gen. nov, sp. nov., del tránsito Jurásico-Cretácico en Galve (Teruel, NE de España). *Naturaleza Aragonesa* **15:** 4–17.

Berman DS, McIntosh JS. 1978. Skull and relationships of the Upper Jurassic sauropod *Apatosaurus* (Reptilia, Saurischia). *Bulletin of the Carnegie Museum of Natural History* **8:** 1–35.

Blakey RC. 2006. Global paleogeographic views of earth history – late Precambrian to Recent. Available at: http://jan.ucc.nau.edu/~rcb/globaltext2.html2006 Accessed on 06/11/11.

Bonaparte JF. 1986. The early radiation and phylogenetic relationships of sauropod dinosaurs, based on vertebral anatomy. In: Padian K, ed. *The beginning of the age of dinosaurs*. Cambridge: Cambridge University Press, 247–258.

Bonaparte JF. 1999. Tetrapod faunas from South America and India: a palaeobiogeographic interpretation. *Proceedings of the Indian National Science Academy* **65A:** 427–437.

Bonaparte JF, Coria RA. 1993. Un nuevo y gigantesco saurópodo titanosaurio de la Formación Río Limay (Albiano-Cenomanio) de la Provincia del Neuquén, Argentina. *Ameghiniana* **30:** 271–282.

Bonaparte JF, González Riga BJ, Apesteguía S. 2006. *Ligabuesaurus leanzai* gen. et sp. nov. (Dinosauria, Sauropoda), a new titanosaur from the Lohan Cura Formation (Aptian, Lower Cretaceous) of Neuquén, Patagonia, Argentina. *Cretaceous Research* **27:** 364–376.

Bonaparte JF, Heinrich WD, Wild R. 2000. Review of *Janenschia* Wild, with the description of a new sauropod from the Tendaguru beds of Tanzania and a discussion on the systematic value of procoelous caudal vertebrae in the Sauropoda. *Palaeontographica Abteilung A Band* **256:** 25–76.

Borsuk-Bialynicka M. 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii*, gen. n., sp. n. from the Upper Cretaceous of Mongolia. *Palaeontologia Polonica* **37:** 1–64.

Bremer K. 1994. Branch support and tree stability. *Cladistics* **10:** 295–304.

Britt BB, Scheetz RD, McIntosh JS, Stadtman KL. 1998. Osteological characters of an Early Cretaceous titanosaurid sauropod from the Cedar Mountain Formation of Utah. *Journal of Vertebrate Paleontology* **18:** 29A.

Calvo JO, Bonaparte JF. 1991. *Andesaurus delgadoi* n. g. n. sp. (Saurischia, Sauropoda) a titanosaurid dinosaur from the Río Limay Formation (Albian-Cenomanian), Neuquén, Argentina. *Ameghiniana* **28:** 303–310.

Calvo JO, González Riga BJ. 2003. *Rinconsaurus caudamirus* gen. et sp nov., a new titanosaurid (Dinosauria, Sauropoda) from the Late Cretaceous of Patagonia, Argentina. *Revista Geologica de Chile* **30:** 333–353.

Calvo JO, González Riga BJ, Porfiri JD. 2007. A new titanosaur sauropod from the Late Cretaceous of Neuquén, Patagonia, Argentina. *Arquivos do Museu Nacional, Rio de Janeiro* **65:** 485–504.

Calvo JO, González Riga BJ, Porfiri JD. 2008. A new titanosaur sauropod from the Late Cretaceous of Neuquén, Patagonia, Argentina. *Arquivos do Museu Nacional, Rio de Janeiro* **65:** 485–504.

Canudo J, Royo-Torres R, Cuenca-Bescós G. 2008. A new sauropod: *Tastavinsaurus sanzi* gen et. sp. nov. from the Early Cretaceous (Aptian) of Spain. *Journal of Vertebrate Paleontology* **28:** 712–731.

Carballido JL, Pol D, Cerda I, Salgado L. 2011a. The osteology of *Chubutisaurus insignis* Del Corro, 1975 (Dinosauria: Neosauropoda) from the 'middle' Cretaceous of central Patagonia, Argentina. *Journal of Vertebrate Paleontology* **31:** 93–110.

Carballido JL, Rauhut OWM, Pol D, Salgado L. 2011b. Osteology and phylogenetic relationships of *Tehuelchesaurus benitezii* (Dinosauria, Sauropoda) from the Upper Jurassic of Patagonia. *Zoological Journal of the Linnean Society* **163:** 605–662.

Chure D, Britt BB, Whitlock JA, Wilson JA. 2010. First complete sauropod dinosaur skull from the Cretaceous of the Americas and the evolution of sauropod dentition. *Die Naturwissenschaften* **97:** 379–391.

Cope ED. 1877. On a gigantic saurian from the Dakota epoch of Colorado. *Paleontological Bulletin* **25:** 5–10.

del Corro G. 1975. Un nuevo saurópodo del Cretácico *Chubutisaurus insignis* gen. et sp. nov. (Saurischia-Chubutisauridae nov.) del Cretácico Superior (Chubutiano), Chubut, Argentina, 12–16 August 1974. *Actas I Congreso Argentino De Paleontología Y Bioestratigrafía, Tucuman* **2:** 229–240.

Curry Rogers KA. 2005. Titanosauria: a phylogenetic overview. In: Curry Rogers KA, Wilson JA, eds. *The sauropods: evolution and paleobiology*. Berkeley and Los Angeles: University of California Press, 50–103.

Curry Rogers KA, D'Emic MD, Rogers RR, Vickaryous M, Cagan A. 2011. Sauropod dinosaur osteoderms from the Late Cretaceous of Madagascar. *Nature Communications* **2:** 1–5. doi: 10.1038/ncomms1578.

D'Emic MD. in press. Revision of the sauropod dinosaurs of the Trinity Group (Texas and Oklahoma, USA). *Journal of Systematic Palaeontology* in press.

D'Emic MD, Foreman BZ. 2012. The beginning of the sauropod dinosaur hiatus in North America: insights from the Early Cretaceous Cloverly Formation of Wyoming. *Journal of Vertebrate Paleontology* **32:** 883–902.

D'Emic MD, Wilson JA. 2011. New remains attributable to the holotype of the sauropod dinosaur *Neuquensaurus australis*, with implications for saltasaurine systematics. *Acta Palaeontologica Polonica* **56:** 61–73.

D'Emic MD, Wilson JA, Chatterjee S. 2009. The titanosaur (Dinosauria: Sauropoda) osteoderm record: review and first definitive specimen from India. *Journal of Vertebrate Paleontology* **29:** 165–177.

D'Emic MD, Wilson JA, Thompson R. 2010. The end of the sauropod dinosaur hiatus in North America. *Palaeogeography, Palaeoclimatology, Palaeoecology* **297:** 486–490.

D'Emic MD, Wilson JA, Williamson TE. 2011. A sauropod dinosaur pes from the latest Cretaceous of North America and the validity of *Alamosaurus sanjuanensis* (Sauropoda: Titanosauria). *Journal of Vertebrate Paleontology* **31:** 1072–1079.

Day JJ, Norman DB, Gale AS, Upchurch P, Powell HP. 2004. A Middle Jurassic dinosaur trackway site from Oxfordshire, UK. *Palaeontology* **47:** 319–348.

Day JJ, Upchurch P, Norman DB, Gale AS, Powell HP. 2002. Sauropod trackways, evolution, and behavior. *Science* **296:** 1659.

Dong Z, Zhou S, Zhang Y. 1983. The dinosaurian remains from Sichuan Basin, China. *Palaeontologica Sinica (Series C)* **23:** 139–145.

Gilmore CW. 1922. Discovery of a sauropod dinosaur from the Ojo Alamo Formation of New Mexico. *Smithsonian Miscellaneous Collections* **81:** 1–9.

Gilmore CW. 1933. Two new dinosaurian reptiles from Mongolia with notes on some fragmentary specimens. *American Museum Novitates* **679:** 1–20.

Gilmore CW. 1946. Reptilian fauna of the North Horn Formation of central Utah. *United States Geological Survey Professional Paper* **210C:** 1–52.

Giménez O. 2007. Skin impressions of *Tehuelchesaurus* (Sauropoda) from the Upper Jurassic of Patagonia. *Revista del Museo Argentino de Ciencias Naturales* **9:** 119–124.

Gomani EM. 2005. Sauropod dinosaurs from the Early Cretaceous of Malawi, Africa. *Palaeontologia Electronica* **8:** 1–37.

Gomani EM, Jacobs LL, Winkler DA. 1999. Comparison of the African titanosaurian, *Malawisaurus*, with an Early Cretaceous North American sauropod. In: Tomida Y, Rich TH, Vickers-Rich, P, eds. *Proceedings of the second Gondwanan dinosaur symposium*. Tokyo: National Science Museum. Monograph **15:** 223–233.

González Riga BJ. 2003. A new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza, Argentina. *Amehginiana* **40:** 155–172.

González Riga BJ, Previtera E, Pirrone CA. 2009. *Malarguesaurus florenciae* gen. et sp. nov., a new titanosauriform (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza, Argentina. *Cretaceous Research* **30:** 135–148.

Gradstein FM, Ogg JG, Smith AG. 2004. *A geologic time scale 2004*. Cambridge: Cambridge University Press.

Grellet-Tinner G, Sim CM, Dong HK, Trimby P, Higa A, An SL, Oh HS, Kim TJ, Kardjilov N. 2011. Description of the first lithostrotian titanosaur embryo in ovo with neutron characterization and implications for lithostrotian Aptian migration and dispersion. *Gondwana Research* **20:** 621–629.

Haughton SH. 1928. On some reptilian remains from the Dinosaur beds of Nyasaland. *Transactions of the Royal Society of South America* **16:** 69–83.

He X, Li K, Cai K. 1988. *[The Middle Jurassic Dinosaur fauna from Dashanpu, Zigong, Sichuan, Vol. IV. Sauropod dinosaurs (2), Omeisaurus tianfuensis]*. Chengdu: Sichuan Scientific and Technical Publishing House, (in Chinese).

Hocknull SA, White MA, Tischler TR, Cook AG, Calleja ND, Sloan T, Elliott DA. 2009. New mid-Cretaceous (latest Albian) dinosaurs from Winton, Queensland, Australia. *PLoS ONE* **4:** e6190.

Ikejiri T. 2005. Distribution and biochronology of *Camarasaurus* (Dinosauria, Sauropoda) from the Jurassic Morrison Formation of the Rocky Mountain Region. *New Mexico Geological Society Field Conference Guidebook, Geology of the Chama Basin* **56:** 367–379.

Ikejiri T, Tidwell V, Trexler DL. 2005. New adult specimens of *Camarasaurus lentus* highlight ontogenetic variation within the species. In: Carpenter K, Tidwell V, eds. *Thunder-Lizards: The Sauropodomorph Dinosaurs*. Bloomington: Indiana University Press, 154–179.

Jacobs LL, Winkler DA, Downs WR, Gomani EM. 1993. New material of an Early Cretaceous titanosaurid sauropod dinosaur from Malawi. *Palaeontology* **36:** 523–534.

Janensch W. 1914. Übersicht über die Wirbeltierfauna der Tendaguru-Schichten, nebst einer kurzen Charakeristierung der neu aufgeführten Arten von Sauropoden. *Archiv Für Biontologie* **3:** 15–58.

Janensch W. 1929. Material und Formengehalt der Sauropoden in der Ausbeute der Tendaguru-Expedition. *Palaeontographica* **2** (Suppl. 7)**:** 1–34.

Janensch W. 1950. Die Wirbelsaule von *Brachiosaurus brancai*. *Palaeontographica* **3** (Suppl. 7)**:** 27–93.

Janensch W. 1961. Die Gliedmaßen und Gliedmaßen Gürtel der Sauropoden der Tendaguru-Schichten. *Palaeontographica* **3** (Suppl. 7)**:** 177–235.

Kearney M. 2002. Fragmentary taxa, missing data, and ambiguity: mistaken assumptions and conclusions. *Systematic Biology* **51:** 369–381.

Krause DW, O'Connor PM, Curry Rogers KC, Sampson SD, Buckley GA, Rogers RR. 2006. Late Cretaceous terrestrial vertebrates from Madagascar, implications for Latin American biogeography. *Annals of the Missouri Botanical Garden* **93:** 178–208.

Ksepka DT, Norell MA. 2006. *Erketu ellisoni*, a long-necked sauropod from Bor Guve (Dornogov Aimag, Mongolia). *American Museum Novitates* **3508:** 1–16.

Ksepka DT, Norell MA. 2010. The illusory evidence for Asian Brachiosauridae: new material of *Erketu ellisoni* and a phylogenetic reappraisal of basal Titanosauriformes. *American Museum Novitates* **3700:** 1–28.

Kues BS, Lehman T, Rigby JK Jr. 1980. The teeth of *Alamosaurus sanjuanensis*, a Late Cretaceous sauropod. *Journal of Paleontology* **54:** 864–868.

Le Loeuff J. 1993. European titanosaurs. *Revue de Paléobiologie* **7:** 105–117.

Lehman TM, Coulson AB. 2002. A juvenile specimen of the sauropod dinosaur *Alamosaurus sanjuanensis* from the Upper Cretaceous of Big Bend National Park, Texas. *Journal of Paleontology* **76:** 156–172.

Lockley MG, Farlow JO, Meyer CA. 1994. *Brontopodus* and *Parabrontopodus* ichnogen. nov. and the significance of wide- and narrow-gauge sauropod trackways. *Gaia* **10:** 135–145.

Longman HA. 1933. A new dinosaur from the Queensland Cretaceous. *Memoirs of the Queensland Museum* **10:** 131–144.

Lucas SG, Hunt AP. 1989. *Alamosaurus* and the sauropod hiatus in the Cretaceous of the North American western interior. *Geological Society of America Special Paper* **238:** 75–85.

Lydekker R. 1893. The dinosaurs of Patagonia. *Anales del Museo de La Plata* **2:** 1–14.

Lydekker R. 1895. On bones of a sauropodous dinosaur from Madagascar. *Quarterly Journal of the Geological Society of London* **51:** 329–336.

Maddison WP, Maddison DR. 1992. *Macclade, Version 3.0*. Sunderland, MA: Sinauer.

Maddison WP, Maddison DR. 2009. *Mesquite: a modular system for evolutionary analysis*, v. 2.71. Available at: http://mesquiteproject.org

Mannion PD. 2011. A reassessment of *Mongolosaurus haplodon* Gilmore, 1933, a titanosaurian sauropod dinosaur from the Early Cretaceous of Inner Mongolia, People's Republic of China. *Journal of Systematic Palaeontology* **9:** 355–378.

Mannion PD, Calvo JO. 2011. Anatomy of the basal titanosaur (Dinosauria, Sauropoda) *Andesaurus delgadoi* from the mid-Cretaceous (Albian–early Cenomanian) Río Limay Formation, Neuquén Province, Argentina: implications for titanosaur systematics. *Zoological Journal of the Linnean Society* **163:** 155–181.

Mantell GA. 1852. On the structure of the *Iguanodon*, and on the fauna and flora of the Wealden Formation. *Proceedings of the Royal Institute of Great Britain* **1:** 141–146.

Marsh OC. 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:** 161–167.

Martin V, Buffetaut E, Suteethorn V. 1994. A new genus of sauropod dinosaur from the Sao Khua Formation (Late Jurassic or Early Cretaceous) of northeastern Thailand. *Comptes Rendus de l'Academie des Sciences de Paris* **319:** 1085–1092.

Martinelli AG, Forasieppi AM. 2004. Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Río Negro Province, Argentina, with the description of a new sauropod dinosaur (Titanosauridae). *Revista del Museo Argentino de Ciencias Naturales* **6:** 257–305.

Mateer NJ, McIntosh JS. 1985. A new reconstruction of the skull of *Euhelopus zdanskyi* (Saurischia: Sauropoda). *Bulletin of the Geological Institutions of the University of Uppsala, New Series* **11:** 125–132.

McIntosh JS. 1990. Sauropoda. In: Weishampel DB, Dodson P, Osmólska H, eds. *The dinosauria*, 1st edn. Berkeley: University of California Press, 345–401.

McIntosh JS, Miles CA, Cloward KC, Parker JR. 1996. A new nearly complete skeleton of *Camarasaurus*. *Bulletin of Gunma Museum of Natural History* **1:** 1–87.

Monbaron M, Russell DA, Taquet P. 1999. *Atlasaurus imelakei*, n. g., n. sp., a brachiosaurid-like sauropod from the Middle Jurassic of Morocco. *Comptes Rendus De l'Académie Des Sciences, Paris* **329:** 519–526.

Naish D, Hutt S, Martill DM. 2001. *Dinosaurs of the Isle of Wight*. The Palaeontological Association, London, 433.

Osborn HF, Mook CC. 1921. *Camarasaurus*, *Amphicoelias*, and other sauropods of Cope. *Memoirs of the American Museum of Natural History* **3:** 247–387.

Ostrom JH, McIntosh JS. 1966. *Marsh's dinosaurs*. New Haven: Yale University Press, 388.

Otero A. 2010. The appendicular skeleton of *Neuquensaurus*, a Late Cretaceous saltasaurine sauropod from Patagonia, Argentina. *Acta Palaeontologica Polonica* **55:** 399–426.

Paul GS. 1988. The brachiosaur giants of the Morrison and Tendaguru with a description of a new subgenus, Giraffatitan, and a comparison of the world's largest dinosaurs. *Hunteria* **2:** 1–14.

Powell JE. 1992. Osteología de *Saltasaurus loricatus* (Sauropoda–Titanosauridae) del Cretácico Superior del noroeste Argentino. In: Sanz J, Buscalioni A, eds. *Los Dinosaurios y Su Entorno*. Biotico: Actas del Segundo Curso de Paleontología en Cuenca, 165–230.

Ratkevitch R. 1998. New Cretaceous brachiosaurid dinosaur, *Sonorasaurus thompsoni* gen. et sp. nov, from Arizona. *Journal of the Arizona-Nevada Academy of Science* **31:** 71–82.

Rauhut OWM. 2006. A brachiosaurid sauropod from the Late Jurassic Cañadón Calcáreo Formation of Chubut, Argentina. *Fossil Record* **9:** 226–237.

Rauhut OWM, Lopez-Arbarello A. 2009. Considerations on the age of the Tiouaren Formation (Iullemmeden Basin, Niger, Africa): implications for Gondwanan Mesozoic terrestrial vertebrate fauna. *Palaeogeography, Palaeoclimatology, Palaeoecology* **271:** 259–267.

Rich TH, Vickers-Rich P, Gimenez O, Cúneo R, Puerta P, Vacca R. 1999. A new sauropod dinosaur from Chubut Province, Argentina. In: Tomida Y, Rich TH, Vickers-Rich, P, eds. *Proceedings of the second Gondwanan dinosaur symposium*. Tokyo: National Science Museum. Monograph 15, 61–84.

Riggs ES. 1903. Structure and relationships of opisthocoelian dinosaurs. Part I: *Apatosaurus* Marsh. *Field Columbian Museum Geological Series* **2:** 165–196.

Romer AS. 1956. *Osteology of the reptiles*. Chicago, IL: University of Chicago Press.

Rose P. 2007. A titanosauriform (Dinosauria: Saurischia) from the Early Cretaceous of Central Texas and its phylogenetic relationships. *Palaeontologica Electronica* **10:** 1–65.

Royo-Torres R. 2009. El saurópodo de Peñarroya de Tastavins. *Monograpfías Turonlenses* **6:** 1–548.

Royo-Torres R, Cobos A, Alcalá L. 2006. A giant European dinosaur and a new sauropod clade. *Science* **314:** 1925–1927.

Royo-Torres R, Alcalá L, Cobos A. 2012. A new specimen of the Cretaceous sauropod *Tastavinsaurus sanzi* from El Castellar (Teruel, Spain), and a phylogenetic analysis of the Laurasiformes. *Cretaceous Research* **34:** 61–83.

Royo-Torres R, Cobos A. 2009. Turiasaur sauropods in the Tendaguru beds of Tanzania. *Journal of Vertebrate Paleontology* **29:** 173A.

Russell DA. 1993. The role of central Asia in dinosaurian biogeography. *Canadian Journal of Earth Science* **30:** 2002–2012.

Salgado L, Azpilicueta C. 2000. Un nuevo saltasaurino (Sauropoda, Titanosauridae) de la provincia de Río Negro (Formación Allen, Cretácico Superior), Patagonia, Argentina. *Ameghiniana* **37:** 259–264.

Salgado L, Coria RA, Calvo J. 1997. Evolution of titanosaurid sauropods. I: phylogenetic analysis based on the postcranial evidence. *Ameghiniana* **34:** 3–32.

Sánchez-Hernández B. 2005. *Galveosaurus herreroi*, a new sauropod dinosaur from Villar del Arzobispo Formation (Tithonian-Berriasian) of Spain. *Zootaxa* **1034:** 1–20.

Sander PM, Mateus O, Laven T, Knötschke N. 2006. Bone histology indicates insular dwarfism in a new Late Jurassic sauropod dinosaur. *Nature* **441:** 739–741.

Santos VF, Lockley MG, Meyer CA, Carvalho J, Galopim de Carvalho AM, Moratalla JJ. 1994. A new sauropod tracksite from the Middle Jurassic of Portugal. *Gaia* **10:** 5–13.

Sanz JL, Powell JE, LeLoeuff J, Martinez R, Pereda-Suberiola X. 1999. Sauropod remains from the Upper Cretaceous of Laño (northcentral Spain), titanosaur phylogenetic relationships. *Estudios del Museo de Ciencias Naturales de Nava* **14:** 235–255.

Sereno PC. 1999. Dinosaurian biogeography: vicariance, dispersal and regional extinction. In: Tomida Y, Rich TH, Vickers-Rich, P, eds. *Proceedings of the second Gondwanan dinosaur symposium*. Tokyo: National Science Museum. Monograph 15, 249–257.

Sereno PC. 2007. Logical basis for morphological characters in phylogenetics. *Cladistics* **23:** 565–587.

Sereno PC. 2009. Comparative cladistics. *Cladistics* **25:** 624–659.

Sereno PC, Beck AL, Dutheil DB, Larssen HCE, Lyon GH, Moussa B, Sadleir RW, Sidor CA, Varricchio DJ, Wilson GP, Wilson JA. 1999. Cretaceous sauropods from the Sahara and the uneven rate of skeletal evolution among dinosaurs. *Science* **286:** 1342–1347.

Smith AB. 1994. *Systematics and the fossil record: documenting evolutionary patterns*. Hoboken: Wiley-Blackwell.

Stein K, Cziki Z, Curry Rogers KC, Weishampel DB, Redelstorff R, Carballido JL, Sander PM. 2010. Small body size and extreme cortical bone remodeling indicate phyletic dwarfism in *Magyarosaurus dacus* (Sauropoda: Titanosauria). *Proceedings of the National Academy of Sciences, USA* **107:** 9258–9263.

Suteethorn S, Le Loeuff J, Buffetaut E, Suteethorn V. 2010. Description of topotypes of *Phuwiangosaurus sirindhornae*, a sauropod from the Sao Khua Formation (Early Cretaceous) of Thailand, and their phylogenetic implications. *Neues Jahrbuch für Geologie und Paläontologie* **256:** 109–121.

Suteethorn S, Le Loeuff J, Buffetaut E, Suteethorn V, Talubmook C, Chonglakmani C. 2009. A new skeleton of *Phuwiangosaurus sirindhornae* (Dinosauria, Sauropoda) from NE Thailand. *The Geological Society, London, Special Publications* **315:** 189–215.

Swofford DL. 2002. *PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4.0b10*. Sunderland, MA: Sinauer Associates.

Tang F, Jing X, Kang X, Zhang G. 2001. *[Omeisaurus maoianus: a complete sauropod from Jingyuan, Sichuan.]* Beijing: China Ocean Press, (in Chinese).

Taylor M. 2009. A reevaluation of *Brachiosaurus altithorax*

Riggs, 1903 (Dinosauria, Sauropoda) and its generic separation from *Brachiosaurus brancai* (Janensch, 1914). *Journal of Vertebrate Paleontology* **29:** 787–806.

Taylor MP, Naish D. 2007. An unusual new neosauropod dinosaur from the Lower Cretaceous Hastings Beds Group of East Sussex, England. *Palaeontology* **50:** 1547–1564.

Taylor MP, Wedel MJ, Cifelli RL. 2011. A new sauropod dinosaur from the Lower Cretaceous Cedar Mountain Formation, Utah, USA. *Acta Palaeontologica Polonica* **56:** 75–98.

Templeton A. 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and apes. *Evolution* **37:** 221–244.

Tidwell V, Carpenter K, Brooks W. 1999. New sauropod from the Lower Cretaceous of Utah, USA. *Oryctos* **2:** 21–37.

Tidwell V, Carpenter K, Meyer S. 2001. New titanosauriform (Sauropoda) from the Poison Strip Member of the Cedar Mountain Formation (Lower Cretaceous), Utah. In: Tanke D, Carpenter K, eds. *Mesozoic vertebrate life: new research inspired by the paleontology of Phillip J. Currie*. Bloomington: Indiana University Press, 139–165.

Tidwell V, Wilhite DR. 2005. Ontogenetic variation and isometric growth in the forelimb of the Early Cretaceous sauropod *Venenosaurus*. In: Carpenter K, Tidwell V, eds. *Thunder-lizards: the sauropodomorph dinosaurs*. Bloomington: Indiana University Press, 187–196.

Upchurch P. 1995. The evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society of London* **349:** 365–390.

Upchurch P. 1998. The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society* **124:** 43–103.

Upchurch P, Barrett PM, Dodson P. 2004. Sauropoda. In: Weishampel DB, Dodson P, Osmólska H, eds. *The dinosauria*, 2nd edn. Berkeley: University of California Press, 259–322.

Upchurch P, Hunn CA, Norman DB. 2002. An analysis of dinosaurian biogeography: evidence for the existence of vicariance and dispersal patterns caused by geological events. *Proceedings of the Royal Society of London B* **269:** 613–621.

Upchurch P, Mannion PD, Barrett PM. 2011. Sauropod dinosaurs. In: Batten D, ed. *English Wealden fossils*. London: The Palaeontological Association, 476–525.

Wedel MJ, Cifelli R. 2005. *Sauroposeidon*: Oklahoma's native giant. *Oklahoma Geology Notes* **65:** 40–57.

Wedel MJ, Cifelli R, Sanders RK. 2000b. Osteology, paleobiology, and relationships of the sauropod dinosaur *Sauroposeidon*. *Acta Paleontologica Polonica* **45:** 343–388.

Wedel MJ, Cifelli RL, Sanders RK. 2000a. *Sauroposeidon proteles*, a new sauropod from the Early Cretaceous of Oklahoma. *Journal of Vertebrate Paleontology* **20:** 109–114.

Whitlock JA. 2011. A phylogenetic analysis of Diplodocoidea (Saurischia: Sauropoda). *Zoological Journal of the Linnean Society* **161:** 872–915.

Whitlock JA, D'Emic MD, Wilson JA. 2011. Cretaceous diplodocids in Asia? Re-evaluating the affinities of a fragmentary specimen. *Palaeontology* **54:** 351–364.

Wild R. 1991. *Janenschia* n. g. *robusta* (E. Fraas 1908) pro *Tornieria robusta* (E. Fraas 1908) (Reptilia, Saurischia, Sauropodomorpha). *Stuttgarter Beiträge Zur Naturkunde, Serie B (Geologie und Paläontologie)* **173:** 1–4.

Wilson JA. 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *Journal of Vertebrate Paleontology* **19:** 639–653.

Wilson JA. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of the Linnean Society* **136:** 217–276.

Wilson JA. 2005. Redescription of the Mongolian sauropod *Nemegtosaurus mongoliensis* Nowinski (Dinosauria: Saurischia) and comments on Late Cretaceous sauropod diversity. *Journal of Systematic Palaeontology* **3:** 283–318.

Wilson JA. 2006. Anatomical nomenclature of fossil vertebrates: standardized terms or lingua franca? *Journal of Vertebrate Paleontology* **26:** 511–518.

Wilson JA, Carrano MT. 1999. Titanosaurs and the origin of 'wide-gauge' trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology* **25:** 252–267.

Wilson JA, D'Emic MD, Curry Rogers KA, Mohabey D, Sen S. 2009. Reassessment of the sauropod dinosaur *Jainosaurus* (='*Antactosaurus*') *septentrionalis* from the Upper Cretaceous of India. *Contributions from the Museum of Paleontology, University of Michigan* **32:** 17–40.

Wilson JA, D'Emic MD, Ikejiri T, Moacdieh E, Whitlock JA. 2011. A nomenclature for vertebral fossae in sauropods and other saurischian dinosaurs. *PLoS ONE* **6:** e17114.

Wilson JA, Sereno PC. 1998. Early evolution and higher level phylogeny of sauropod dinosaurs. *Society of Vertebrate Paleontology Memoir* **5:** 1–68.

Wilson JA, Upchurch P. 2003. A revision of *Titanosaurus* Lydekker (Dinosauria-Sauropoda), the first dinosaur genus with a 'Gondwanan' distribution. *Journal of Systematic Palaeontology* **1:** 125–160.

Wilson JA, Upchurch P. 2009. Redescription and reassessment of the phylogenetic affinities of *Euhelopus zdanskyi* (Dinosauria: Sauropoda) from the Early Cretaceous of China. *Journal of Systematic Palaeontology* **7:** 199–239.

Wiman C. 1929. Die Kreide-Dinosaurier aus Shantung. *Palaeontologia Sinica (Series C)* **6:** 1–67.

Xu X, Zhang X, Tan Q, Zhao X, Tan L. 2006. A new titanosaurian sauropod from Late Cretaceous of Nei Mongol, China. *Acta Geologica Sinica* **80:** 20–26.

You H-L, Li D-Q. 2009. The first well-preserved Early Cretaceous brachiosaurid dinosaur in Asia. *Proceedings of the Royal Society of London, Series B* **276:** 4077–4082. doi:10.1098/rspb.2009.1278.

You H-L, Li D-Q, Zhou L-Q, Ji Q. 2008. *Daxiatitan binglingi*: a giant sauropod dinosaur from the Early Cretaceous of China. *Gansu Geology* **17:** 1–10.

Young CC. 1939. On a new Sauropoda, with notes on other fragmentary reptiles from Szechuan. *Bulletin of the Geological Society of China* **19:** 279–315.

Zaher H, Pol D, Carvalho AB, Nascimento PM, Riccomini C, Larson P, Juarez-Valieri R, Pires-Domingues R, da Silva NJ, Campos DA. 2011. A complete skull of an Early Cretaceous sauropod and the evolution of advanced titanosaurians. *PLoS ONE* **6:** e16663.

APPENDIX 1

CHARACTER-TAXON MATRIX

										010										020										030										040
Shunosaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	1	0	0	0
Omeisaurus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	0
Jobaria	1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Atlasaurus	1	?	?	?	0	1	0	0	?	?	?	?	?	1	?	0	1	0	?	0	?	?	?	0	0	?	?	?	0	?	?	?	?	?	?	?	?	?	0	0
Diplodocoidea	1	0	0	0	1	0	0	0	0	0	0	0	1	2	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Camarasaurus	1	0	0	0	1	0	1	0	0	0	1	1	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0
Tehuelchesaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	1	?	0	0	?	0	0	?	1	1	0
Europasaurus	1	0	0	?	0	0	0	0	1	?	1	1	1	1	1	0	1	?	?	?	1	0	1	0	0	0	0	0	0	?	?	0	?	0	?	?	0	1	1	1
Giraffatitan	1	1	1	1	0	0	0	0	1	1	1	1	1	1	1	0	1	1	0	0	1	0	1	0	0	0	0	0	0	?	?	0	?	?	?	1	0	1	1	1
Brachiosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	1	0	1	1	1
Abydosaurus	1	1	1	1	0	0	0	0	1	1	0	1	1	2	1	0	1	1	?	0	1	?	1	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Cedarosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	1	?	1	1	?
Venenosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ligabuesaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	2	?	?	?	?	?	?	?	?	?	?	?	0	1	0	1	1	1	1	?	1	1	0
Sauroposeidon	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	2	?	?	1	0	1	0	0	0	0	0	0	0	1	0	1	1	1	1	0	1	1	?
Tastavinsaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	1	?
Qiaowanlong	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	1	1	1	0	1	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?
Erketu	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	?	0	1	1	1	0	1	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?
Euhelopus	1	?	?	0	?	?	?	?	0	0	?	1	0	2	0	0	1	2	1	0	1	1	1	1	0	1	?	0	1	1	0	2	0	0	0	0	1	1	1	0
Daxiatitan	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	?	?	?	1	1	1	?	1	?	0	1	1	?	?	?	0	0	0	?	1	1	?
Tangvayosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	0	?	?	?	?	1	?
Phuwiangosaurus	?	0	?	?	?	1	0	0	?	?	?	?	1	2	0	1	1	0	1	0	1	1	1	1	1	1	0	0	1	1	0	2	0	0	0	0	1	1	1	0
Chubutisaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0
Andesaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	1	?
Malawisaurus	?	?	0	?	1	1	1	1	?	?	?	1	1	2	0	1	1	2	?	?	0	0	1	0	0	0	?	1	0	1	1	0	1	1	1	0	1	1	1	0
Opisthocoelicaudia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	0	?	1	1	?	0	1	1	1	1	0
Alamosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	2	?	1	1	2	?	1	0	0	1	0	0	0	1	1	0	?	?	0	1	1	1	0	1	1	1	0
‘Saltasaurini’	?	?	?	?	1	1	1	1	?	?	?	?	?	?	?	?	1	2	?	1	1	0	?	0	0	0	1	1	0	?	1	0	1	1	1	0	1	1	1	0

										050										060										070										080
Shunosaurus	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Omeisaurus	1	0	0	0	0	0	0	0	?	0	1	0	0	?	0	0	0	1	0	0	0	0	?	?	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0
Jobaria	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Atlasaurus	0	0	0	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Diplodocoidea	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Camarasaurus	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Tehuelchesaurus	1	0	1	0	0	0	0	0	0	?	1	?	?	?	0	?	?	?	?	?	?	?	0	1	?	?	?	?	0	0	0	0	0	0	?	?	?	0	1	0
Europasaurus	1	0	1	1	0	0	0	0	?	0	?	?	?	0	0	?	?	1	?	0	0	0	?	?	1	?	1	?	?	0	?	0	0	?	0	0	?	0	1	0
Giraffatitan	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	1	1	1	0	1	0	1	0	1	0	0	0	0	0	0	1	1	0
Brachiosaurus	1	0	1	1	0	0	0	0	0	0	1	?	?	0	0	?	?	1	?	0	?	?	1	1	?	?	?	?	?	?	?	0	0	0	?	?	?	1	0	0
Abydosaurus	?	?	1	?	?	?	?	?	?	?	1	?	1	0	0	1	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?
Cedarosaurus	1	0	1	?	0	0	0	0	0	?	?	0	?	0	0	1	?	1	1	1	0	0	?	1	1	0	1	?	1	0	?	0	0	0	0	0	0	1	0	0

Venenosaurus	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	1	?	1	1	1	0	0	1	?	1	0	1	0	?	0	?	?	?	?	?	?	?	?	?	?
Ligabuesaurus	1	?	1	?	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	0	0	?	?	?	1	1	0
Sauroposeidon	1	0	1	0	0	0	0	0	0	0	1	0	?	0	0	0	0	1	1	0	0	0	1	1	?	?	?	1	2	1	0	0	0	0	0	0	0	1	1	0
Tastavinsaurus	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	?	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Qiaowanlong	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Erketu	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?
Euhelopus	1	0	1	1	0	0	1	?	1	1	1	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	1	1	1	0	0	0	0	?	?	?	0	1	0
Daxiatitan	1	?	0	?	?	0	1	0	?	?	?	?	?	?	?	?	?	1	?	0	1	?	1	1	0	?	?	?	1	?	0	0	0	0	?	?	?	?	?	?
Tangvayosaurus	?	0	1	?	?	?	?	0	1	?	?	0	?	0	0	0	1	1	?	0	0	0	?	?	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Phuwiangosaurus	1	0	0	1	0	0	1	0	1	1	1	0	1	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1	1	0	0	0	?	0	?	0	?	1	1	0
Chubutisaurus	?	0	?	?	0	1	?	0	0	?	?	?	?	0	0	0	0	1	1	?	0	0	1	1	1	?	?	?	1	1	0	?	?	?	?	?	?	0	1	0
Andesaurus	1	0	1	?	0	?	?	0	0	?	?	0	1	1	0	0	0	1	1	0	0	0	?	1	1	0	1	?	?	?	?	?	?	?	?	?	?	0	1	?
Malawisaurus	1	0	1	1	1	1	1	1	?	1	1	0	0	1	1	0	0	1	1	0	0	0	1	1	1	0	1	?	?	?	?	?	1	0	1	1	1	0	1	0
Opisthocoelicaudia	1	1	0	1	1	1	0	1	1	1	1	1	0	1	?	0	1	1	1	0	0	0	1	1	1	?	1	1	2	0	0	1	1	1	1	0	1	0	1	1
Alamosaurus	1	1	1	1	1	1	1	1	0	?	?	1	0	1	1	0	1	1	1	0	1	1	1	1	1	0	1	1	2	1	0	1	1	1	1	1	1	0	1	1
'Saltasaurini'	0	1	1	1	1	1	1	1	0	1	1	?	0	1	1	0	1	1	1	0	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	0	1	1
										090										100										110									119	
Shunosaurus	0	0	0	0	0	?	0	0	0	0	0	1	?	?	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	?	0	0	0	0	?	?	0	
Omeisaurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	?	0	0	0	?	0	0	0	
Jobaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Atlasaurus	?	?	?	?	?	?	?	1	?	0	?	?	0	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	
Diplodocoidea	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Camarasaurus	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Tehuelchesaurus	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	0	
Europasaurus	?	0	?	0	1	?	?	?	?	?	1	?	0	?	1	1	1	1	0	1	?	?	0	0	1	?	1	0	0	?	?	?	?	?	?	?	?	?	0	
Giraffatitan	2	0	0	0	1	1	0	1	1	1	1	1	?	0	1	1	1	1	1	1	1	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	1	0	
Brachiosaurus	2	0	?	0	?	?	?	?	?	?	?	?	?	?	1	?	1	1	?	1	?	?	?	?	?	?	1	0	0	0	?	?	?	?	?	?	?	?	0	
Abydosaurus	?	0	?	0	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	1	0	1	0	?	?	?	?	?	?	?	1	0	
Cedarosaurus	2	0	0	0	1	?	0	?	1	?	?	?	1	?	1	1	?	?	?	?	?	0	0	?	?	?	1	0	1	?	?	?	?	?	?	?	?	?	0	
Venenosaurus	?	?	?	?	1	1	0	?	1	?	?	?	1	0	1	1	?	?	?	?	1	0	0	0	1	1	?	?	?	?	?	?	?	?	0	0	1	1	?	
Ligabuesaurus	1	0	0	0	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	1	0	1	0	0	1	0	1	0	?	1	0	0	
Sauroposeidon	1	0	0	0	1	1	0	?	1	?	?	?	0	?	1	1	1	1	0	1	1	1	0	0	0	1	1	0	1	0	1	1	0	0	?	?	?	?	0	
Tastavinsaurus	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	1	1	0	1	1	1	0	0	0	1	1	0	1	0	1	1	1	0	?	0	1	0	?	
Qiaowanlong	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	1	1	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
Erketu	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	0	1	?	?	?	
Euhelopus	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	1	0	0	0	0	0	1	1	0	1	0	1	1	1	0	0	1	0	0	0	
Daxiatitan	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	?	?	?	?	?	?	?	?	0	
Tangvayosaurus	?	?	?	?	?	?	?	?	?	?	?	?	0	?	1	1	?	?	?	?	1	1	0	0	0	?	1	0	1	0	1	1	0	0	0	1	?	?	?	
Phuwiangosaurus	1	0	0	0	1	?	0	?	?	?	?	?	0	?	1	1	0	1	0	1	1	1	0	0	0	1	1	0	1	0	1	1	1	0	0	?	?	?	0	
Chubutisaurus	1	0	1	0	?	1	0	?	1	1	1	1	0	?	1	1	?	?	?	?	?	?	0	0	0	?	1	0	1	0	?	?	?	?	?	?	1	0	?	
Andesaurus	?	0	?	?	?	?	?	?	?	?	1	1	?	?	1	1	?	?	?	?	1	1	1	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	
Malawisaurus	?	0	1	0	1	1	0	?	1	?	1	1	?	?	1	1	?	?	?	?	?	?	1	1	0	1	1	0	1	?	1	1	1	0	?	?	?	?	1	
Opisthocoelicaudia	0	1	1	0	1	0	1	2	1	1	1	1	0	1	1	1	?	1	?	?	1	1	1	?	0	1	1	0	0	1	1	1	1	0	1	1	1	?	?	
Alamosaurus	?	1	1	1	1	1	1	2	1	1	1	1	0	1	1	1	1	1	1	1	?	?	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	0	1	
'Saltasaurini'	0	1	1	1	1	1	1	?	?	?	?	?	0	?	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	?	?	1	

APPENDIX 2

Characters ordered by anatomical region. The original author or modifications to pre-existing characters are listed where appropriate.

1. Posterolateral process of premaxilla and lateral process of maxilla, shape: without midline contact (0); with midline contact forming marked narial depression, subnarial foramen not visible laterally (1). (Wilson, 2002.)
2. Premaxilla–maxilla suture, shape: planar (0); twisted along its length, giving the contact a sinuous appearance in lateral view (1). (Chure *et al*., 2010.)
3. Premaxilla, small, finger-like, vertically orientated premaxillary process near anteromedial corner of external naris: absent (0); present (1).
4. Lacrimal, anteriorly projecting vertical plate of bone: absent (0); present (1). (Modified from Chure *et al*., 2010.)
5. Parietal, distance separating supratemporal fenestrae: less than (0) or twice (1) the long axis of supratemporal fenestra. (Wilson, 2002.)
6. Supraoccipital, height: twice (0) subequal to or less than (1) height of foramen magnum. (Wilson, 2002.)
7. Basal tubera, width relative to occipital condyle: less than 1.4 (0); greater than 1.6 (1). (Modified from Mannion, 2011.)
8. Paroccipital process, ventral non-articular process: absent (0); present (1). (Wilson, 2002.)
9. Quadradojugal, anterior ramus, ventral triangular projection: absent (0); present (1).
10. Dentary, posteroventral process, shape: single (0); divided (1). (Modified from Chure *et al*., 2010.)
11. Surangular depth: less than twice (0) or more than two and a half times (1) maximum depth of the angular (Wilson, 2002.)
12. Dentary teeth, number: greater than 20 (0); 17 or fewer (1). (Wilson, 2002.)
13. Tooth crowns, orientation: aligned anterolingually, tooth crowns overlap (0); aligned along jaw axis, crowns do not overlap (1). (Modified from Wilson, 2002.)
14. Marginal tooth denticles: present on anterior and posterior edges of tooth (0); only present in posterior-most few teeth (1); absent on both anterior and posterior edges (2). (Modified from Wilson, 2002.)
15. Maxillary teeth, shape: straight along axis (0); twisted axially through an arc of 30–45° (1). (Modified from Chure *et al*., 2010.)
16. Teeth, average slenderness index (= crown height/crown width): > 3.0 (0); < 3.0 (1). (Modified from Upchurch, 1998.)
17. Presacral vertebrae, pneumatopores in centra (pleurocoels): absent (0); present (1). (Wilson, 2002.)
18. Presacral neural arch bone texture: camerate, with a few, large cavities (0); spongy, with centimetre-scale internal cells and walls, 'semi-camellate' (Wedel *et al*., 2000b) (1); camellate to somphospondylous, with subcentimetre-scale cells and walls (2). (Wilson, 2002.)
19. Cervical vertebrae, number: 14 or fewer (0); 15 or more (1). (Modified from Wilson, 2002.)
20. Axis, centrum, shape: over two and a half times as long as tall (0); less than twice as long as tall (1).
21. Cervical pneumatopores (pleurocoels), shape: complex, divided by bony septa (0); simple, undivided (1). (Wilson, 2002.)
22. Middle cervical neural spines, shape: single (0); bifid (1). (Wilson, 2002.)
23. Middle cervical centra, anteroposterior length/average of width and height of posterior face: < 2.5 (0); > 3.0 (1). (Modified from Upchurch, 1998; Wilson, 2002; Chure *et al*., 2010.)
24. Cervical vertebrae, epipophyses, shape: stout, pillar-like expansions above postzygapophyses (0); posteriorly projecting prongs (1).
25. Cervical vertebrae, epipophyseal prezygapophyseal lamina, morphology: thin lamina passing nearly horizontally across the neural arch (0); thick, subvertically orientated strut that joins the spinopostzygapophyseal lamina at the neural spine (1).
26. Cervical vertebrae, intrapostzygapophyseal lamina, shape: has little or no relief past margin of centropostzygapophyseal lamina (cpol) when viewed laterally (0); projects beyond cpol in lateral view, with distinct 'kink' (1).
27. Middle cervical vertebrae, neural canal, shape: roughly same diameter throughout length (0); mediolaterally narrows towards mid-length of vertebra (1). (Curry Rogers, 2005.)
28. Middle and posterior cervical vertebrae, parapophyses, shape: subcircular or only slightly longer than tall (0); elongate, making up more than half the functional centrum length in posterior cervical vertebrae (1).
29. Cervical vertebrae, parapophyses, shape and orientation: weakly developed, project laterally or slightly ventrally from the centrum (0); broad and project ventrally such that cervical ribs are displaced ventrally more than the height of the centrum (1). (Modified from Wilson & Upchurch, 2009.)
30. Posterior cervical and anterior dorsal vertebrae, neural spines, height: tall, height approaches or

exceeds centrum height (0); very short, height less than centrum height (1).

31. Posterior cervical and anterior dorsal vertebrae, spinodiapophyseal laminae (spdl) single (0); divided, with low relief on the front of the neural spine (1). (Modified from Salgado *et al*., 1997.)
32. Posterior cervical and anterior dorsal vertebrae, neural spine, shape: single (0); bifid (1); trifid (2). (Modified from Upchurch, 1995.)
33. Posterior cervical and anterior dorsal vertebrae, prespinal lamina: absent (0), present (1). (Salgado *et al*., 1997.)
34. Posterior-most cervical vertebrae, region between centrum and prezygapophyses, height: tall, around centrum height (0); low, much less than centrum height (1). (Bonaparte *et al*., 2006.)
35. Anterior dorsal vertebrae, neural spines, shape: taper along their length (0), expand distally and end in a rounded, anteroposteriorly thin blade ('paddle-shaped') (1).
36. Middle dorsal vertebrae, posterior centrodiapophyseal lamina: single (0); double, with low relief (1).
37. Middle and posterior dorsal vertebrae, spinopostzygapophyseal lamina: divided (0); single (1). (Wilson, 2002.)
38. Anterior dorsal centra, articular face shape: amphicoelous (0); opisthocoelous (1). (Wilson, 2002.)
39. Posterior dorsal centra, articular face shape: amphicoelous (0); opisthocoelous (1). (Wilson & Sereno, 1998.)
40. Middle and posterior dorsal vertebrae, diapophyses, shape: short and dorsoventrally tall (0); long and dorsoventrally short, rod-like (1). (Janensch, 1950.)
41. Middle dorsal vertebrate, diapophyses, orientation: directed dorsally at an angle of about 45° (0); directed horizontally (1). (Modified from Salgado *et al*. 1997.)
42. Middle dorsal vertebrae, postzygapophyseal–diapophyseal lamina: present (0); absent (1). (Salgado *et al*., 1997.)
43. Middle and posterior dorsal vertebrae, posterior centrodiapophyseal lamina: single and of constant width (0); ventrally widened or forked (1). (Salgado *et al*., 1997.)
44. Middle and posterior dorsal neural spines, breadth: much narrower (0); equal to or broader (1) transversely than anteroposteriorly. (Modified from Wilson, 2002.)
45. Middle and posterior dorsal vertebrae, prespinal lamina, shape: present and bifurcates toward its ventral end (0); present and remains a single lamina throughout its length (1). (Upchurch *et al*., 2004.)
46. Middle and posterior dorsal neural spines, orientation: vertical (0); posterior, neural spine summit approaches level of diapophyses (1). (Wilson, 2002.)
47. Middle and posterior dorsal vertebrae, diapophyses: dorsal surface grades smoothly towards midline (0); dorsal surface flat and set off from rest of diapophysis by a lip (1). (Modified from Sanz *et al*., 1999.)
48. Posterior dorsal neural arches, hyposphene–hypantrum articulations: present (0); absent (1). (Wilson, 2002.)
49. Middle and posterior dorsal vertebral centra, keel: absent (0); present (1).
50. Sacral vertebrae, number: five (0); six (1). (Modified from Upchurch, 1995.).
51. Sacricostal yoke: absent (0); present (1). (Riggs, 1903; Wilson, 2002.)
52. Anterior caudal vertebrae, transverse processes, ventral 'bulge' or 'kink' visible in anteroposterior views: absent (0); present (1). (Modified from Chure *et al*., 2010.)
53. Caudal vertebrae, number: more than 50 (0); fewer than 35 (1). (Wilson, 2002.)
54. Anterior and middle caudal centra, ventral longitudinal hollow: absent (0); present (1) (Wilson, 2002.)
55. Anterior caudal vertebral centra, articular faces, shape: anterior face concave and posterior face weakly concave to flat; anterior more concave (0); procoelous (1). (Modified from Wilson, 2002.)
56. Anterior and middle caudal vertebrae, blind fossae in lateral centrum: absent (0); present, often sporadically along the vertebral series (1).
57. Anterior caudal vertebrae, tubercle or subtle blade-like process on spinoprezygapophyseal lamina near prezygapophysis: absent (0); present (1).
58. Anterior and middle caudal vertebrae, neural arches, location: over the midpoint of the centrum with approximately subequal amounts of the centrum exposed at either end (0), on the anterior half of the centrum (1). (Salgado *et al*., 1997; Upchurch *et al*., 2004.)
59. Middle caudal vertebrae, transverse processes, orientation: roughly perpendicular (0); swept backwards, usually reaching posterior margin of centrum (excluding posterior ball if present) (1).
60. Middle caudal vertebrae, neural spines, orientation: upright or lean posteriorly (0); lean anteriorly (1). (Modified from Rose, 2007.)
61. Middle to distal caudal vertebral centra, articular shape: amphiplatyan (0); procoelous (1). (Upchurch, 1995.)

62. Distal caudal vertebral centra, shape: subcircular (0); around twice as wide as tall (1) (Wilson, 2002.)
63. Dorsal ribs, proximal pneumatocoels: absent (0); present (1). (Wilson & Sereno, 1998.)
64. Anterior dorsal ribs, cross-sectional shape: subcircular (0); plank-like, anteroposterior breadth more than three times mediolateral breadth (1). (Wilson & Sereno, 1998.)
65. Chevrons, 'crus' bridging dorsal margin of haemal canal: present (0); absent (1). (Upchurch, 1995.)
66. Anterior and middle chevrons, articular facets: contiguous (0); each facet divided into an anterior and posterior section, separated by a furrow (1).
67. Anterior chevrons excluding the first, haemal canal, depth: short, approximately 25 per cent (0) or long, approximately 50 per cent (1) chevron length. (Wilson, 2002.)
68. Scapular glenoid, orientation: relatively flat or laterally facing (0); bevelled medially (1). (Wilson & Sereno, 1998).
69. Scapula, processes on ventral margin near base of blade, number: zero (0); one (1), two (2) (Modified from Carballido *et al*., 2011.)
70. Scapular blade, cross-section near base: D-shaped, wide lateral ridge present (0); flat or slightly curved, no lateral ridge (1). (Modified from Wilson, 2002.)
71. Scapula, acromial side of blade, shape: straight (0); curved, flaring (1). (Wilson, 2002.)
72. Scapulocoracoid suture, shape: suture ends before dorsal margin of acromion and coracoid (0); suture extends to dorsal margin of acromion and coracoid (= flush dorsal margin) (1). (Modified from Upchurch, 1995, 1998.)
73. Coracoid, shape: anteroposterior dimension more than 1.5 times proximodistal dimension (0); anteroposterior dimension less than proximodistal dimension (1). (Modified from Wilson, 2002.)
74. Coracoid, anteroventral margin: rounded (0); square (1). (Upchurch, 1998; Wilson, 2002.)
75. Sternal plate, shape: oval with nearly straight lateral margin (0); crescentic, lateral margin strongly curved (1). (Wilson, 2002.)
76. Sternal plate, shape: posterolateral margin curved (0); posterolateral margin expanded as a corner (1).
77. Sternal plate length/humerus length: about 0.5 (0); more than 0.7 (1) (Modified from Upchurch, 1998.)
78. Humerus, robustness: robust (length/midshaft width < 7) (0); gracile (length/ midshaft width > 7.5 (1) (Modified from Curry Rogers, 2005.)
79. Humerus, proximolateral corner, shape: forms an obtuse angle, head of humerus raised (0); forms a right angle or acute angle, head of humerus flat (1). (Modified from Wilson, 2002.)
80. Humerus, strong posterolateral bulge on around level of the deltopectoral crest, absent (0); present (1).
81. Humerus-to-femur ratio: ≤ 0.80 (0); 0.85 to 0.95 (1); > 1.0. (2). (Modified from Wilson, 2002.)
82. Humerus, deltopectoral crest, shape: narrow throughout length (0); strongly expanded distally (1). (Modified from Wilson, 2002.)
83. Humerus, radial and ulnar condyles, shape: radial condyle divided on anterior face by a notch (0); undivided (1).
84. Humerus, distal condyles, shape: flat or convex in distal profile (0); concave/ divided distally (1). (Modified from Wilson, 2002.)
85. Ulna, proximal arms, shape: anterior and medial arms subequal in development (0); anterior arm longer and wider than medial arm (1). (Modified from Wilson, 2002.)
86. Ulna, distal end: expanded posteriorly (0); unexpanded (1).
87. Radius, distal end, orientation: perpendicular to (0) or bevelled approximately 20° proximolaterally (1) relative to long axis of shaft. (Wilson, 2002.)
88. Carpal bones, number: three or more (0); two or one (1); none (2). (Modified from Upchurch, 1998; Wilson, 2002.)
89. Longest metacarpal-to-radius ratio: close to 0.3 (0); 0.45 or more (1). (Wilson & Sereno, 1998.)
90. Metacarpal I, length: less than (0) or subequal to/longer than (1) metacarpal IV. (Modified from Wilson, 2002.)
91. Metacarpal I, distal condyle shape: divided (0); undivided (1). (Wilson, 2002.)
92. Metacarpal I distal condyle, transverse axis orientation: bevelled approximately 20° proximodistally (0) or perpendicular (1) with respect to axis of distal shaft (i.e. not angled because of bowing of bone). (Modified from Wilson, 2002.)
93. Metacarpal IV, articulation for metacarpal V, shape: anteroposteriorly long, broad articular surface (0); articular surface forms a near right angle, transverse and anteroposterior dimensions of proximal end subequal (1).
94. Metacarpal V, proximal end, size: much smaller than proximal end of metacarpal I (0); subequal to or larger than proximal end of metacarpal I (1).
95. Metacarpus, shape: spreading (0); bound, with subparallel shafts and articular surfaces that extend half their length (1). (Wilson, 2002.)
96. Metacarpals, distal articular facets, shape: present and extend well onto external/ anterior

face of bone (0); reduced almost entirely to distal face of the bone except in metatarsal IV (1). (Modified from Wilson, 2002.)

97. Ilium, preacetabular process, shape: dorsoventrally short and tapering anteriorly (0); expanded into a semicircle anteriorly (1) (Modified from Salgado *et al*., 1997.)
98. Ilium, preacetabular process, orientation: directed anteriorly (0); flared laterally at least 45° (1). (Wilson, 2002.)
99. Ilium, preacetabular process, kink on ventral margin, absent (0); present (1).
100. Ilium, pubic peduncle, shape: anteroposterior and transverse dimensions subequal (0); transverse dimension more than 1.5 times anteroposterior dimension (1).
101. Pubis, length relative to puboischial contact: greater than or equal to 3 (0); less than or equal to 2.5 (1). (Modified from Salgado *et al*., 1997; Wilson, 2002.)
102. Ischial blade, length: equal to or longer than (0); shorter than (1) pubic blade. (Modified from Wilson, 2002.)
103. Ischial blade, shape: emarginated distal to pubic peduncle (0); no emargination distal to pubic peduncle (1). (Wilson, 2002.)
104. Ischium, acetabular margin, shape: margin forms short, obtuse angle (0); margin strongly embayed, forming acute angle with tall iliac peduncle (1).
105. Ischium, pubic peduncle, shape: anteroposteriorly long, large ischial contribution to acetabulum (0); anteroposteriorly abbreviate, short ischial contribution to acetabulum (1). (Modified from Wilson, 2002.)
106. Ischium, tubercle on lateroventral face, shape: set in fossa (0); raised on surface (1).
107. Femoral shaft, lateral margin shape: straight (0); proximal one-third deflected medially (1). (Wilson, 2002.)
108. Femur, longitudinal ridge on anterior face: absent (0); present (1). (Otero, 2010.)
109. Femur, fourth trochanter, shape: raised ridge, projects prominently in lateral view (0); low ridge or absent, barely or not visible in anterior view (1). (Modified from Whitlock, 2011.)
110. Femur, distal condyles: roughly perpendicular to long axis of shaft (0); bevelled dorsomedially approximately 10° (1). (Wilson, 2002.)
111. Fibula, proximal end, anterior crest: absent or poorly developed (0); well developed, creating interlocking proximal crus (1). (Modified from Royo-Torres, 2009; Wilson & Upchurch, 2009.)
112. Fibula, proximomedial end, raised triangular scar, present (0); absent (1).
113. Fibula, shaft, shape: straight (0); sigmoid, such that proximal and distal faces are angled relative to midshaft (1). (Royo-Torres, 2009.)
114. Fibula, distal end, shape: unexpanded or gently expanding distally (0); abruptly expands to form a medial lip (1). (Modified from Wilson, 2002.)
115. Astragalus, shape: at least 1.5 times wider than anteroposteriorly long (0); anteroposterior and transverse dimensions subequal (1).
116. Astragalus, posterior end of proximal face, tubercle: present (0); absent (1).
117. Metatarsal IV, proximomedial end, shape: flat or slightly convex (0); possesses a distinct embayment (1).
118. Metatarsal IV, distal end, orientation: roughly perpendicular to long axis of bone (0); bevelled upwards medially (1).
119. Osteoderms: absent (0); present (1). (Wilson, 2002.)

APPENDIX 3

SYNAPOMORPHIES

Shared derived features supporting various neosauropod clades are listed below in order of decreasing inclusiveness. Characters are optimized according to delayed transformations (DELTRAN). See Tables 5 and 6 for ambiguous synapomorphies owing to character conflict or missing data. Numbers in brackets refer to characters in Appendix 2.

Atlasaurus + Neosauropoda

1. Marginal tooth denticles present only in posteriormost few teeth (modified from Wilson, 2002). [14]

Neosauropoda (Bonaparte, 1986)

1. Distance separating supratemporal fenestrae twice long axis of fenestra (Wilson, 2002). [5]
2. Middle and posterior dorsal vertebral neural spines broader transversely than anteroposteriorly (modified from Wilson, 2002). [44]
3. Chevrons open proximally (Wilson, 2002). [65]
4. Only one carpal bone (modified from Wilson, 2002). [88]
5. Fibula abruptly expanded distally to form medial lip (modified from Wilson, 2002). [114]

Macronaria (Wilson & Sereno, 1998)

1. Surangular tall, forming coronoid eminence (Wilson, 2002). [11]
2. Dentary teeth 17 or fewer in number (Wilson, 2002). [12]
3. Posterior dorsal vertebrae opisthocoelous (Wilson, 2002). [39]
4. Middle dorsal vertebral diapophyses project horizontally (Wilson, 2002). [41]

5. Humerus with squared proximolateral corner (modified from Wilson, 2002). [79]
6. Longest metacarpal at least 45% radius length (Wilson, 2002). [89]

Tehuelchesaurus + Titanosauriformes

1. Middle and posterior dorsal vertebrae with ventrally widened or forked posterior centrodiapophyseal lamina (modified from Salgado *et al*., 1997). [43]
2. Anterior dorsal ribs plank-like, at least three times wider than broad (Wilson, 2002). [64]
3. Femur with proximolateral bulge, proximal one-third deflected medially (McIntosh, 1990; Salgado *et al*., 1997). [107]

Titanosauriformes (Salgado et al.*, 1997)*

1. Tooth crowns do not overlap (Wilson & Sereno, 1998). [13]
2. Presacral vertebrae 'semicamellate', branching centimetre to decimetre-scale cells that do not fully permeate centrum. [18]
3. Middle cervical vertebral centra, anteroposterior length/average of width and height of posterior face > 3.0 (modified from Wilson, 2002; Chure *et al*., 2010). [23]
4. Middle dorsal vertebrae with divided posterior centroparapophsyeal lamina (pcpl). [36]
5. Anterior caudal vertebrae with bulge or 'kink' on ventral margin of transverse process (Chure *et al*., 2010). [52]
6. Anterior and middle caudal vertebrae with neural arches set on anterior half of centrum (Salgado *et al*., 1997). [58]
7. Middle caudal vertebrae with posteriorly projecting transverse processes. [59]
8. Dorsal ribs pneumatic (Wilson & Sereno, 1998). [63]
9. Anterior chevrons (excluding the first) with haemal canal at least 50% the length of the bone (Wilson, 2002). [67]
10. Scapula with tubercle on ventral margin of base of blade. [69]
11. Humerus length between 85 and 95% femur length (modified from Wilson, 2002). [81]
12. Ulna with anterior arm much longer and wider than medial arm (modified from Wilson, 2002). [85]
13. Ulna with unexpanded posterodistal end. [86]
14. Metacarpal I subequal to or longer than metacarpal IV (modified from Wilson, 2002). [90]
15. Metacarpal I distal condyle undivided (Wilson, 2002). [91]
16. Metacarpal I distal condyle perpendicular to long axis of shaft (Wilson, 2002). [92]
17. Metacarpal distal articular facets reduced (except for that of metacarpal IV). [96]
18. Ilium preacetabular process expanded, semicircular (Salgado *et al*., 1997). [97]
19. Ilium preacetabular process flared laterally 45° or more (modified from Salgado *et al*., 1997). [98]
20. Iliac pubic peduncle more than 1.5 times wider than long anteroposteriorly. [100]
21. Pubis at least three times as long as puboischial contact (modified from Wilson, 2002). [101]
22. Ischium with raised tubercle on lateroventral face. [106]
23. Fibular proximomedial end lacks corrugated triangular scar. [112]

Brachiosauridae (Riggs, 1903)

1. Distance separating supratemporal fenestrae less than long axis of fenestra (Wilson, 2002). [5]
2. Quadratojugal with ventral triangular projection on anterior ramus. [9]
3. Maxillary teeth twisted axially through an arc of 30–45° (modified from Chure *et al*., 2010). [15]
4. Middle and posterior dorsal vertebrae with long, dorsoventrally short transverse processes, 'rod-like'. [40]
5. Ischium with abbreviate pubic peduncle (Wilson, 2002). [105]

Giraffatitan + ((Brachiosaurus + (Abydosaurus, Cedarosaurus, Venenosaurus))

1. Premaxilla–maxilla suture sinuous. (Chure *et al*. 2010). [2]
2. Premaxilla with small, finger-like process near anteromedial corner of external naris. [3]
3. Lacrimal with anteriorly projecting plate of bone at dorsal end (modified from Chure *et al*., 2010). [4]
4. Dentary with divided posteroventral process (modified from Chure *et al*., 2010). [10]
5. Anterior and middle caudal vertebrae with sporadically distributed, shallow fossae in lateral faces of centrum. [56]
6. Humerus gracile, length/midshaft width > 7.5. [78]
7. Humerus length more than 95% femur length (modified from McIntosh, 1990; Wilson, 2002) [81]
8. Metatarsal IV with distal end bevelled upwards medially. [118]

Brachiosaurus + (Abydosaurus, Cedarosaurus, Venenosaurus)

1. Humerus with rounded proximolateral corner (modified from Wilson, 2002). [79]

Abydosaurus, Cedarosaurus, Venenosaurus

1. Middle caudal vertebrae with neural spines that lean anteriorly (modified from Rose, 2007). [60]

2. Metacarpal IV embraces metacarpal V; proximal articular surface forms a near right angle. [93]
3. Femoral fourth trochanter reduced to subtle bulge. [109]

Somphospondyli (Wilson & Sereno, 1998)

1. Presacral vertebrae with subcentimetre-scale pneumatic chambers that permeate the entire vertebra. [18]
2. Posterior cervical and anterior dorsal vertebrae with spinodiapophyseal laminae that are low in relief on the front of the neural spine (modified from Salgado *et al*., 1997). [31]
3. Posterior cervical and anterior dorsal vertebrae with a prespinal lamina (modified from Salgado *et al*., 1997). [33]
4. Posterior-most cervical vertebrae with low 'infrazygapophyseal region'; region between centrum and prezygapophyses shorter than centrum height (modified from Bonaparte *et al*., 2006). [34]
5. Anterior dorsal vertebrae with plate-like, 'paddle-shaped' neural spines. [35]
6. Scapular glenoid bevelled medially (Wilson, 2002). [68]
7. Scapular blade straight on acromial side. [71]
8. Femoral fourth trochanter reduced to subtle bulge. [109]
9. Metatarsal IV with embayed medial face of proximal end. [117]

Sauroposeidon + (Tastavinsaurus + (Euhelopodidae + (Chubutisaurus + Titanosauria)))

1. Scapular blade flat in cross-section (modified from Wilson, 2002). [70]
2. Ischial blade shorter than pubic blade (modified from Wilson, 2002). [102]
3. Fibula with anterior crest on proximal end that is embraced by the cnemial crest of the tibia (modified from Wilson & Upchurch, 2009; Royo-Torres, 2009). [111]
4. Fibula with distal end that is unexpanded, or gradually and subtly expanded; medially facing lip absent. [114]

Tastavinsaurus + (Euhelopodidae + (Chubutisaurus + Titanosauria))

1. Middle dorsal vertebrae, pcpl undivided. [36]
2. Middle and posterior dorsal vertebrae with single spinopostzygapophyseal lamina. [37]
3. Fibula sigmoid; proximal and distal faces angled relative to shaft (Royo-Torres, 2009). [113]

Euhelopodidae + (Chubutisaurus + Titanosauria)

1. Supraoccipital subequal to or less than height of foramen magnum (Wilson, 2002). [6]
2. Tooth denticles absent (modified from Wilson, 2002). [14]
3. Middle and posterior dorsal vertebrae with flat-topped diapophyses (modified from Sanz *et al*., 1999). [47]
4. Six sacral vertebrae (Wilson, 2002). [50]
5. Sternal plate crescentic (Wilson, 2002). [75]
6. Astragalus lacks tubercle on posterior proximal face. [116]

Euhelopodidae

1. Middle cervical neural spines bifid (Wilson, 2002). [22]
2. Cervical vertebrae with thick, subvertically orientated epipophyseal–prezygapophyseal lamina. [25]

Erketu + (Euhelopus, Daxiatitan + (Tangvayosaurus + Phuwiangosaurus))

1. Cervical vertebrae with 'kinked' intrapostzygapophyseal lamina (tpol); tpol visible in lateral view. [26]
2. Cervical vertebrae with pendant parapophyses; cervical ribs displaced ventrally more than the height of the centrum (modified from Wilson & Upchurch, 2009). [29]

Euhelopus, Daxiatitan + (Tangvayosaurus + Phuwiangosaurus)

1. Fifteen or more cervical vertebrae. [19]
2. Cervical vertebral epipophyses form long, posteriorly projecting prongs. [24]
3. Posterior cervical and anterior dorsal vertebrae with neural spines shorter than centrum height. [30]
4. Posterior cervical and anterior dorsal vertebrae with single spinodiapophyseal laminae that are sharp in relief on the side of the neural spine (modified from Salgado *et al*., 1997). [31]
5. Posterior cervical and anterior dorsal vertebral neural spines trifid. [32]
6. Posterior cervical and anterior dorsal vertebrae lack prespinal lamina. [33]
7. Posterior-most cervical vertebrae with tall 'infrazygapophyseal region'; region between centrum and prezygapophyses exceeds centrum height (modified from Bonaparte *et al*., 2006). [34]
8. Anterior dorsal neural spines taper along their length. [35]
9. Middle and posterior dorsal vertebral centra with ventral keel. [49]
10. Ilium with pointed, low preacetabular process (modified from Wilson, 2002). [97]

Tangvayosaurus + Phuwiangosaurus

1. Presacral vertebrae lack camellae; internal pneumaticity restricted to one or a few large chambers in the centrum. [18]

2. Anterior caudal vertebrae with tubercle on dorsal margin of prezygapophyses. [57]
3. Anterior and middle caudal vertebral chevrons with proximal articular facets divided into anterior and posterior segments. [66]

Chubutisaurus + Titanosauria
1. Dorsal vertebrae with reclined neural spines (Wilson, 2002) [46].
2. Humerus with undivided radial condyle (condyle lacks 'notch'). [83]

Titanosauria (Bonaparte & Coria, 1993)
1. Anterior and middle caudal vertebrate with ventral longitudinal hollow (Wilson, 2002). [54]
2. Ischium plate-like, no emargination distal to pubic peduncle (Wilson, 2002). [103]

Lithostrotia (Upchurch et al.*, 2004)*
1. Basal tubera width more than 1.6 times occipital condyle width (modified from Mannion, 2011). [7]
2. Paroccipital processes with ventral, non-articular processes (Wilson, 2002). [8]
3. Teeth slender, average slenderness index less than 3. [16]
4. Middle and posterior cervical vertebrae with elongate parapophyses; parapophyses make up more than half the functional centrum length in posterior cervical vertebrae [28]
5. Middle and posterior dorsal vertebrae with a single prespinal lamina (Upchurch *et al*., 2004). [45]
6. Posterior dorsal neural arches lack hyposphene–hypantrum articulations (Wilson, 2002). [48]
7. Anterior caudal vertebrae with bulge or 'kink' on ventral margin of transverse process (Chure *et al*., 2010). [52]
8. Anterior caudal vertebrae procoelous (Wilson, 2002). [55]
9. Coracoid proximodistally long (modified from Wilson, 2002). [73]
10. Sternal plate more than 70% humerus length. [77]
11. Ischial margin of acetabulum strongly embayed, margin acute. [104]
12. Osteoderms present. [119]

Saltasauridae (Powell, 1992)
1. Middle dorsal vertebrae lack postzygapophyseal–diapophyseal lamina (modified from Salgado *et al*., 1997). [42]
2. Thirty-five or fewer caudal vertebrae (Wilson, 2002). [53]
3. Anterior caudal vertebrae with tubercle on dorsal margin of prezygapophyses. [57]
4. Scapulocoracoid suture flush, no embayment at suture. [72]
5. Coracoid anteroventral margin square (Wilson, 2002). [74]
6. Humerus with strong posterolateral bulge around level of deltopectoral crest. [80]
7. Humerus length less than 80% femur length (modified from Wilson, 2002). [81]
8. Humeral deltopectoral crest strongly expanded distally (Wilson, 2002). [82]
9. Radius distal end bevelled approximately 20° proximolaterally relative to shaft (Wilson, 2002). [87]
10. Carpus unossified or absent (Wilson, 2002). [88]
11. Metacarpal V proximal end subequal in size to proximal end of metacarpal I. [94]
12. Femoral distal condyles bevelled 10° dorsomedially relative to shaft (Wilson, 2002). [110]
13. Astragalus transversely narrow (modified from Wilson, 2002). [115]

Alamosaurus + 'Saltasaurini'
1. Axis short, less than twice as long as tall. [20]
2. Middle cervical vertebrae, neural canal dramatically narrows at mid-length of centrum (Curry Rogers, 2005). [27]
3. Middle and distal caudal vertebrae procoelous (Wilson, 2002). [61]
4. Distal caudal vertebral centra about twice as wide as tall. [62]
5. Humeral radial and ulnar condyles divided distally (Wilson, 2002). [84]
6. Ilium with kink on ventral margin of preacetabular process. [99]
7. Femur with longitudinal ridge on anterior face of shaft (Otero, 2010). [108]

APPENDIX 4

Autapomorphies diagnosing each taxon are listed below. Numbers in brackets refer to autapomorphies resolved in the phylogenetic analysis and correspond to character numbers given in Appendix 2. Features listed without a number following them are unique autapomorphies and are absent from the data matrix

Shunosaurus lii (Dong et al.*, 1983)*
1. Strap-shaped pterygoid (Wilson, 2002).
2. Teeth lack marginal denticles. [14]
3. Anterior portion of the axial neural spine prominent (Wilson & Sereno, 1998).
4. Dorsal vertebrae with divided spinopostzygapophyseal lamina. [37]
5. 'Postparapophyses' on posterior dorsal vertebrae (Wilson & Sereno, 1998).
6. Terminal tail club composed of enlarged and co-ossified caudal vertebrae (Wilson, 2002).

7. Metacarpal I distal articular surface bevelled 20° with respect to shaft. [92]

Omeisaurus (Young, 1939)

1. Maxillary ascending ramus with dorsoventrally expanded distal end (Wilson & Sereno, 1998).
3. More than 15 cervical vertebrae. [19]
4. Middle cervical vertebral centra, anteroposterior length/average of width and height of posterior face > 3.0. [23]
5. Posterior dorsal vertebral centra opisthocoelous. [39]
6. Middle dorsal vertebral diapophyses directed horizontally. [41]
7. Anterior and middle caudal vertebrae with neural arches situated anteriorly on the centrum. [58]
8. Distal-most caudal chevrons fused to anterior-most portion of ventral centrum (Wilson, 2002).
9. Scapular blade unexpanded on acromial side. [71]

Jobaria tiguidensis (Sereno et al.*, 1999)*

1. Cervical vertebral epipophyses form long, posteriorly projecting prongs. [24]
2. Cervical vertebrae with 'kinked' intrapostzygapophyseal lamina (tpol); tpol visible in lateral view. [26]
3. Cervical ribs with secondary anterior projection (Wilson, 2002).
4. Dorsal neural arches with well-developed, paired coels below diapophysis (Sereno *et al*., 1999).
5. Anterior caudal neural spines with circular depression at base of prespinal lamina (Sereno *et al*., 1999).
6. Middle caudal vertebrae with posteriorly projecting transverse processes. [59]
7. U-shaped first caudal chevron (Sereno *et al*., 1999).
8. Middle caudal chevrons with pronounced ligamentous scar encircling distal end (Sereno *et al*., 1999).

Atlasaurus imelaki (Monbaron et al.*, 1999)*

1. Paroccipital processes extend nearly horizontally (Monbaron *et al*., 1999).
2. Width of paroccipital processes nearly half mandible length (Monbaron *et al*., 1999).
3. Jugal process of postorbital orthogonal to dorsal ramus.
4. Supratemporal fenestrae occupy over 80% of skull width.
5. Ulna 115% length of tibia (Monbaron *et al*., 1999).

Diplodocoidea (Marsh, 1884; Upchurch, 1995)

1. Tooth crowns do not overlap (Wilson & Sereno, 1998). [13]
2. Marginal tooth denticles present only in posteriormost few teeth (modified from Wilson, 2002). [14]
3. Teeth slender, average slenderness index less than 3. [16]
4. Cervical ribs short, not overlapping posterior centra (Berman & McIntosh, 1978).
5. Fibular facet of astragalus faces posterolaterally (Whitlock, 2011).

Camarasaurus (Cope, 1877)

1. Lacrimal with long axis directed anterodorsally (Wilson & Sereno, 1998).
2. Quadratojugal with short anterior ramus that does not extend anterior to the laterotemporal fenestra (Wilson & Sereno, 1998).
3. Quadratojugal anterior process shorter than dorsal process. (Wilson, 2002).
4. Pterygoid with dorsomedially orientated basipterygoid hook (Wilson, 2002).
5. Basal tubera width more than 1.6 times occipital condyle width (modified from Mannion, 2011). [7]
6. Splenial posterior process separating anterior portions of angular and prearticular (Wilson, 2002).
7. Middle cervical neural spines bifid (Wilson, 2002). [22]
8. Posterior cervical and anterior dorsal neural spines bifid. [32]
9. Conspicuous groove passing anteroventrally from the surangular foramen to the ventral margin of the dentary (Wilson & Sereno, 1998).
10. Forked chevrons restricted to distal tail (Wilson, 2002).
11. Metacarpal V proximal end subequal in size to proximal end of metacarpal I. [94]
12. Ischial blade directed posteriorly so that the long axis of its shaft passes through the pubic peduncle (Wilson & Sereno, 1998).

Tehuelchesaurus benitezii (Rich et al.*, 1999)*

1. Posterior cervical vertebrae with neural spines less than centrum height. [30]
2. Dorsal vertebrae with very short diapophyses.
3. Middle and posterior dorsal vertebral neural spines broader transversely than anteroposteriorly [44]
4. Acromion process of scapula tall, over four times minimum height of scapular blade (Carballido *et al*., in press).
5. Scapular blade unexpanded on acromial side. [71]
6. Humerus subcircular in cross-section (Upchurch *et al*., 2004).

Europasaurus holgeri (Sander et al.*, 2006)*

1. Small body size.
2. Premaxilla with anteriorly projecting nasal process (Sander *et al*., 2006).

Giraffatitan brancai (Janensch, 1914)
1. Snout elongate (Wilson, 2002).
2. Posterior dorsal vertebral centra about twice as wide as tall.
3. Anterior caudal vertebrae with tubercle on dorsal margin of prezygapophyses. [57]
4. Ilium with kink on ventral margin of preacetabular process [99]
5. Pubis with well-developed ambiens process.

Brachiosaurus altithorax (Riggs, 1903)
1. Posterior dorsal vertebral column long relative to humerus length (Paul, 1988).

Cedarosaurus weiskopfae (Tidwell et al.*, 1999)*
1. Radius with well-developed flange lateral to ulnar articulation (Tidwell *et al*., 1999).
2. Radius with subtle tubercle on anterior face of shaft, one-third of the way from proximal end.
3. Metatarsal II with well-developed medial and lateral tubercles at mid-shaft.
4. Metatarsal V rod-like, unexpanded proximally.
5. Metatarsal V longer than metatarsals II or III.
6. Phalanx on metatarsal V.

Venenosaurus dicrocei (Tidwell et al.*, 2001)*
1. Anterior and posterior faces of anterior and middle caudal vertebrae equally flat to slightly concave.
2. Metatarsal II with collateral ligament pits.
3. Metacarpal I proximal end more than twice as broad as wide.
4. Metacarpals II–IV with distal articular facets divided.
5. Metatarsal IV with embayed medial face of proximal end. [117]

Abydosaurus mcintoshi (Chure et al.*, 2010)*
1. Foramen on lateral aspect of postorbital at juncture of the three processes.
2. Lacrimal angled anteriorly in lateral view.
3. Two exits for cranial nerve V.
4. Surangular short, lacking coronoid eminence. [11]
5. Tooth denticles absent. [14]
6. Caudal vertebral transverse processes with deep fossa into ventral face.
7. Collateral ligament pits on metatarsals II–IV.

Ligabuesaurus leanzi (Bonaparte et al.*, 2006)*
1. Distal scapular blade with rounded dorsal expansion.
2. Humeral head expanded posteriorly.
3. Humerus gracile, length/midshaft width > 7.5. [78]
4. Fossae on proximoventral faces of metatarsals II and III.
5. Deep pit on ventrodistal face of manual phalanx I.1.

Sauroposeidon proteles (Wedel et al.*, 2000a)*
1. Middle cervical vertebrae with elongation index greater than 6 (Wedel *et al*., 2000a).
2. Pneumatic fossa developed posteriorly to the cotyle in middle cervical vertebrae (Wedel *et al*., 2000a).
3. Neural spines perforated in middle cervical vertebrae (Wedel *et al*., 2000a).
4. Top of neural spine with broad midline ridge flanked by small fossae at its anterior and posterior ends.
5. Narrow middle and posterior dorsal neural spines that taper distally. [44]
6. Spinoprezygapophyseal laminae divergent, forming wide spinoprezygapophyseal fossa in anterior caudal vertebrae.
7. Anterior caudal vertebral centra roughly square in cross-section.
8. Scapula with two processes at the base of the blade. [69]
9. Humerus gracile, length/midshaft width > 7.5. [78]

Tastavinsaurus sanzi (Canudo et al.*, 2008)*
1. Distal neural spines of dorsal vertebrae with small fossae and foramina.
2. Distal neural spines of dorsal vertebrae with upwardly directed hook-like processes.
3. Sacrum narrow.
4. Sacricostal yoke projects well below ventral margin of sacral centra.
5. Fifth sacral rib dorsoventrally deep, flaring distally.
6. Metatarsal I with ventrally expanded distal condyles.
7. Metatarsal I without ventrally expanded proximal articular surface.
8. Metatarsals II–IV divided distally.
9. Metatarsal IV with divided distal articular surface.
10. Metatarsal V with proximoventral flange.
11. Pedal phalanx I.1 subrectangular.

Qiaowanlong kangxii (You & Li, 2009)
1. Cervical vertebral centra large, taller than the neural arch and spines.
2. Pubic articulation of ischium more than 50% ischium length (You & Li, 2009).

Erketu ellisoni (Ksepka & Norell, 2006)
1. Axis extremely elongate (more than three times longer than tall).
2. Spinodiapophyseal and centrodiapophyseal neural arch fossae extremely subdivided in cervical vertebrae.

Euhelopus zdanskyi (Wiman, 1929)
1. Maxillary ascending process flush with anterior margin of bone; subnarial fossa reduced.

2. Teeth procumbent with asymmetrical crown-root margin (i.e. the mesial margin closer to the apex of the crown) (Wilson & Upchurch, 2009).
3. Tooth crowns overlap. [13]
4. Third cervical vertebral neural spine with laterally compressed, anteriorly projecting triangular process (Wilson & Upchurch, 2009).
5. Anterior cervical vertebrae with three costal spurs on tuberculum and capitulum (Wilson & Upchurch, 2009).
6. Cervical vertebrae with thin, horizontally orientated epipophyseal–prezygapophyseal lamina. [25]
7. Ilium pneumatic (Wilson & Upchurch, 2009).
8. Pubis less than 2.5 times as long as puboischial contact. [101]
9. Ischial blade longer than pubic blade. [102]
10. Metatarsal IV with straight medial face of proximal end. [117]

Daxiatitan binglingi (You et al.*, 2008)*

1. Middle and posterior dorsal vertebrae with single, unexpanded posterior centrodiapophyseal lamina (pcdl). [43]
2. Middle and distal caudal vertebrae procoelous. [61]
3. Chevrons closed proximally. [65]
4. Femoral distal condyles bevelled 10° dorsolaterally with respect to shaft (You *et al.*, 2008).

Phuwiangosaurus sirindhornae
(Martin et al.*, 1994)*

1. Quadrate with kinked posteromedial margin of quadrate fossa.
2. Teeth slender, average slenderness index less than 3. [16]
3. Axial centrum without paramedian fossae on anterior half of ventral centrum.
4. Posterior cervical and anterior dorsal vertebrae with tubercle on prdl.
5. Middle dorsal vertebrae with dorsally acuminate pneumatic openings.
6. Middle and posterior dorsal vertebrae with single, unexpanded pcdl. [43]
7. Middle caudal vertebrae with kinked neural arch pedicle below postzygapophyses.
8. Scapular blade D-shaped (with expanded lateral ridge) in cross-section. [70]
9. Humerus gracile, length/midshaft width > 7.5. [78]

Tangvayosaurus hoffeti (Allain et al.*, 1999)*

1. Fibular shaft straight. [113]

Chubutisaurus insignis (del Corro, 1975)

1. Centroprezygapophyseal fossa subdivided in anterior dorsal vertebrae (Carballido *et al.*, 2011).
2. Metacarpal I with posteriorly expanded distal condyle.
3. Metacarpal III with distomedial flange.

Andesaurus delgadoi (Calvo & Bonaparte, 1991)

1. Middle dorsal vertebrae with divided posterior centroparapophsyeal lamina (pcpl). [36]
2. Posterior dorsal vertebrae with neural spines more than twice height of centrum (Mannion & Calvo, 2011).
3. Caudal vertebral centra transversely narrow.
4. Metacarpals I and V with elongate ridges on their internal faces (Mannion & Calvo, 2011).

Malawisaurus dixeyi (Haughton, 1928)

1. Abbreviate premaxillary portion of snout, dentary arched ventrally (Wilson, 2002).
2. Surangular notch and groove on dentary (Wilson, 2002).
3. Cervical vertebrae with undivided pleurocoels. [21]
4. Posterior cervical vertebrae with neural spines less than centrum height. [30]
5. Neural spines of anterior caudal vertebrae very short.
6. Sternal plate with squared posterolateral margin. [76]

Opisthocoelicaudia skarzynskii
(Borsuk-Bialynicka, 1977)

1. Posterior cervical and anterior dorsal neural spines bifid. [32]
2. Middle dorsal vertebrae with divided pcpl. [36]
3. Middle and posterior dorsal vertebrae with single, unexpanded pcdl. [43]
4. Middle and posterior dorsal vertebrae lack flat-topped diapophyses (modified from Sanz *et al.*, 1999). [47]
5. Middle and posterior dorsal vertebral centra with ventral keel. [49]
6. Scapula with two processes at the base of the blade. [69]
7. Scapular blade D-shaped (with expanded lateral ridge) in cross-section. [70]
8. Ulna with expanded posterodistal end. [86]
9. Femoral fourth trochanter raised as a prominent ridge. [109]
10. Femoral fourth trochanter positioned at mid-shaft, near midline of femur.
11. Second muscle attachment surface lateral to fourth trochanter on femur.

Alamosaurus sanjuanensis (Gilmore, 1922)

1. Cervical vertebrae with undivided pleurocoels. [21]
2. Biconvex first caudal vertebra with circumferential depression on anterior condyle limited to ventral half of bone (D'Emic *et al.*, 2011).
3. Cross-section of scapular blade asymmetrical, thicker ventral margin (D'Emic *et al.*, 2011).

4. Scapula with two processes at the base of the blade. [69]
5. Ventral edge of scapular blade nearly straight, dorsal edge expanded distally (D'Emic *et al*., 2011).
6. Sternal plate with squared posterolateral margin. [76]
7. Ilium pneumatic.

'Saltasaurini'

1. Zygapophyses of cervical vertebrae set posteriorly; postzygapophyses overhang the centrum.
2. Middle dorsal vertebral diapophyses directed horizontally. [41]
3. Posterior caudal centra dorsoventrally flattened, breadth of posterior centrum at least twice height (Wilson, 2002).
4. Scapula with medial tuberosity on acromial side (Wilson, 2002).
5. Femoral distal condyles exposed on anterior portion of femoral shaft (Wilson, 2002).