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.

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).
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; Carbal lido 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 Som phospondyli; 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**

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). 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).

### MRCA, MOST RECENT COMMON ANCESTOR.

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

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

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

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

MPTs, most parsimonious trees; TSFs, Titanosauriformes.
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 as 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 scoreings 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). *Malawiensisaurus* 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 Saltasaursaenae, 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, diplodocids, 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.
Wilson (2002) did not include *Andesaurus* et al. (Fig. 2). Most of the other titanosauriform nodes in *Malawisaurus* and *Lithostrotia* was arbitrary. Consequently, the titanosaur membership of *Titanosauriformes* was defined as a stem-based taxon 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 titanosaurians. 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 Phuwiangosaurus, 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, Venenosauroidea, 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 polytomous. 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* revealed that of the 289 characters presented, 99% (227) were parsimony-informative. Their data set was re-run in PAUP*, three unambiguous sauropod synapomorphies were recovered. All three recovered sauropod synapomorphies (characters 101, 158, 173) have a homoplasy distribution amongst basal titanosaurs, 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 sauropod 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 titanosaurs. 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-titanosaurs (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 tianfuentesis He, Li & Cai, 1988 and Omeisaurus maotiansus 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 titanosaurs. Several taxa were not included in the analysis because their validity could not be evaluated or substantiated (e.g. Aragosaurus, Fukuittitan, Fusuisaurus, Pukyongosaurus) see ‘Relationships of fragmentarily represented taxa’ below). Fragmentarily represented taxa were not excluded a priori because anatomical completeness
<table>
<thead>
<tr>
<th>Taxon</th>
<th>Geological age (stage)</th>
<th>Geographical range</th>
<th>References</th>
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</thead>
<tbody>
<tr>
<td><em>Shunosaurus lii</em></td>
<td>Middle Jurassic (Bathonian–Callovian)</td>
<td>Asia (China)</td>
<td>Dong <em>et al.</em>, 1983</td>
</tr>
<tr>
<td><em>Omeisaurus</em></td>
<td>Middle Jurassic (Bathonian–Callovian)</td>
<td>Asia (China)</td>
<td>Young, 1939</td>
</tr>
<tr>
<td><em>Jobaria tiguidensis</em></td>
<td>Middle or Late Jurassic (Bathonian–Oxfordian)</td>
<td>Africa (Niger)</td>
<td>Sereno <em>et al.</em>, 1999</td>
</tr>
<tr>
<td><em>Atlasaurus imelaki</em></td>
<td>Middle Jurassic (Bathonian–Callovian)</td>
<td>Africa (Morocco)</td>
<td>Monbaron <em>et al.</em>, 1999</td>
</tr>
<tr>
<td>Diplodocoidea</td>
<td>Late Jurassic–Late Cretaceous</td>
<td>North America (USA), Europe (various), Africa (Niger), South America (Argentina)</td>
<td>Marsh, 1884; Upchurch, 1995; Whitlock, 2011</td>
</tr>
<tr>
<td><strong>Camarasaurus</strong></td>
<td>Late Jurassic (Kimmeridgian–Tithonian)</td>
<td>North America (USA)</td>
<td>Cope, 1877</td>
</tr>
<tr>
<td><em>Tehuelchesaurus benitezii</em></td>
<td>Late Jurassic (Kimmeridgian–Tithonian)</td>
<td>South America (Argentina)</td>
<td>Rich <em>et al.</em>, 1999; Carballido <em>et al.</em>, 2011b</td>
</tr>
<tr>
<td><em>Europasaurus holgeri</em></td>
<td>Late Jurassic (Kimmeridgian)</td>
<td>Europe (Germany)</td>
<td>Sander <em>et al.</em>, 2006</td>
</tr>
<tr>
<td><em>Giraffatitan brancai</em></td>
<td>Late Jurassic (Kimmeridgian–Tithonian)</td>
<td>Africa (Tanzania)</td>
<td>Janensch, 1914, 1929, 1950, 1961; Paul, 1988</td>
</tr>
<tr>
<td><em>Brachiosaurus altithorax</em></td>
<td>Late Jurassic (Kimmeridgian–Tithonian)</td>
<td>North America (USA)</td>
<td>Riggs, 1903</td>
</tr>
<tr>
<td><em>Cedarosaurus weiskopfae</em></td>
<td>Early Cretaceous (Aptian–Albian)</td>
<td>North America (USA)</td>
<td>Tidwell <em>et al.</em>, 1999</td>
</tr>
<tr>
<td><em>Abydosaurus micintoshi</em></td>
<td>Early Cretaceous (late Albian)</td>
<td>North America (USA)</td>
<td>Tidwell <em>et al.</em>, 2001; Tidwell and Wilhite, 2005</td>
</tr>
<tr>
<td><em>Ligabuesaurus lezai</em></td>
<td>Early Cretaceous (Aptian–Albian)</td>
<td>South America (Argentina)</td>
<td>Chure <em>et al.</em>, 2010</td>
</tr>
<tr>
<td><em>Sauropowidon proteles</em></td>
<td>Early Cretaceous (Aptian–Albian)</td>
<td>North America (USA)</td>
<td>Bonaparte <em>et al.</em>, 2006</td>
</tr>
<tr>
<td><em>Chubutisaurus insignis</em></td>
<td>Early or Late Cretaceous (Aptian–Cenomanian)</td>
<td>South America (Argentina)</td>
<td>Wedel <em>et al.</em>, 2000a, b; Rose, 2007; D'Emic &amp; Foreman, 2012</td>
</tr>
<tr>
<td><em>Tastavinsaurus sanzi</em></td>
<td>Early Cretaceous (Aptian)</td>
<td>Europe (Spain)</td>
<td>Canudo <em>et al.</em>, 2008; Royo-Torres, 2009; Royo-Torres <em>et al.</em>, 2012</td>
</tr>
<tr>
<td><em>Qiouawanlong hangxii</em></td>
<td>Early Cretaceous (Aptian–Albian)</td>
<td>Asia (China)</td>
<td>You &amp; Li, 2009</td>
</tr>
<tr>
<td><em>Erketu ellisoni</em></td>
<td>Late Cretaceous (Cenomanian–Santonian)</td>
<td>Asia (Mongolia)</td>
<td>Ksepka &amp; Norell, 2006, 2010</td>
</tr>
<tr>
<td><em>Dacriatitan binglingi</em></td>
<td>Early Cretaceous (Aptian–Albian)</td>
<td>Asia (China)</td>
<td>You <em>et al.</em>, 2008</td>
</tr>
<tr>
<td><em>Euhelopus zaniszy</em></td>
<td>Early Cretaceous (Barremian–Aptian)</td>
<td>Asia (China)</td>
<td>Wiman, 1929; Wilson &amp; Upchurch, 2009</td>
</tr>
<tr>
<td><em>Phuwiangosaurus sirindhornae</em></td>
<td>Early Cretaceous (Barremian–Aptian)</td>
<td>Asia (Thailand)</td>
<td>Martin <em>et al.</em>, 1994; Suteethorn <em>et al.</em>, 2009, 2010</td>
</tr>
<tr>
<td><em>Tangvayosaurus hoffeti</em></td>
<td>Early Cretaceous (Aptian–Albian)</td>
<td>Asia (Laos)</td>
<td>Allain <em>et al.</em>, 1999</td>
</tr>
<tr>
<td><em>Andesaurus delgadoi</em></td>
<td>Early or Late Cretaceous (Albian–Cenomanian)</td>
<td>South America (Argentina)</td>
<td>Calvo &amp; Bonaparte, 1991, Mannion &amp; Calvo, 2011</td>
</tr>
<tr>
<td><em>Malawisaurus diceyi</em></td>
<td>Early Cretaceous (Aptian)</td>
<td>Africa (Malawi)</td>
<td>Haughton, 1928; Jacobs <em>et al.</em>, 1993; Gomani, 2005</td>
</tr>
<tr>
<td><em>Opisthocoelicaudia skarzynskii</em></td>
<td>Late Cretaceous (Maastrichtian)</td>
<td>Asia (Mongolia)</td>
<td>Borsuk-Bialynicka, 1977</td>
</tr>
<tr>
<td><em>Alamosaurus sanjuanensis</em></td>
<td>Late Cretaceous (Maastrichtian)</td>
<td>North America (USA)</td>
<td>Gilmore, 1922; Lehman &amp; Coulson, 2002; D'Emic <em>et al.</em>, 2011</td>
</tr>
<tr>
<td>‘Saltasaurini’ (Saltasaurus, Neuquensaurus, Rocasaurus)</td>
<td>Late Cretaceous (Campanian–Maastrichtian)</td>
<td>South America (USA)</td>
<td>Powell, 1992; Lydekker, 1893; Salgado &amp; Azpilicueta, 2000; D'Emic &amp; Wilson, 2011</td>
</tr>
</tbody>
</table>
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 specialists 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, Atlanosaurus, Omeisaurus, Euhelopus, and Taotavinsaurus. 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 hypophene 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 centrum 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 *Giraffatitans* 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 Mengyn 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 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 firsthand 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-
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-

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.
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 Diplodocidea, *Camarasaurus*, and *Tehuelchusaurus* as successive outgroups to Titanosauriformes. Titanosauriformes is composed of two sister clades, Brachiosauridae and Somphospondylidae. Brachiosauridae contains a mix of Late Jurassic and Early Cretaceous Laurasian and Gondwanan taxa. Basal members of Somphospondylidae 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 titanosaurans 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.

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

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Cranial</th>
<th>Axial</th>
<th>Appendicular/dermal</th>
<th>Total</th>
</tr>
</thead>
<tbody>
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<td>8</td>
<td>15</td>
<td>10</td>
</tr>
<tr>
<td><em>Omeisaurus</em></td>
<td>0</td>
<td>10</td>
<td>10</td>
<td>8</td>
</tr>
<tr>
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<td>2</td>
<td>2</td>
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<td>75</td>
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<tr>
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</tr>
<tr>
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<td><em>Giraffatitan brancai</em></td>
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<td><em>Tastavinsaurus sanzi</em></td>
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</tr>
<tr>
<td><em>Tangvayosaurus hoffeti</em></td>
<td>100</td>
<td>49</td>
<td>75</td>
<td>67</td>
</tr>
<tr>
<td><em>Andesaurus delgadoi</em></td>
<td>100</td>
<td>59</td>
<td>62</td>
<td>67</td>
</tr>
<tr>
<td><em>Malawisaurus dixeyi</em></td>
<td>38</td>
<td>8</td>
<td>40</td>
<td>26</td>
</tr>
<tr>
<td><em>Opisthocoelicaudia skarzynskii</em></td>
<td>100</td>
<td>31</td>
<td>12</td>
<td>32</td>
</tr>
<tr>
<td><em>Alamosaurus sanjuanensis</em></td>
<td>88</td>
<td>10</td>
<td>6</td>
<td>18</td>
</tr>
<tr>
<td>‘Saltasaurini’ (Saltasaurus, Neuquensaurus, Rocasaurus)</td>
<td>75</td>
<td>8</td>
<td>16</td>
<td>20</td>
</tr>
<tr>
<td>Average</td>
<td>63</td>
<td>36</td>
<td>41</td>
<td>42</td>
</tr>
</tbody>
</table>
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;
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.

### 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

<table>
<thead>
<tr>
<th>Character number</th>
<th>ACCTRAN</th>
<th>DELTRAN</th>
</tr>
</thead>
<tbody>
<tr>
<td>44, 65, 115</td>
<td>Atlasaurus + Neosauropoda</td>
<td>Neosauropoda</td>
</tr>
<tr>
<td>39, 41</td>
<td>Neosauropoda</td>
<td>Macronaria</td>
</tr>
<tr>
<td>31, 118</td>
<td>Tehuelchesaurus + Titanosauriformes</td>
<td>Somphospondyli</td>
</tr>
<tr>
<td>33, 35</td>
<td>Titanosauriformes, Euhelopodidae</td>
<td>Somphospondyli, Euhelopus + mde</td>
</tr>
<tr>
<td>4, 10, 56, 82, 118</td>
<td>Brachiosauridae</td>
<td>Giraffatitan + mdb</td>
</tr>
<tr>
<td>57</td>
<td>Brachiosauridae</td>
<td>Giraffatitan</td>
</tr>
<tr>
<td>95</td>
<td>Giraffatitan + mdb</td>
<td>Abydosaurus + mdb</td>
</tr>
<tr>
<td>100</td>
<td>Giraffatitan + mdb, (Chubutisaurus + Titanosauria)</td>
<td>Giraffatitan, Saltasaurinae</td>
</tr>
<tr>
<td>11</td>
<td>Brachiosaurus + mdb</td>
<td>Abydosaurus</td>
</tr>
<tr>
<td>14</td>
<td>Brachiosaurus + mdb; Somphospondyli</td>
<td>Abydosaurus + mdb; (Chubutisaurus + Titanosauria) + Euhelopodidae</td>
</tr>
<tr>
<td>6, 15</td>
<td>Somphospondyli</td>
<td>Euhelopodidae + (Chubutisaurus + Titanosauria)</td>
</tr>
<tr>
<td>103</td>
<td>Somphospondyli</td>
<td>Sauroposeidon + mdo</td>
</tr>
<tr>
<td>19</td>
<td>Somphospondyli</td>
<td>Euhelopus + mde</td>
</tr>
<tr>
<td>90</td>
<td>Somphospondyli</td>
<td>Saltasauridae</td>
</tr>
<tr>
<td>75</td>
<td>Tastavinsaurus + mdo</td>
<td>Euhelopodidae + (Chubutisaurus + Titanosauria)</td>
</tr>
<tr>
<td>77</td>
<td>Tastavinsaurus + mdo</td>
<td>Lithostrotia</td>
</tr>
<tr>
<td>26</td>
<td>Euhelopodidae</td>
<td>Erketu + mde</td>
</tr>
<tr>
<td>31, 32, 33, 49</td>
<td>Euhelopodidae</td>
<td>Euhelopus + mde</td>
</tr>
<tr>
<td>117</td>
<td>Euhelopodidae</td>
<td>Euhelopus</td>
</tr>
<tr>
<td>57, 66</td>
<td>Euhelopodidae</td>
<td>Phuwiangosaurus + Tangvayosaurus</td>
</tr>
<tr>
<td>97</td>
<td>Erketu + mde</td>
<td>Euhelopus + mde</td>
</tr>
<tr>
<td>70, 78</td>
<td>Phuwiangosaurus + Tangvayosaurus</td>
<td>Phuwiangosaurus</td>
</tr>
<tr>
<td>7, 8, 28, 73, 119</td>
<td>Chubutisaurus + Titanosauria</td>
<td>Lithostrotia</td>
</tr>
<tr>
<td>20</td>
<td>Chubutisaurus + Titanosauria</td>
<td>Saltasaurinae</td>
</tr>
<tr>
<td>72, 115</td>
<td>Chubutisaurus + Titanosauria</td>
<td>Saltasauridae</td>
</tr>
<tr>
<td>76</td>
<td>(Chubutisaurus + Titanosauria), – Opisthocoelicaudia</td>
<td>Malawisaurus, Alamosaurus</td>
</tr>
<tr>
<td>81, 110</td>
<td>Titanosauria</td>
<td>Saltasauridae</td>
</tr>
</tbody>
</table>

mdb, more derived brachiosaurids; mde, more derived euhelopodids; mdo, 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.

### 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)

<table>
<thead>
<tr>
<th>Character number</th>
<th>ACCTRAN</th>
<th>DELTRAN</th>
</tr>
</thead>
<tbody>
<tr>
<td>13</td>
<td>(Atlasaurus + Neosauropoda), – Camarasaurus</td>
<td>Diplodocoidea, Titanosaurusiformes</td>
</tr>
<tr>
<td>95</td>
<td>Macronaria, – Brachiosauridae</td>
<td>Camarasaurus, Saltasauridae</td>
</tr>
<tr>
<td>117</td>
<td>– Giraffatitan</td>
<td>Venenosaurus</td>
</tr>
<tr>
<td>71</td>
<td>(Tehuelchesaurus + Titanosaurusformes), Brachiosauridae</td>
<td>– Tehuelchesaurus, – Somphospondyli</td>
</tr>
<tr>
<td>78</td>
<td>Europasaurus, Titanosaurusformes, –Tastavinsaurus + mdso</td>
<td>Giraffatitan + mdbo, Ligabuesaurus, Sauroposeidon</td>
</tr>
<tr>
<td>30</td>
<td>Tastavinsaurus + mdso, Saltasauridae</td>
<td>Malawisaurus, Euhelopus + mde</td>
</tr>
<tr>
<td>16</td>
<td>Tastavinsaurus + mdso, –Euhelopus</td>
<td>Lithostrotia, Phuwiangosaurus</td>
</tr>
<tr>
<td>69</td>
<td>Titanosauria, – ‘Saltasaurini’</td>
<td>Opisthocoelicaudia, Alamosaurus</td>
</tr>
<tr>
<td>21</td>
<td>(Chubutisaurus + Titanosauria), ‘Saltasaurini’</td>
<td>Malawisaurus, Alamosaurus</td>
</tr>
</tbody>
</table>

ACCTRAN, accelerated transformation; DELTRAN, delayed transformation; mdbo, 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 Cedarsaurus, 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 abbreviated 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 titanosaursiforms.

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. Cedarsaurus, 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...
distal end), a medially bevelled scapular glenoid, and an embryonic 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 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)

<table>
<thead>
<tr>
<th>Node</th>
<th>Decay index</th>
<th>Rank</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neosauropoda</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Macronaria</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Tarchuelchesaurus + Titanosauriformes</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Titanosauriformes</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Brachiosauridae</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Somphospondyli</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td><em>Sauroposeidon</em> + more derived somphospondylys</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Tastavinsaurus + more derived somphospondylys</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Euhelopodidae</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Lithostrotia</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Saltasauridae</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Saltasaurinae</td>
<td>3</td>
<td>3</td>
</tr>
</tbody>
</table>

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 resoring 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: Qiawonlong, Erketu, Daxiatitan, Euhelopus, Phuwiangosaurus, and Tanguyosaurus. 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, Qiawonlong) 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 Qiawonlong 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).

Qiawonlong 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 Qiawonlong 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. Afamosaurus 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 Titanosauria, because in those cases the missing data often occur in non-overlapping anatomical regions amongst Titanosauria, because in those cases the missing data often occur in non-overlapping anatomical regions amongst Titanosauria, because in those cases the
<table>
<thead>
<tr>
<th>Character state</th>
<th>Comments</th>
<th>Analysis</th>
<th>Character state</th>
<th>Comments</th>
<th>Analysis</th>
<th>Character state</th>
<th>Comments</th>
<th>Analysis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hypophene-hypantrum articulations only present in middle and posterior dorsal vertebrae</td>
<td>Characterizes most saurischians; absent in derived titanosaurs.</td>
<td>Royo-Torres (2009)</td>
<td>Hypophene-hypantrum articulations only present in middle and posterior dorsal vertebrae</td>
<td>Characterizes most saurischians; absent in derived titanosaurs.</td>
<td>Royo-Torres (2009)</td>
<td>Hypophene-hypantrum articulations only present in middle and posterior dorsal vertebrae</td>
<td>Characterizes most saurischians; absent in derived titanosaurs.</td>
<td>Royo-Torres (2009)</td>
</tr>
<tr>
<td>Anterior caudal vertebrae (excluding the first weakly procoelous)</td>
<td>Feature common to most non-lithostrotian sauropods, e.g. Patagosaurus, Giraffatitan, Chubutisaurus; subtlety is serially variable.</td>
<td>Royo-Torres (2009)</td>
<td>Anterior caudal vertebrae (excluding the first weakly procoelous)</td>
<td>Feature common to most non-lithostrotian sauropods, e.g. Patagosaurus, Giraffatitan, Chubutisaurus; subtlety is serially variable.</td>
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<td>Anterior caudal vertebrae (excluding the first weakly procoelous)</td>
<td>Feature common to most non-lithostrotian sauropods, e.g. Patagosaurus, Giraffatitan, Chubutisaurus; subtlety is serially variable.</td>
<td>Royo-Torres (2009)</td>
</tr>
<tr>
<td>Sacrum narrow (width 50–70% length)</td>
<td>Only Tastavinsaurus has this feature amongst neosauropods.</td>
<td>Royo-Torres (2009)</td>
<td>Sacrum narrow (width 50–70% length)</td>
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<td>Royo-Torres (2009)</td>
<td>Sacrum narrow (width 50–70% length)</td>
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<td>Royo-Torres (2009)</td>
</tr>
<tr>
<td>Anterior caudal vertebral centra concave anteriorly, flat posteriorly</td>
<td>Feature common to most non-lithostrotian sauropods, e.g. Patagosaurus, Giraffatitan, Chubutisaurus; subtlety is serially variable.</td>
<td>Royo-Torres (2009)</td>
<td>Anterior caudal vertebral centra concave anteriorly, flat posteriorly</td>
<td>Feature common to most non-lithostrotian sauropods, e.g. Patagosaurus, Giraffatitan, Chubutisaurus; subtlety is serially variable.</td>
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<td>Feature common to most non-lithostrotian sauropods, e.g. Patagosaurus, Giraffatitan, Chubutisaurus; subtlety is serially variable.</td>
<td>Royo-Torres (2009)</td>
</tr>
<tr>
<td>‘Wrinkle’ on lateral face of neural arch of middle–posterior caudal vertebrae</td>
<td>Remnant of neurocentral suture; present in all sauropods at some ontogenetic stage. Displays variation within some genera (e.g. Camarasaurus).</td>
<td>Royo-Torres (2009)</td>
<td>‘Wrinkle’ on lateral face of neural arch of middle–posterior caudal vertebrae</td>
<td>Remnant of neurocentral suture; present in all sauropods at some ontogenetic stage. Displays variation within some genera (e.g. Camarasaurus).</td>
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<td>Royo-Torres (2009)</td>
</tr>
<tr>
<td>Neural spines of anterior caudal vertebrae bulbous</td>
<td>Displays variation within some genera (e.g. Camarasaurus). Also present in some brachiosaurids.</td>
<td>Royo-Torres (2009)</td>
<td>Neural spines of anterior caudal vertebrae bulbous</td>
<td>Displays variation within some genera (e.g. Camarasaurus). Also present in some brachiosaurids.</td>
<td>Royo-Torres (2009)</td>
<td>Neural spines of anterior caudal vertebrae bulbous</td>
<td>Displays variation within some genera (e.g. Camarasaurus). Also present in some brachiosaurids.</td>
<td>Royo-Torres (2009)</td>
</tr>
<tr>
<td>Metatarsal III more than 30% thibia length</td>
<td>Not found in any sauropod.</td>
<td>Royo-Torres (2009)</td>
<td>Metatarsal III more than 30% thibia length</td>
<td>Not found in any sauropod.</td>
<td>Royo-Torres (2009)</td>
<td>Metatarsal III more than 30% thibia length</td>
<td>Not found in any sauropod.</td>
<td>Royo-Torres (2009)</td>
</tr>
</tbody>
</table>
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 ‘Saltasaurni’ 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 titanosaurids. A ‘dendritical enamel pattern’ and ‘homogenous slender-ness’ were features used to refer these teeth to titanosaurids (Apesteguía, 2007: 539), but titanosaur enamel is not diagnostic (Upchurch et al., 2004), and diplodocids 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 Abdysaurus 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 mcintoshii* 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.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Age</th>
<th>Area</th>
<th>Clade/validity</th>
<th>Characters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agustinia ligabuei</td>
<td>EK</td>
<td>SA</td>
<td>nd</td>
<td>—</td>
</tr>
<tr>
<td>Amargatitanis macni</td>
<td>EK</td>
<td>SA</td>
<td>nd</td>
<td>—</td>
</tr>
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<td>Angolotitan adamastor</td>
<td>LK</td>
<td>AF</td>
<td>Lithostrotia</td>
<td>83</td>
</tr>
<tr>
<td>Aragosaurus ischiaticus</td>
<td>LJ–EK</td>
<td>EU</td>
<td>TSF; !Titanosauria</td>
<td>106; !103</td>
</tr>
<tr>
<td>Argentinaurus hunculensis</td>
<td>LK</td>
<td>SA</td>
<td>Tsastavinsaurus + mdso; !Euhelopodida; !Lithostrotia</td>
<td>36; !22; !48</td>
</tr>
<tr>
<td>Australodocus bohettii</td>
<td>LJ</td>
<td>AF</td>
<td>TSF</td>
<td>18, 23</td>
</tr>
<tr>
<td>Baotianmansaurus henanensis</td>
<td>LK</td>
<td>AS</td>
<td>Euhelopus + mde</td>
<td>30</td>
</tr>
<tr>
<td>Brontomerus mcintoshi</td>
<td>EK</td>
<td>NA</td>
<td>nd</td>
<td>—</td>
</tr>
<tr>
<td>Daanosaurus zhangi</td>
<td>LJ</td>
<td>AS</td>
<td>Macronaria</td>
<td>39</td>
</tr>
<tr>
<td>Diamantinasaurus matildae</td>
<td>EK</td>
<td>AU</td>
<td>Saltasaurida</td>
<td>110</td>
</tr>
<tr>
<td>Dongbeitian dongo</td>
<td>EK</td>
<td>AS</td>
<td>Somphospondyli</td>
<td>68</td>
</tr>
<tr>
<td>Dongyangosaurus sinensis</td>
<td>LK</td>
<td>AS</td>
<td>Euhelopus + mde</td>
<td>30, 97</td>
</tr>
<tr>
<td>Fukuiptitan nipponensis</td>
<td>EK</td>
<td>AS</td>
<td>Macronaria</td>
<td>89</td>
</tr>
<tr>
<td>Fusuisaurus zhaoi</td>
<td>EK</td>
<td>AS</td>
<td>Tehuelchesaurus + Titanosauriformes</td>
<td>64</td>
</tr>
<tr>
<td>‘French Bothiospondylus’/</td>
<td>LJ</td>
<td>EU</td>
<td>Giraffatitan + mdb</td>
<td>78, 79, 81, 93</td>
</tr>
<tr>
<td>Damparis sauropod</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Galvesaurus herreroi</td>
<td>LJ–EK</td>
<td>EU</td>
<td>TSF; !Titanosauria</td>
<td>23, 58, 106; !103</td>
</tr>
<tr>
<td>Gobititan shenzhouensis</td>
<td>EK</td>
<td>AS</td>
<td>Sauroposeidon + mdso</td>
<td>111</td>
</tr>
<tr>
<td>Huabeisaurus allocotus</td>
<td>LK</td>
<td>AS</td>
<td>Euhelopus + mde</td>
<td>97</td>
</tr>
<tr>
<td>Huanghettian liujiaxaoensis</td>
<td>EK</td>
<td>AS</td>
<td>Somphospondyli</td>
<td>69</td>
</tr>
<tr>
<td>‘Huanghetitan’ ruyangensis</td>
<td>LK</td>
<td>AS</td>
<td>Euhelopodida + (Chubutisaurus + Titanosauria)</td>
<td>50</td>
</tr>
<tr>
<td>Janenschia robusta</td>
<td>LJ</td>
<td>AF</td>
<td>TSF; !TSF; !Sauroposeidon + mdso; !Euhelopodida + (Chubutisaurus + Titanosauria)</td>
<td>112; !86; !111; !116</td>
</tr>
<tr>
<td>Jiangshanosaurus lixianensis</td>
<td>EK</td>
<td>AS</td>
<td>Saltasaurida</td>
<td>72, 74</td>
</tr>
<tr>
<td>Jiutaissaurus xidiensis</td>
<td>EK</td>
<td>AS</td>
<td>TSF</td>
<td>67</td>
</tr>
<tr>
<td>Lusotitan atalaiensis</td>
<td>LJ</td>
<td>EU</td>
<td>Brachiosaurus + mdb</td>
<td>79</td>
</tr>
<tr>
<td>Malarguesaurus florenceae</td>
<td>LK</td>
<td>SA</td>
<td>Tehuelchesaurus + TSF; !Lithostrotia</td>
<td>107; !55</td>
</tr>
<tr>
<td>Mongolosaurus haplodon</td>
<td>EK</td>
<td>AS</td>
<td>Euhelopodida + (Chubutisaurus + Titanosauria)</td>
<td>7, 22</td>
</tr>
<tr>
<td>MPEF PV 3098 (partial skeleton)</td>
<td>LJ</td>
<td>SA</td>
<td>Brachiosaurus + mdb</td>
<td>79</td>
</tr>
<tr>
<td>NHMUK R5333 (isolated caudal</td>
<td></td>
<td></td>
<td></td>
<td>55</td>
</tr>
<tr>
<td>vertebrae)</td>
<td>EK</td>
<td>AS</td>
<td>Lithostrotia</td>
<td></td>
</tr>
<tr>
<td>NSF 60104403-20554450 (embryo)</td>
<td>EK</td>
<td>AS</td>
<td>Tehuelchesaurus + TSF</td>
<td>107</td>
</tr>
<tr>
<td>‘Pelorosaurus’ becklesi</td>
<td>EK</td>
<td>EU</td>
<td>TSF; !Chubutisaurus + Titanosauria</td>
<td>85, 183</td>
</tr>
<tr>
<td>Pukyongosaurus milleniumi</td>
<td>EK</td>
<td>AS</td>
<td>Somphospondyli</td>
<td>18</td>
</tr>
<tr>
<td>Qinxiuissaurus youjiangensis</td>
<td>LK</td>
<td>AS</td>
<td>Lithostrotia</td>
<td>83*</td>
</tr>
<tr>
<td>Rugocaudia cooneyi</td>
<td>EK</td>
<td>NA</td>
<td>nd</td>
<td>—</td>
</tr>
<tr>
<td>Ruyangosaurus giganteus</td>
<td>LK</td>
<td>AS</td>
<td>Somphospondyli</td>
<td>18</td>
</tr>
<tr>
<td>SMU 61732 (partial skeleton)</td>
<td>EK</td>
<td>NA</td>
<td>Sauroposeidon + mdso; !Titanosauria</td>
<td>70, !103</td>
</tr>
<tr>
<td>Sonidosaurus saithangaoiensis</td>
<td>LK</td>
<td>AS</td>
<td>Euhelopodida + (Chubutisaurus + Titanosauria)</td>
<td>30, 48</td>
</tr>
<tr>
<td>Sonorasaurus thompsoni</td>
<td>EK/LK</td>
<td>NA</td>
<td>Giraffatitan + mdb</td>
<td>78, 118</td>
</tr>
<tr>
<td>Wintonotitan wattsi</td>
<td>EK</td>
<td>AU</td>
<td>TSF; !Abydosaurus + mdb; !Titanosauria</td>
<td>96; 193; !54</td>
</tr>
<tr>
<td>Xenoposeidon proneneukos</td>
<td>EK</td>
<td>EU</td>
<td>nd</td>
<td>—</td>
</tr>
<tr>
<td>Xianshanosaurus shijaguouensis</td>
<td>LK</td>
<td>AS</td>
<td>Lithostrotia</td>
<td>55</td>
</tr>
</tbody>
</table>

*Qingxiuissaurus 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 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.

Iuticosaurus valdensis (Le Loeuff, 1993)

Iuticosaurus was named on the basis of two procoelous caudal vertebrae (NHMUK R151, lectotype and R146a, paratype; 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, Somphospondylidae, 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 titanosaurans, 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 euohelopodid 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 euohelopodids, 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 euohelopod 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 euohelopodid synapomorphies in the analysis presented herein (Baotianmansaurus, Dongyangosaurus, Huabeisaurus, Mongolosaurus; Table 9). Other genera may belong to Euhelopodidae, but euohelopodid synapomorphies are not evident in them given the data at hand (Fukuititan, Gobititan, Huanghetitan liujiangiensis, ‘Huanghetitan’ ruyangensis, Jiutaisaurus, Pukyongosaurus, Ruyangosaurus; Table 9).

Still other Cretaceous East Asian genera appear to lie outside Euhelopodidae because they lack euohelopodid 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 euohelopodid 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 Alguï 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 (cited 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 (cited as a similarity to *Diamantinasaurus*), and (5) two longitudinal fossae on the posterior face of the femur, one around mid-length 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 (*Teherulichesaurus* + 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. *Teherulichesaurus*, 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 brachiosaur and is important because of its Albiano-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, metacarpals with reduced or absent distal articular facets, and a fibula that lacks a corrugated subtriangular proximal scar (Appendix 3).

Brachiosaur 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 brachiosaur 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 titanosaurans (e.g. *Andesaurus*, *Malawisaurus*). Further data are needed to firmly establish the affinities of *Sonorasaurus*.

**Wintonotitan wattsii** (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 *Rincosaurus* (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 PRONEUKOS**
*(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 infrarapophyseal 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 purnmaticity 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 titanosaurans (*Janenschia, Amargasaitanis, Iuticosaurus, Pelorosaurus‘ becklesi*) do not pertain to Titanosaurus. Thus, the oldest known titanosaur forms 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 Titanosaurus.

Furthermore, the Barremian–Aptian (c. 128–112 Mya) age for these oldest titanosaurans is far younger than the Middle Jurassic (Bathonian, c. 163 Mya) age of origin for Titanosaurus 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 titanosaurans. In turn, wide-gauge track-ways are thought to have been produced by titanosaurans 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 titanosaurans 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-titanosaurans as well. Wilson & Carrano (1999) noted that one of the features hypothesized to be related to wide-gauge track-making – a proximolateral femoral
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 pre-dated the break-up of Pangaea; (2) the existence of several Laurasian titanosaurines. The first objection is resolved by this study, because the revised picture of titanosaur evolution presented herein suggests that titanosaurines 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 titanosaurines by Wilson & Upchurch (2003) have been shown above to be either non-titanosaurs (Phuwiangosaurus, Tangaysaurus, D’Emic and Foreman, 2012; Table 9). Other Laurasian titanosaurs are the 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 titanosaurines and more precise age dates. Basal titanosaurines (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 titanosaurines 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 titanosaurines 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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## APPENDIX 1

### CHARACTER-TAXON MATRIX

| Character | Shunosaurus | Omeisaurus | Jobaria | Atlasaurus | Diplodocidae | Camarasaurus | Tehuelchesaurus | Europasaurus | Giraffatitan | Brachiosaurus | Abydosaurus | Cedarosaurus | Venosaurus | Ligabuesaurus | Sauroposeidon | Tastavinsaurus | Quoawanlong | Erhetu | Euhelopus | Daxiatitan | Tangvayosaurus | Pliosaurus | Chubutisaurus | Andesaurus | Malawisaurus | Opisthocoelicaudia | Alamosaur | 'Saltasaurini' |
|-----------|-------------|------------|---------|------------|--------------|--------------|----------------|-------------|-------------|-------------|------------|--------------|-----------|--------------|--------------|--------------|-------------|----------|------------|-----------|--------------|---------|--------------|-------------|---------------|-------------|
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
| 0000000000 | 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         |
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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 oriented premaxillary process near anteromedial corner of external naris: absent (0); present (1). (Modified from Chure et al., 2010.)
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). (Wilson, 2002.)
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 shape: camerate, with a few, large cavities (0); spongy, with centimetre-scale internal cells and walls, ‘semi-camerate’ (Wedel et al., 2000b) (1); camellate to somphospondyly, 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
31. Posterior cervical and anterior dorsal vertebrae, spinodiaphyseal 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 centriodiaphyseal 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, diaphyses, shape: short and dorsoventrally tall (0); long and dorsoventrally short, rod-like (1). (Janensch, 1950.)
41. Middle dorsal vertebrae, diaphyses, orientation: directed dorsally at an angle of about 45° (0); directed horizontally (1). (Modified from Salgado et al. 1997.)
42. Middle dorsal vertebrae, postzygapophyseal–diaphysyal lamina: present (0); absent (1). (Salgado et al., 1997.)
43. Middle and posterior dorsal vertebrae, posterior centriodiaphyseal 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, diaphyses: dorsal surface grades smoothly towards midline (0); dorsal surface flat and set off from rest of diaphysis by a lip (1). (Modified from Sanz et al., 1999.)
48. Posterior dorsal neural arches, hypospheno–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. Sacrocostal 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 half 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); plack-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 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 abbreviated, 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, proximomedical 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, proximomedical 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 posterior-most 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)
2. Dentine 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 centrodiaaphysal 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)
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 centroparapophyseal 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]
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))
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]
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]
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]

_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]
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]
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. Sterna! 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]
4. Dorsal vertebrae with divided spinopostzygapophyseal lamina. [37]
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)
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)
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)
2. Marginal tooth denticles present only in posterior-most few teeth (modified from Wilson, 2002). [14]
3. Teeth slender, average slenderness index less than 3. [16]

Camarasaurus (Cope, 1877)
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).
6. Splenial posterior process separating anterior portions of angular and prearticular (Wilson, 2002).
7. Middle cervical neural spines bifid (Wilson, 2002).
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.
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]

Abidosaurus mcintoshi (Chure et al., 2010)
1. Foramen on lateral aspect of postorbital at junction of the three processes.
2. Lacrimal angled anteriorly in lateral view.
3. Two exits for cranial nerve V.
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.

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]
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.
4. Sacricostal yoke projects well below ventral margin of sacral centra.
5. Fifth sacral rib dorsoventrally deep, flaring distally.
6. Metatarsal I without ventrally expanded proximal articular surface.
7. Metatarsal IV with divided distal articular surface.
8. Metatarsals II–IV divided distally.
11. Pubic articulation of ischium more than 50% ischium length (You & Li, 2009).

Qiaowanlong kangxii (You & Li, 2009)
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]
5. Anterior cervical vertebrae with three costal spurs on tuberculum and capitulum (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 pdcl. [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 centroparapophyseal 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 pdcl. [43]
4. Middle and posterior dorsal vertebrae lack flat-topped diapophys (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).