



An Overview of Titanosaur Evolution and Phylogeny

Una revisión de la evolución y filogenia de los Titanosaurios

J. A. Wilson

Museum of Paleontology and Department of Geological Sciences, University of Michigan,
1109 Geddes Road, Ann Arbor, Michigan 48109-1079, U.S.A.; wilsonja@umich.edu

Recibido el 17 de marzo de 2005, aceptado el 15 de febrero de 2006.

Abstract

Titanosaurus was named in 1877 for two caudal vertebrae and an isolated femur from Cretaceous rocks of central India. Titanosauridae was coined soon afterwards to encompass numerous taxa, despite their often tenuous associations and limited morphological overlap. Long recognized as wastebasket taxa, “*Titanosaurus indicus*”, “Titanosauridae” and coordinated rank-taxa are now considered invalid, but the unranked taxon Titanosauria remains valid. Titanosauria currently includes 40+ species and first appeared during the Middle Jurassic in the form of “wide-gauge” trackways. Titanosaur body fossils do not appear until the Late Jurassic, but they are inferred to have occupied nearly all continental landmasses during the Early Cretaceous. Titanosaurs are the predominant or exclusive sauropods during the Late Cretaceous and represent a key clade for investigation of survivorship patterns and the effects of major tectonic rearrangements on dinosaur evolution. Titanosauria includes several large-bodied species (e.g., *Antarctosaurus giganteus*, *Argyrosaurus superbus*, *Argentinosaurus huinculensis*), as well as species that are diminutive by sauropod standards (e.g., *Saltasaurus loricatus*, *Neuquensaurus australis*).

Evaluation of previous phylogenetic analyses of Titanosauria provides insight into the structure of the character data thus far generated and a starting point for future studies. Where comparable, analyses agree on several topological points, including (1) the basal position of *Andesaurus* and *Malawisaurus* and (2) the derived position of *Saltasaurus*, *Neuquensaurus*, *Opisthocoelicaudia*, and *Alamosaurus*. This investigation identifies several stable titanosaur nodes and a core of character data for future analysis. However, many titanosaur species have yet to be included in a phylogenetic analysis. A comprehensive phylogenetic analysis of Titanosauria will require incorporating these taxa as well as new character data. Resolution of titanosaur interrelationships will spur investigation into Mesozoic paleobiogeography, changes in body size distribution through time, wide-gauge limb posture and its biomechanical significance, and patterns in herbivorous apomorphies of Cretaceous dinosaurs. These and other avenues will be explored in future research.

Key words: Dinosauria, Phylogeny, Paleobiogeography, Titanosauria, Sauropoda

Resumen

Titanosaurus fue erigido en 1877 para dos vértebras caudales y un fémur aislado procedentes de rocas cretácicas de India central. Seguidamente, fue acuñado Titanosauridae al cual se asignaron numerosos taxones a pesar, a menudo, de las dudosas asociaciones y limitado solapamiento morfológico. Mientras que taxones como “*Titanosaurus*

indicus”, “Titanosauridae” y varios taxones de rango han sido ya reconocidos desde hace largo tiempo como inválidos, el taxón sin rango Titanosauria permanece válido. Titanosauria incluye actualmente más de 40 especies y se lo registra por primera vez durante el Jurásico Medio en forma de rastrilladas con una postura ancha de los miembros. Restos óseos de titanosaurios no se conocen hasta el Jurásico Tardío, aunque se infiere que estuvieron presentes en todas las zonas continentales en el Cretácico Temprano. Los titanosaurios fueron los más abundantes o los únicos saurópodos durante el Cretácico Tardío y representan un clado clave para el estudio de los patrones de supervivencia y los efectos de la reestructuración tectónica en la evolución de los dinosaurios. Titanosauria incluye varias especies de gran tamaño (ej., *Antarctosaurus giganteus*, *Argyrosaurus superbus*, *Argentinosaurus huinculensis*) y también especies diminutas de saurópodos estándar (ej., *Saltasaurus loricatus*, *Neuquensaurus australis*).

El estudio de análisis filogenéticos previos de Titanosauria aporta una visión más completa acerca de la estructura de los caracteres, lo que supone un avance sobre los datos existentes y es un punto de partida para estudios posteriores. Donde es posible compararlos, los análisis coinciden en varios puntos de su topología, incluyendo (1) la posición basal de *Andesaurus*, y *Malawisaurus* y (2) la posición derivada de *Saltasaurus*, *Neuquensaurus*, *Opisthocoelicaudia* y *Alamosaurus*. Este estudio identifica varios nodos estables y un núcleo de caracteres para futuros análisis. Sin embargo, muchas especies de titanosaurios aun no han sido incluidas en un análisis filogenético. Un análisis filogenético abarcativo de todos los titanosaurios requiere incorporar estos taxones así como también datos de nuevos caracteres. La resolución de las interrelaciones de los titanosaurios dará soporte a futuras investigaciones sobre la paleobiogeografía mesozoica, los cambios en la distribución del tamaño corporal a través del tiempo, la postura ancha de los miembros y su significado biomecánico y los patrones de las apomorfías relacionadas con la herbivoría en los dinosaurios del cretácico. Estas y otras vías serán exploradas en futuros estudios.

Palabras clave: Dinosauria, Filogenia, Paleobiogeografía, Titanosauria, Saurópoda

Introduction

Sauropod dinosaurs are perceived as ‘monolithic’ by enthusiasts and specialists alike, due to their enormous body size, their obvious and memorable body plan that appears early in their history, and a misconception that sauropods were replaced by more specialized herbivores at the end of the Jurassic (Wilson and Curry Rogers, 2005). Although these perceptions may hold true for some sauropod lineages, Titanosauria is a good example of why sauropods are not monolithic. They acquired locomotor features that depart in important ways from those of other sauropods, experienced one or more evolutionary body size reductions, diversified during the fragmentation of Gondwana, and are now known from every continent but Antarctica during the Cretaceous (Curry Rogers, 2005). Despite these attributes, the origin of Titanosauria has only recently been agreed upon, and its species-level relationships remain poorly resolved. Below I describe the spatial, temporal, and character distributions within Titanosauria, provide a rationale for investigating their relationships, and summarize previous efforts to resolve their interrelationships to provide a framework for future work on the clade.

Titanosauria: predominant sauropods of the cretaceous

Discovered in 1828 and first described by Falconer (1868) in his posthumous memoirs, the eponymous titanosaur species *Titanosaurus indicus* was named by Lydekker in 1877 for two caudal vertebrae and an isolated femur from Cretaceous rocks of central India (Fig. 1). Like other early dinosaur discoveries (e.g., *Iguanodon anglicus*, *Megalosaurus bucklandii*, *Cetiosaurus medius*), *T. indicus* was founded on fragmentary remains with few diagnostic characters. Over time, many new and often fragmentary specimens were referred to the genus or named as closely related genera, based on the presence of socket-and-ball (i.e., procoelous) articulations between caudal vertebrae. Lydekker (1893:3) and Depéret (1899) described species of *Titanosaurus* from South America and Madagascar, recognizing a “remarkable community of type which undoubtedly exists between the faunas of southern continents of the world”. *Titanosaurus* and the Family Titanosauridae (Lydekker, 1893) soon swelled to include numerous constituent taxa, many among them from southern landmasses. Fifty years later, Gilmore (1946:29) recognized that the family represented a wastebasket taxon:

“Titanosauridae has since [its first usage in 1893] become the repository of practically all the Cretaceous sauropods that have been described...it would appear that the Titanosauridae have the widest geographical range of any known family of the Dinosauria”.

Gilmore’s comment is apt, because it recognizes the taxonomic disorder of the group but acknowledges its temporal and spatial breadth.

Titanosauria was the predominant sauropod clade during the Cretaceous, maintaining high species richness and a near-global distribution during peak Mesozoic continental fragmentation (Fig. 2). According to a recent summary, Titanosauria comprises 35 species, which represent 29% of the 121 sauropod species and 5% of the 661 dinosaur species (tabulated from Upchurch *et al.*, 2004). This tally is augmented to 41 species with the inclusion of newly named titanosaur species (see below), reinstatement of species considered by most to be members of that group (*Nemegtosaurus mongoliensis*, *Quaesitosaurus orientalis*, *Mongolosaurus haplodon*; Wilson, 2005a), and exclusion of invalid species (Wilson and Upchurch, 2003). According to this revised estimate, titanosaur species represent 34% of sauropod species and 6% of dinosaur species. Although most titanosaur species come from southern landmasses (26 species), many are known from northern landmasses (15 species).

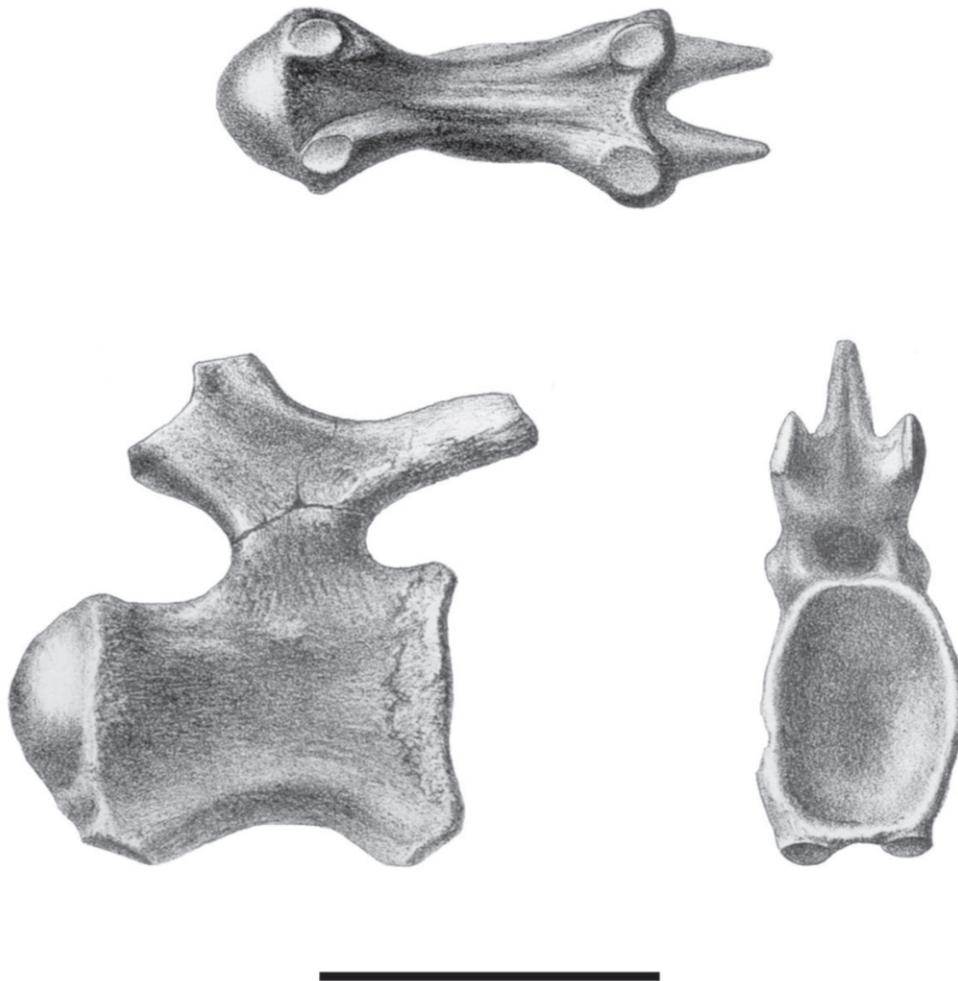


Figure 1. Holotypic distal caudal vertebra of "*Titanosaurus indicus*" in ventral (top), right lateral (left), and anterior (right) views. From Falconer (1868: pl. 34, figs 3-5). Scale equals 15 cm.

Rationale for phylogenetic study of titanosauria

Although there are intrinsic merits for systematic studies, especially those focusing on poorly understood groups, there are several factors motivating phylogenetic analysis of Titanosauria. Titanosauria is morphologically distinct, includes the smallest and the largest sauropods, has ontogenetic series for some species, and is a key clade for understanding Cretaceous paleobiogeography. Moreover, cladistic analysis of Titanosauria is timely because well preserved cranial and postcranial remains have been recently discovered on several landmasses.

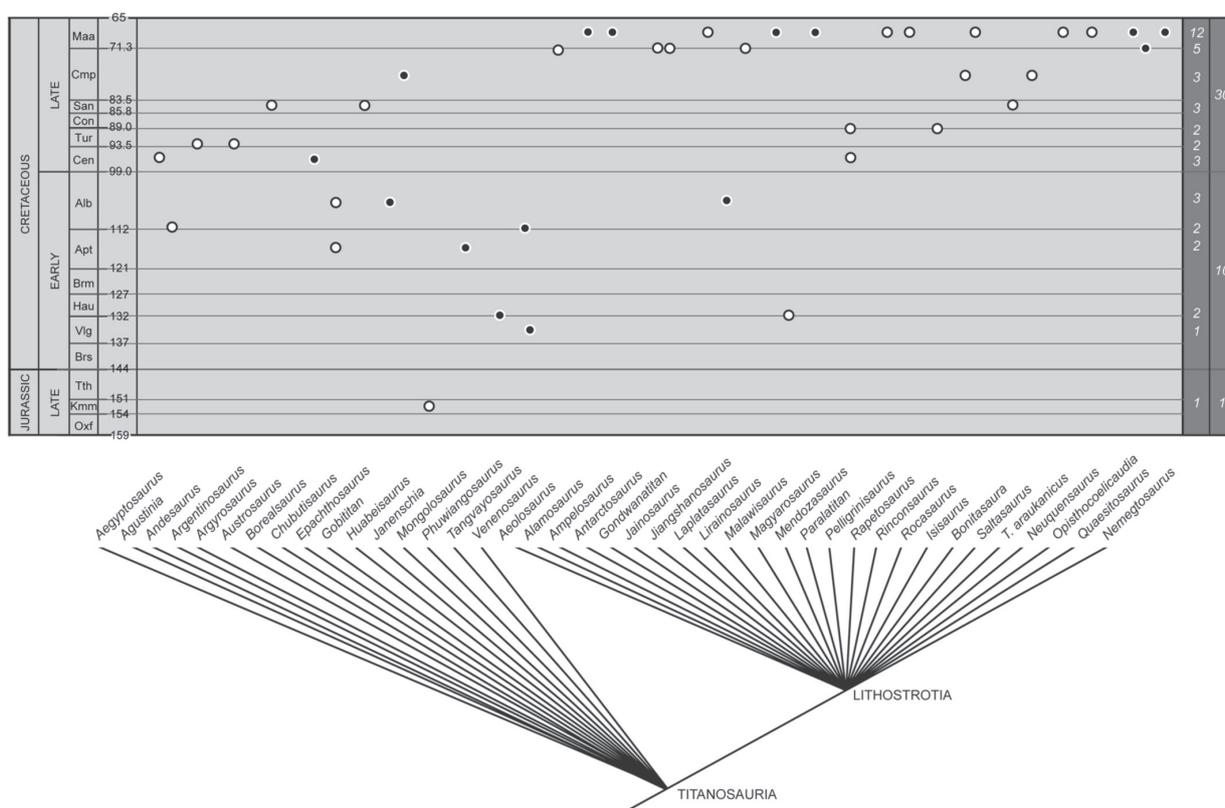


Figure 2. Phylogenetic, stratigraphic and geographic distribution of titanosaur species. Black-filled circles with white borders indicate species from northern landmasses; white-filled circles with black borders indicate species from southern landmasses. Based on data from Upchurch *et al.* (2004), with modifications from Wilson and Upchurch (2003) and Wilson (2005a).

Autapomorphic morphology.

The morphological distinctiveness of titanosaurs has facilitated referral of many genera to the group. However, the distribution of many of these features amongst titanosaurs is poorly known due to missing or inadequate data.

Until recently, titanosaurs were thought to be *Diplodocus*-like sauropods, based on the shared presence of narrow tooth crowns (e.g., Huene, 1929; Romer, 1966; McIntosh, 1990). More recent analyses, however, have shown that narrow crowns appear independently within these two groups (Wilson and Sereno, 1998) and that titanosaurs are most closely related to broad-crowned taxa such as *Brachiosaurus* (Salgado *et al.*, 1997). In addition, the recent discovery of the associated cranial and postcranial remains of *Rapetosaurus* clearly demonstrated the anatomy of a titanosaur skull and provided ample evidence that the isolated skulls of *Nemegtosaurus* and *Quaesitosaurus* are titanosaurs (Curry Rogers and Forster, 2001, 2004; contra Upchurch, 1999). The skulls of

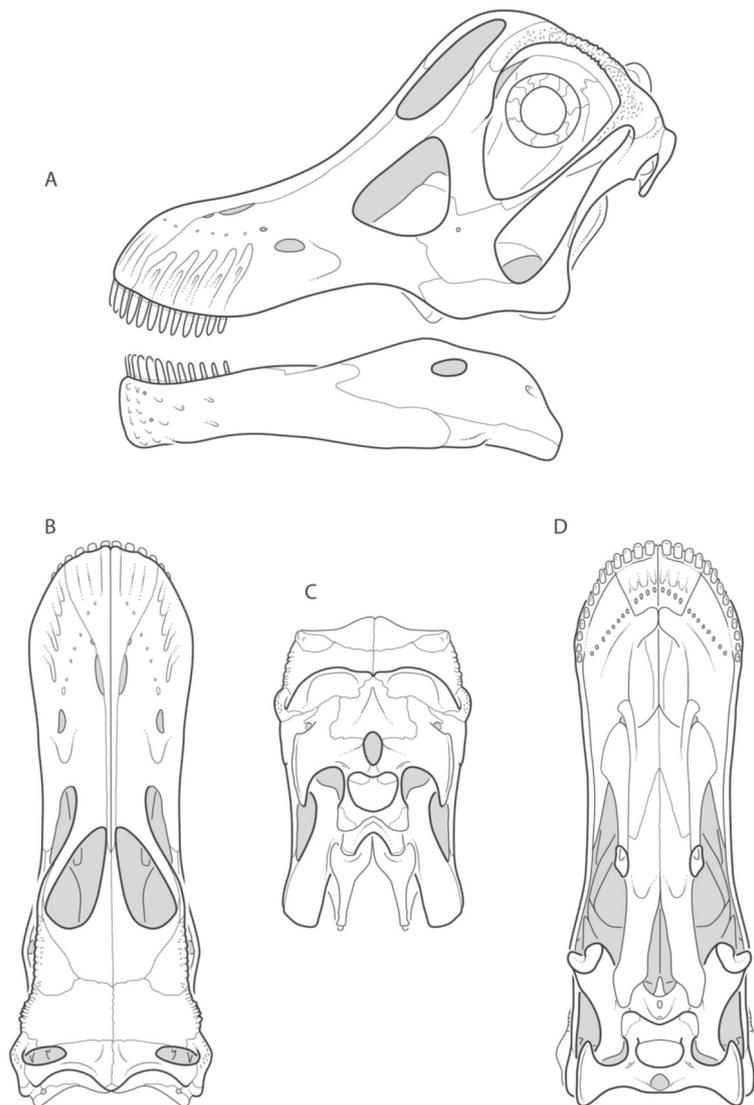


Figure 3. Reconstruction of the skull of *Nemegtosaurus mongoliensis* in left lateral (A), dorsal (B), posterior (C), and ventral (D) views. From Wilson (2005a: fig. 16).

Rapetosaurus, *Nemegtosaurus*, and *Quaesitosaurus* are generally elongate and rotated posteriorly relative to the braincase and share many additional features (Wilson, 2005a; Fig. 3). A novel quadrate-basipterygoid process contact is established between the braincase and palate, and the squamosal is excluded from the supratemporal fenestra. The external nares are exposed laterally but fully retracted. In *Nemegtosaurus* and *Quaesitosaurus*, the upper teeth are larger than the lower teeth, but they appear to occlude to produce both V-shaped and apical wear facets. Numerous openings in the premaxilla, anterior maxilla, and anterior dentary suggest a highly vascularized snout. Although several titanosaur species share one or more of these

features with *Nemegtosaurus*, their distribution remains poorly constrained and cannot yet be used to identify groupings within Titanosauria. As more well-preserved titanosaur skulls are discovered and described (see below), the distribution of characters *Nemegtosaurus* and *Quaesitosaurus* will likely broaden to diagnose more inclusive groups.

The vertebral column of titanosaurs is also diagnostic. Although there is not sufficient articulated material to establish vertebral counts or evaluate changes in vertebral counts in the group, novel features are present in each region of the column. Presacral and occasionally sacral and caudal vertebrae are characterized by varying degrees of camellate pneumatization, in which vertebrae have a honeycomb-like internal structure. Other features include reduced cervical neural arch lamination, loss of the hyposphene-hypantrum articulations in dorsal vertebrae, posterior inclination of dorsal neural spines, addition of a sixth sacral vertebra, and procoelous caudal centra (Fig. 1; Salgado *et al.*, 1997; Upchurch, 1998; Wilson, 2002; Curry Rogers, 2005). Some titanosaurs are characterized by a short tail of approximately 35 stout caudal vertebrae, many fewer than in primitive sauropods (~50 caudal vertebrae) and less than half the number in diplodocids (~80 caudal vertebrae). The articular surfaces of all titanosaur caudal centra are concavo-convex; in all but *Opisthocoelicaudia* the anterior face of the centrum is concave (i.e., procoelous). Borsuk-Bialynicka (1977) and Wilson and Carrano (1999) suggested that this shortened tail might have functioned as a third support when derived titanosaurs reared during feeding or mating.

Numerous changes in the limb skeleton are related to the acquisition of a wide-gauge limb posture (Figs. 4-5). Although most sauropod trackways resemble those of other large animals with a parasagittal limb stance, in which the manus and pes contact the substrate near the trackway midline, some sauropods produced tracks in which manus and pes impressions are “well away from the trackway midline” (Farlow, 1992: 108, 109). This variation in “gauge width” is inferred to be taxonomic. The more widespread narrow-gauge stance is interpreted to be primitive, and the wide-gauge stance is a derived feature of titanosaurs (Wilson and Carrano, 1999). Many appendicular features of titanosaurs appear to be related to a broader limb stance, more flexed limb posture, and increasingly cartilaginous joint surfaces (Fig. 5). The anterior thorax and shoulder girdle are broader in derived titanosaurs than in other sauropods, owing to the combined effects of the elongate coracoids and the enlarged, crescentic sternal plates. The humerus in derived titanosaurs bears a prominent deltopectoral crest, and its distal condyles are both divided and exposed anteriorly, features not present in other sauropods. A prominent olecranon process projects above the articular surface of the ulna, as it does in sauropod outgroups but not in most other sauropods. The radius is typically transversely expanded near the wrist joint. Carpal elements have not been found associated with manual elements in any titanosaur and are not present among the articulated forelimb elements of *Alamosaurus* or *Opisthocoelicaudia* (Gilmore, 1946: pl. 4; Borsuk-Bialynicka, 1977: 29). In both cases, radius, ulna,



Figure 4. Wide-gauge trackways preserved in the Lower Cretaceous Glen Rose Formation near the Paluxy River, Texas (from Bird, 1941: 78). Hindfoot prints are large, ovoid, and bear digit and ungual impressions; forefoot impressions are smaller, arcuate or D-shaped, and do not bear digit or ungual impressions.

and metacarpals were all preserved in articulation, but no intervening carpal ossifications were found. Only extremely reduced manual phalanges have been reported in association with titanosaur skeletons (e.g., Borsuk-Bialynicka, 1977), and it is likely that some titanosaurs lacked fleshy manual digits. Like the carpus and manus, the tarsus is extremely reduced in the some titanosaurs. The preacetabular process of the ilium is enlarged and flared laterally, superficially resembling that of the giant ground sloth *Megatherium*. The femur is specialized in titanosaurs, with the proximal one-third of its shaft bent medially, its distal femoral condyles beveled 10 degrees dorsomedially, and a highly eccentric midshaft cross-section. The relatively small, pyramidal astragalus of *Opisthocoelicaudia* and other titanosaurs contacts the fibula and the lateral aspect of the tibia, but does not reach the medial extreme of the distal tibia (Fig. 5, right).

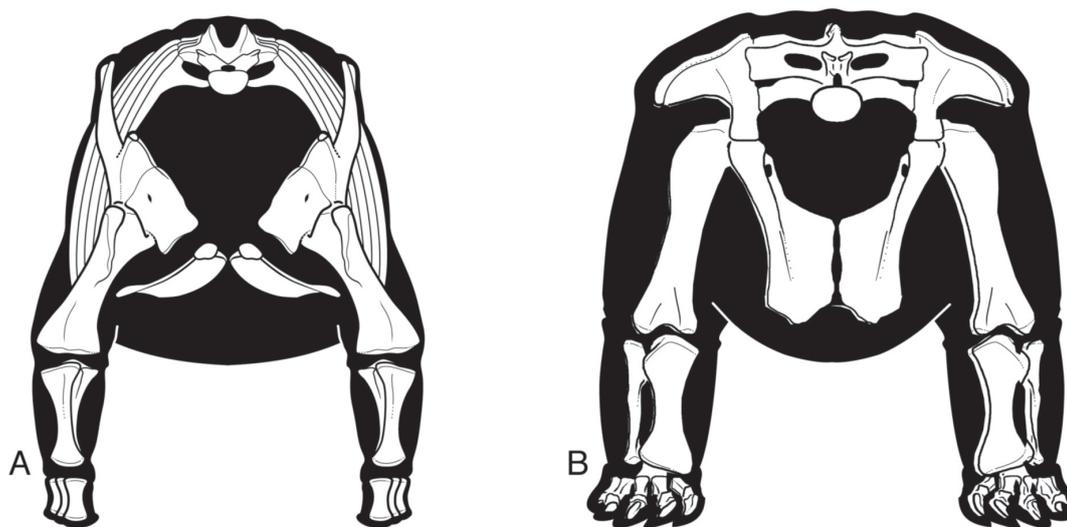


Figure 5. Wide-gauge limb posture in the forelimb (A) and hind limb (B) of *Opisthocoelicaudia* (from Wilson, 2005b).

Body size range.

Although newly hatched sauropods may have measured less than half a meter and weighed less than 10 kg (Britt and Naylor, 1994; Chiappe *et al.*, 2001), they grew to adult sizes rivaling whales (Appenzeller, 1994; Seebacher, 2001; Erickson *et al.*, 2001)

Sauropods are the largest known land vertebrates, but adult body size varies among sauropods. In general, the earliest appearing sauropods (e.g., *Antenonitrus*, *Vulcanodon*) were smaller than the later appearing neosauropods, most of which are several times larger (Yates, 2004). A notable exception is the relatively large Triassic sauropod material recovered from Thailand (Buffetaut *et al.*, 2002; Sander *et al.*, 2004). Interestingly, the largest sauropod genera are not restricted to one clade but are distributed throughout Sauropoda and include basal forms (*Mamenchisaurus*), diplodocoids (*Seismosaurus*), and macronarians (*Brachiosaurus*). Titanosauria has the broadest range of adult body size amongst sauropods and provides an opportunity to evaluate spatial and temporal patterns of body size change within the group, once a species-level phylogeny is established. Figure 6 compares the diminutive saltasaurid *Neuquensaurus australis* (adult body length ~7m; body weight ~100,000 kg; Powell, 1986, 1992, 2003) to the large-bodied *Antarctosaurus giganteus* (adult body length 30+ m, body weight 30-100 tons; Peczki, 1994). The life history changes that led to this great disparity in body size amongst titanosaurs are still not understood.

Descent during continental fragmentation.

Definitive titanosaur body fossils make their first appearance in Lower Cretaceous horizons of North America (Ostrom, 1970; Britt *et al.*, 1998), South America (Calvo and Bonaparte, 1991), Australia (Coombs and Molnar, 1981), Africa (Jacobs *et al.*, 1993), and Europe (Mantell, 1850).

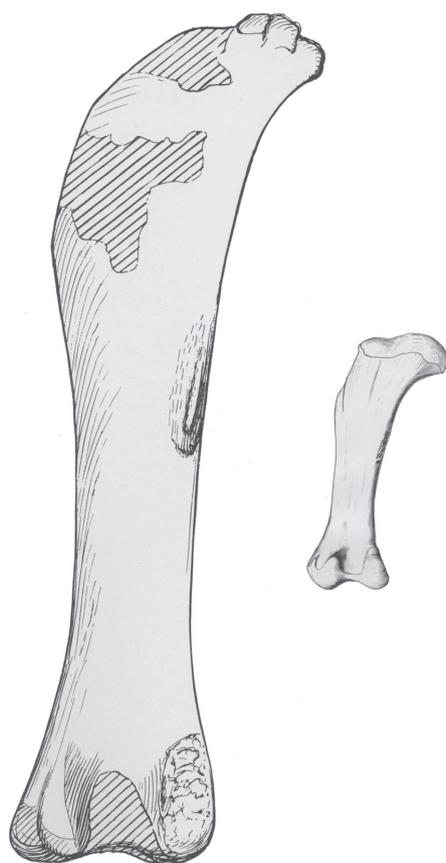


Figure 6. Left femora (posterior view) of the titanosaur species *Antarctosaurus giganteus* (length, 231cm) and *Neuquensaurus australis* (length, 70cm). To scale (from Huene 1929:pls. 20, 36). Both correspond to adult individuals.

In India and Madagascar, which have poorly sampled Lower Cretaceous strata, titanosaurs appear in the first sampled Cretaceous rocks, which are Turonian (Khosla *et al.*, 2003) or Maastrichtian (Curry Rogers and Forster, 2001, 2004) in age, respectively. Given the near-global Early Cretaceous distribution of Titanosauria, it is surprising that only one putative pre-Cretaceous titanosaur body fossil is known, the Late Jurassic *Janenschia* (Janensch 1961; Bonaparte *et al.*, 2000). However, wide-gauge trackways attributed to titanosaurs (Wilson and Carrano, 1999; Fig. 3) suggest that they were present as early as the Middle Jurassic (Santos *et al.*, 1994; Day *et al.*, 2002, 2004). Thus the geographic dispersion of titanosaurs was underway during the Late Jurassic, when substantial connections between landmasses remained. By the latest Cretaceous, titanosaurs were the predominant (or exclusiv) sauropods worldwide, represented on all continental landmasses except Antarctica, which has not yet yielded sauropod body fossils.

Competing hypotheses have been proposed to explain the paleobiogeographic distribution of Gondwanan terrestrial vertebrates. The first, recently reformulated and labeled the “pan-Gondwana” hypothesis by Sereno *et al.* (2004), stipulates that various clades of terrestrial

vertebrates, including titanosaurs, were broadly distributed throughout Gondwana during the Early Cretaceous, and that subsequent faunal disparity developed as a result of differential extinction and diversification. In this context, the latest Cretaceous survival and predominance of titanosaurs on each landmass may have been independent if sub-aerial connections were severed by the Cenomanian. An alternative hypothesis, formulated by the Mahajanga Basin Project working group (Krause *et al.* 1999, Sampson *et al.* 1998, 2001) and recently dubbed the “Africa-first” hypothesis by Sereno *et al.* (2004), posits cosmopolitanism of Late Cretaceous terrestrial Gondwanan faunas exclusive of Africa. More specifically, the latter model, consistent with the paleogeographic reconstruction of Hay *et al.* (1999), invokes Antarctica (in combination with two key land bridges) as a dispersal route between Indo-Madagascar and South America following isolation of Africa by a circum-African seaway sometime in the mid Cretaceous. According to this model, titanosaurs of South America, Madagascar and India are expected to share closer affinities with one another than any shares with African titanosaurs. Titanosaur distributions provide an opportunity to evaluate Cretaceous survivorship patterns and the effects of major tectonic rearrangements on their evolutionary history.

Timeliness.

Analysis of titanosaur relationships is timely because it follows closely on the recent description of several key specimens. These include (1) the first titanosaur with associated cranial and postcranial remains (*Rapetosaurus*; Curry Rogers and Forster, 2001, 2004), (2) first embryonic titanosaur remains (Chiappe *et al.*, 1998, 2001; Salgado *et al.*, 2005), and (3) nearly complete associated or articulated postcranial skeletons from South America (*Mendozasaurus* González Riga, 2003; *Epachthosaurus* Martínez *et al.*, 2004; *Gondwanatitan* Kellner and Azevedo, 1999; *Bonatitan* Martinelli and Farasiepi, 2004), Asia (*Phuwiangosaurus* Martin *et al.*, 1994; *Tangvayosaurus* Allain *et al.*, 1999), India (*Isisaurus* Jain and Bandyopadhyay 1997), Europe (*Lirainosaurus* Sanz *et al.*, 1999; *Ampelosaurus* Le Loeuff, 1995; 2003), and Africa (*Malawisaurus* Jacobs *et al.*, 1993; Gomani, 2005; *Paralatitan* Smith *et al.*, 2001). Most of these important specimens have not yet been incorporated into cladistic analysis and will provide important character combinations for resolving titanosaur phylogeny.

Previous systematic analyses of titanosaurs

Initial work by Lydekker (1877, 1893), Marsh (1895), and Huene (1929, 1932) established Titanosauridae as a unique sauropod subgroup diagnosed on the basis of procoelous caudal vertebrae (Fig. 1). In the first higher-level classification of Sauropoda, Janensch (1929) grouped Titanosauridae with Diplodocidae on the basis of narrow tooth crowns and elevated external nares as suggested by Huene’s reconstruction of *Antarctosaurus* (1929: fig. 31). This classification

was widely accepted and became the paradigm for sauropod taxonomy (Lapparent and Lavocat, 1955; Romer, 1966; Steel, 1970; Carroll, 1988).

Few fossil discoveries or taxonomic revisions of “*Titanosaurus*”-like animals occurred until the 1970s, when field exploration in southern South America yielded several new and well-preserved specimens (reviewed in Bonaparte, 1996). This field work led to the first taxonomy for South American Titanosauridae, which established the Late Cretaceous Subfamilies Titanosaurinae, Saltosaurinae, Argysaurinae, and Antarctosaurinae but provided no hierarchical structure within the group (Powell, 1986, 2003). Subsequent discovery of Early Cretaceous sauropods that resembled typical titanosaurs but lacked procoelous caudal centra and other titanosaurid features (e.g., *Andesaurus*; Calvo and Bonaparte, 1991) led Bonaparte and Coria (1993) to create the new higher taxon Titanosauria, which they divided into the earlier-appearing, primitive Andesauridae and the later-appearing, more derived Titanosauridae. Although Andesauridae is now acknowledged to be a paraphyletic assemblage linked by plesiomorphic features (i.e., Salgado *et al.*, 1997), and Titanosauridae is likewise recognized to be invalid (Wilson and Upchurch, 2003), the basic recognition of a derived subgroup of titanosaurs is agreed upon by recent cladistic analyses, as discussed below.

The first cladistic analyses of Sauropoda addressed higher-level relationships of the group, with little investigation of its subgroups (Calvo and Salgado, 1995; Upchurch, 1995; Salgado *et al.*, 1997; Wilson and Sereno, 1998). Although the analysis of Upchurch (1995) supported the traditional dichotomy of sauropods into broad- and narrow-crowned clades first suggested by Janensch (1929), the analyses of Salgado *et al.* (1997) and Wilson and Sereno (1998) provided evidence that titanosaurs share closest ancestry with *Brachiosaurus*-like taxa. This result has been corroborated in subsequent cladistic analyses focusing on lower-level relationships of Sauropoda (Upchurch, 1998; Wilson, 2002). These latter analyses and several others (Salgado *et al.*, 1997; Sanz *et al.*, 1999; Curry Rogers and Forster, 2001; Curry, 2001; Calvo and González Riga, 2003; González Riga, 2003; Upchurch *et al.*, 2004; Curry Rogers, 2005) evaluated the evolutionary history of titanosaurs. These analyses provide the foundation for future work on titanosaur systematics, and their results are discussed below.

Comparison of data.

Analyses addressing the interrelationships of Titanosauria have each employed different numbers of taxa and characters, as well as different types of characters (Table 1). Most analyses included ten or fewer terminal taxa, but Curry (2001) and Curry Rogers (2005) included 27, which was pruned down to 15 due to the high number of resultant most parsimonious trees. Despite inclusion of numerous terminal taxa, however, Curry Rogers (2005) identified a comparable number of synapomorphies as did analyses considering fewer taxa.

analysis	taxa	characters	cranial		axial		limb		dermal	
			raw	%	raw	%	raw	%	raw	%
Upchurch 1995*	4	12	0	0	5	42	6	50	1	8
Salgado <i>et al.</i> 1997	10	28	0	0	17	61	11	39	0	0
Upchurch 1998	6	28	1	4	14	50	13	46	0	0
Sanz <i>et al.</i> 1999	7	43	1	2	27	63	14	33	1	2
Curry Rogers & Forster 2001*	10	228	74	32	86	38	67	29	1	1
Curry 2001, Curry Rogers 2005	19	364	109	30	140	38	113	31	2	1
Wilson 2002	8	77	22	29	27	35	27	35	1	1
González-Riga 2003*	10	39	0	0	24	62	15	38	0	0
Calvo & González-Riga 2003	10	46	3	7	27	59	16	34	0	0
Upchurch <i>et al.</i> 2004*	10	241	41	17	91	38	109	45	0	0
<i>TOTAL</i>	—	<i>1106</i>	<i>251</i>	<i>22.7</i>	<i>458</i>	<i>41.4</i>	<i>391</i>	<i>35.4</i>	<i>6</i>	<i>0.5</i>

Table 1. Character data used in cladistic analyses of titanosaur interrelationships. Asterisks (*) indicate that either matrices or synapomorphy list were not provided. Only characters that varied within Titanosauria were tallied.

The anatomical composition of the character data summarized in Table 1 provides insight into the structure of the data supporting titanosaur interrelationships. First, early analyses used no or very few cranial features (i.e., narrow tooth crowns). The description of *Rapetosaurus* (Curry Rogers and Forster, 2001) and the re-description of *Nemegtosaurus* and *Quaesitosaurus* (Wilson, 2002, 2005a) provided the first opportunity to discover cranial synapomorphies supporting interrelationships of Titanosauria; later analyses identified many diagnostic cranial features. Owing to the rarity of titanosaur skulls, however, the distributions of these features are not yet well constrained. The recent and upcoming description of new cranial material of titanosaur (Calvo *et al.*, 1997; Martínez, 1998; Gomani, 2005; Chiappe *et al.*, 2001; Salgado *et al.*, 2005) will allow documentation of these and additional cranial features that resolve the relationships of the group. Second, despite the fact that few complete vertebral columns are known among titanosaur, axial characters make up the majority of characters determining titanosaur interrelationships. Of these, three-quarters are characters pertaining to the dorsal and caudal vertebrae. Third, appendicular synapomorphies contribute substantial character support in most analyses. These data are relatively evenly distributed amongst the pectoral girdle, pelvic girdle, forelimb, and hindlimb. The relatively high proportion and evenness of distribution of appendicular features may relate to overall changes in limb morphology associated with acquisition of wide-gauge limb posture.

Core Characters.

The 1,106 characters used by previous analyses can be distilled into a core of 255 independent characters, indicating substantial overlap of character data amongst analyses. As a result, the core character data profile resembles that of the gross tally of characters in Table 1.

Like the gross tally, the core characters are predominantly axial (40%) but include slightly higher relative amounts of cranial (29%) and appendicular (30%) data. Dermal features contributed only 1% of character data.

Topology.

Twenty-six titanosaur species have been evaluated in one or more of the ten analyses shown in Figure 7. (Note: I used the pruned version of Curry Rogers [2005] for comparison, and the branch leading to *Nemegtosaurus* and *Quaesitosaurus* is detached in the Upchurch analyses because he considers those taxa to be diplodocoids). Ten terminal taxa appear in only one or two analyses, but 10 appear in at least half (≥ 5) the analyses. Pruning those infrequently-used terminal taxa and retaining those 10 that appear in half the analyses yield the modified cladograms shown in Figure 8, which can more easily be compared.

The five analyses that include *Andesaurus* resolve it as the basalmost titanosaur. All but two analyses place *Malawisaurus* as the basalmost or next-most basal titanosaur, depending on whether *Andesaurus* was included. Alternative placements for *Malawisaurus* resolve it as more closely related *Saltasaurus* and *Neuquensaurus* than is *Opisthocoelicaudia* (Upchurch, 1995; Curry Rogers, 2005). *Saltasaurus*, which was included in all analyses, was always resolved as the most derived titanosaur. *Neuquensaurus*, when included, is always the sister-taxon of *Saltasaurus*. *Alamosaurus* and *Opisthocoelicaudia* are recovered as outgroups to *Neuquensaurus* and/or *Saltasaurus* in most analyses, but their relative proximity to derived titanosaurs is inconsistent. A notable exception is Curry Rogers (2005), who resolved both as basal to *Malawisaurus*. *Isisaurus* (= “*Titanosaurus*”) and *Lirainosaurus* are typically nested between *Malawisaurus* and more derived titanosaurs. Sanz *et al.* (1999), however, placed *Lirainosaurus* in a more derived position between *Opisthocoelicaudia* and *Saltasaurus*. *Nemegtosaurus* and *Quaesitosaurus* have been resolved as basal diplodocoids (Upchurch 1995, 1998; Upchurch *et al.* 2004) or as titanosaurs phylogenetically between *Malawisaurus* and *Saltasaurus* (Curry Rogers and Forster, 2001; Curry Rogers, 2005; Wilson, 2002) when included in cladistic analyses. Despite this disagreement, they are usually resolved as sister-taxa.

These analyses suggest that there is agreement on the basic framework for titanosaur phylogeny. A 50% majority-rule consensus of these 10 pruned cladograms preserves the following common nodes: *Andesaurus* (*Malawisaurus* (*Isisaurus/Lirainosaurus* (*Opisthocoelicaudia/Alamosaurus* (*Neuquensaurus, Saltasaurus*))))). While the resolution of these basic nodes is promising, many valid titanosaur species have yet to be included in a phylogenetic analysis. Moreover, the substantial overlap of character data between analyses makes their agreement more likely. Novel characters and character combinations from new taxa and continued collections research will test the consensus reached in these preliminary 10 analyses.

An Overview of Titanosaur Evolution and Phylogeny

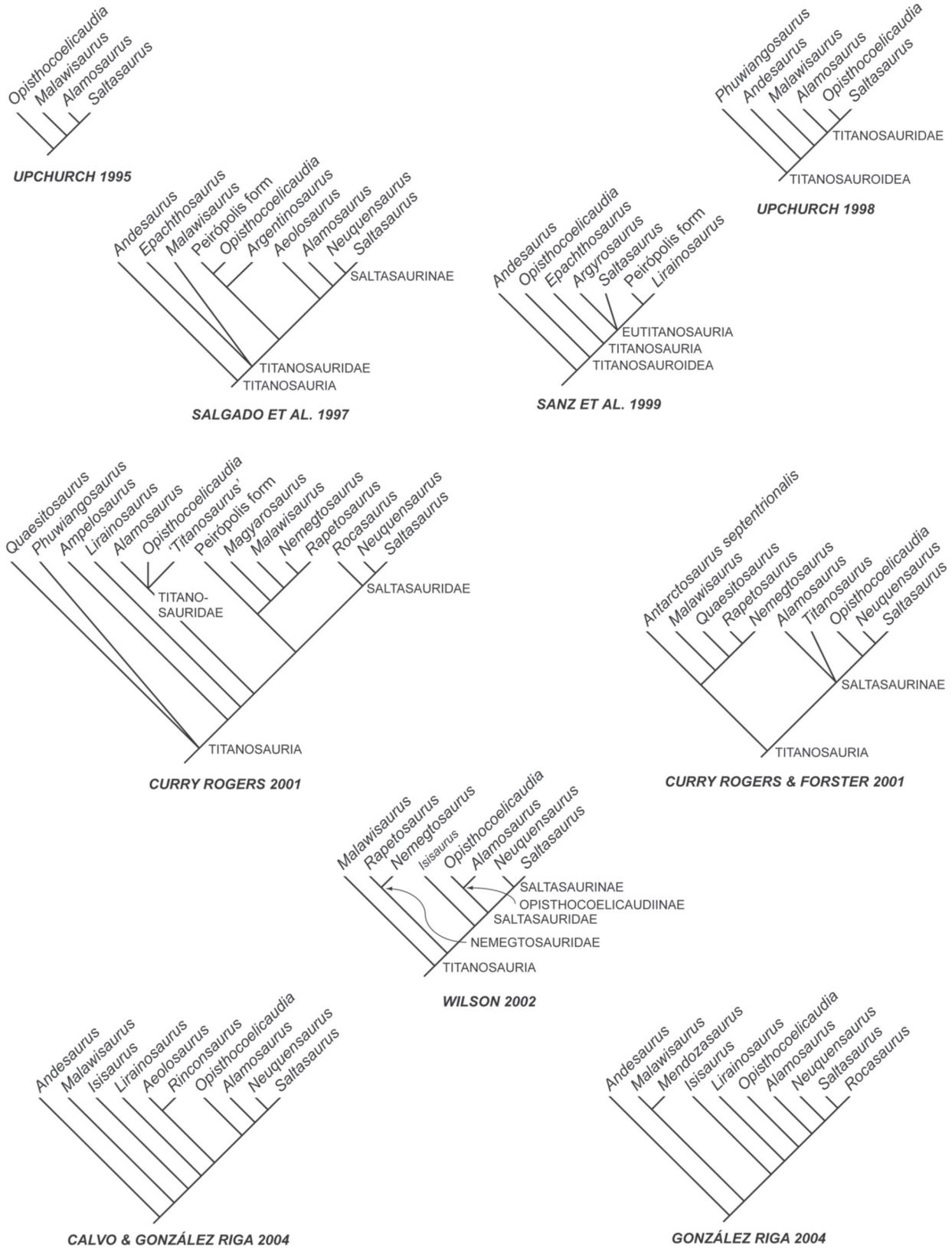


Figure 7. Summary of cladistic analyses including titanosaur species. The pruned Adams consensus tree from Curry (2001)/Curry Rogers (2005) analysis was used. In all three Upchurch analyses, *Nemegtosaurus* and *Quaesitosaurus* were resolved as non-titanosaurs (*diplocoids*), as indicated by the detached branch. “*Titanosaurus*” is equivalent to *Isisaurus*.

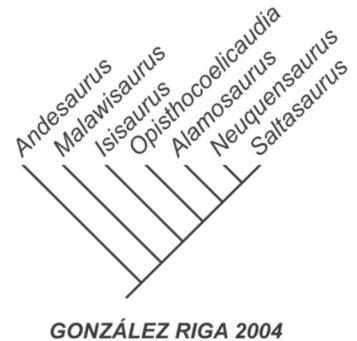
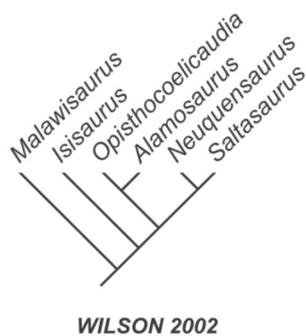
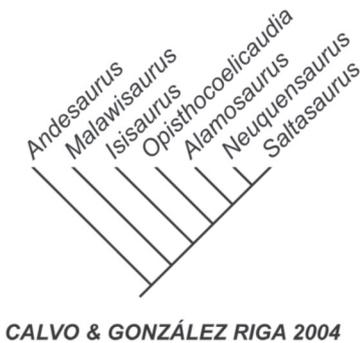
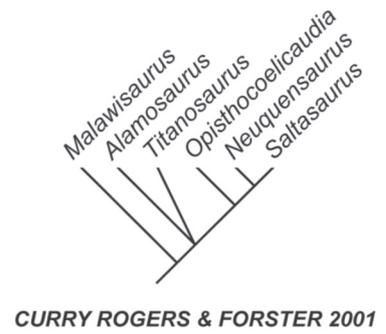
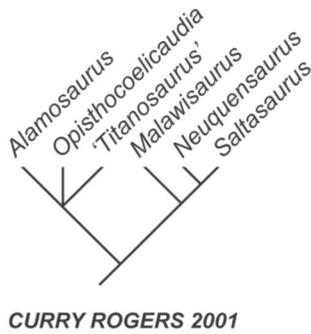
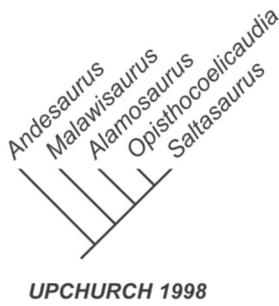
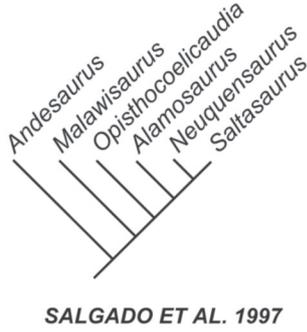
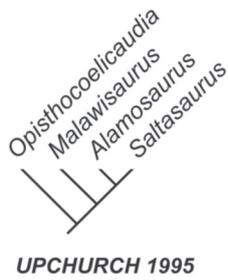


Figure 8. Comparison of the cladistic topologies from Figure 7 ‘pruned’ to include only taxa that appear in at least half of the 10 analyses. “Titanosaurus” is equivalent to *Isisaurus*.

Conclusion

The interrelationships of Titanosauria remain as one of the last frontiers in dinosaur systematics. Currently more than 10 phylogenetic analyses have investigated titanosaur relationships. There are many points of agreement amongst analyses, but much of the character

data used by these analyses are shared. Although new characters have been added to datasets, most are derived from analyses aimed at much broader phylogenetic questions, such as the interrelationships of sauropods. Although discovery and description of more complete titanosaur species will allow more complete scoring of these core characters and improve resolution of titanosaur relationships, more novel characters are needed.

A species-level phylogeny for Titanosauria will allow assessment of basic questions that include exploration of the Mesozoic paleobiogeography, examination of changes in body distribution through time, investigation into the distribution of morphological features related to adoption of a wide-gauge limb posture and its biomechanical significance, and exploration of patterns in herbivorous apomorphies of Cretaceous dinosaurs. These and other avenues of research will be explored in future projects.

Acknowledgments

I am grateful to F. Torcida and P. Huerta for inviting me to participate in the excellent 3^{as} Jornadas Internacionales Sobre Paleontología de Dinosaurios y su Entorno. I thank B. Miljour for Figures 3 and 5, which were based on my preliminary sketches. Discussions with K. Curry Rogers, P. Sereno, P. Upchurch, and G. P. Wilson improved this paper. An anonymous reviewer also provided useful comments on an earlier draft of this manuscript. This research was supported by grants from the Dinosaur Society, the Scott Turner Fund (University of Michigan) and the American Institute for Indian Studies.

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