

A REVISION OF *Titanosaurus* LYDEKKER (DINOSAURIA – SAUROPODA), THE FIRST DINOSAUR GENUS WITH A ‘GONDWANAN’ DISTRIBUTION

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SYNOPSIS Titanosaurs represent approximately one-third of sauropod diversity and were geographically widespread throughout the Cretaceous, especially on southern continents. Titanosaurs evolved numerous appendicular synapomorphies that account for their specialised ‘wide-gauge’ limb posture, which can be recognised in their trackways. The macronarian origin of titanosaurs is only recently agreed upon and aspects of their inter-relationships remain poorly understood.

Titanosauria is named for the poorly known genus *Titanosaurus*, which was coined by Lydekker in 1877 on the basis of a partial femur and two incomplete caudal vertebrae. Fourteen species have since been referred to *Titanosaurus*, which distribute the genus across Argentina, Europe, Madagascar, India and Laos, and throughout 60 million years of the Cretaceous. Despite its centrality to titanosaur systematics and biogeography, the genus *Titanosaurus* has never been revised.

A re-evaluation of all *Titanosaurus* species recognises as diagnostic only five. The type species *T. indicus* is invalid because it is based on ‘obsolescent’ characters – once diagnostic features that have gained a broader taxonomic distribution over time. Consequently, the genus *Titanosaurus* and its co-ordinated rank-taxa (e.g. Titanosaurinae, Titanosauridae, Titanosauroidae) must be abandoned. The unranked taxon Titanosauria, however, remains valid. A new phylogenetic taxonomy is proposed for Titanosauria that utilises nodes that have been judged stable by the most recent cladistic analyses. The early appearance of titanosaur ichnofossils (Middle Jurassic) and body fossils (Late Jurassic) precludes a vicariant origin for the group, but such a pattern cannot yet be ruled out for lower-level taxa within Titanosauria.

KEY WORDS vertebrate palaeontology, evolution, biogeography, Mesozoic, Saurischia, *Isisaurus*

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INTRODUCTION

Titanosauria is the most diverse and geographically widespread clade of sauropod dinosaurs, represented by more than 30 genera that have been recorded from all continental landmasses except Antarctica during the Cretaceous (Weishampel 1990; Hunt *et al.* 1994). The distribution of titanosaur body fossils is complemented by their abundant footprint record, which hints at a much earlier origin, in the Early or Middle Jurassic (Santos *et al.* 1994; Day *et al.* 2002). Titanosaurs are one of the few dinosaur subgroups whose appendicular morphology can be recognised in their trackways – unique ‘wide-gauge’ tracks in which the limbs were distanced from the body midline during locomotion (Wilson & Carrano 1999). However, despite the breadth of their distribution, the novelty of their locomotor style and their centrality in palaeobiogeographical scenarios, titanosaur origins have only recently been agreed upon and aspects of their interrelationships remain poorly established (Salgado *et al.* 1997; Upchurch 1998; Wilson & Sereno 1998; Sanz *et al.* 1999; Curry Rogers & Forster 2001; Wilson 2002).

A central issue in titanosaur systematics is the validity of the genus *Titanosaurus* (Lydekker 1877), namesake for several higher-level taxa (e.g. Titanosauria, Titanosauroidae, Titanosauridae). As the first sauropod discovered on a southern continent, *Titanosaurus* was coined despite its fragmentary nature and the presence of only one unique feature – procoelous caudal centrum articulations. By 1896, discoveries of sauropods with similar tail morphology in Argentina and Madagascar were attributed to the same genus, making *Titanosaurus* the first dinosaur genus with a Gondwanan

distribution. As Lydekker (1893:3) noted, ‘the occurrence of *Titanosaurus* (or of that and a closely allied genus) in both India and South America affords one more instance of that remarkable community of type which undoubtedly exists between the faunas of southern continents of the world’. This notion has persisted into the present and has formed the basis for considering titanosaurs to be ‘Gondwanan’ elements, whose vicariant origin was guided by the fragmentation of Pangaea in the Late Jurassic (Bonaparte 1984, 1999; Bonaparte & Kielan-Jaworowska 1987; Le Loeuff 1993). In all, studies from Lydekker (1877) to Jain & Bandyopadhyay (1997) have produced 14 *Titanosaurus* species, which, if valid, give the genus a geographical distribution covering Argentina, Europe, Madagascar, India and Laos, and a temporal distribution spanning 60 million years of the Cretaceous. Most recent treatments of the genus have focused on particular geographical areas, such as Europe (Le Loeuff 1993; Upchurch 1993), South America (Bonaparte & Gasparini 1979; Powell 1986) and India (Jain & Bandyopadhyay 1997). McIntosh (1990), however, considered the genus in its entirety. Together, these studies accept a handful of valid *Titanosaurus* species, including four from India and one or two from South America. None of these studies, however, provided an adequate diagnosis for the genus or evaluated the original remains.

In this paper, we evaluate the validity of all *Titanosaurus* species and of the genus itself. Firstly, we provide a historical context for the paper by reviewing the early history of *Titanosaurus* discoveries and underscoring early taxonomic choices that have coloured subsequent studies. Secondly, we discuss all named species of *Titanosaurus*, assessing the diagnostic

nature of the original and referred materials and identifying comparisons that can be made to the type species. Thirdly, we assess the validity of the genus itself and discuss the implications of our conclusions on titanosaur systematics and palaeobiogeography.

Institutional abbreviations

AMNH	= American Museum of Natural History, New York
BMNH	= The Natural History Museum, London
CM	= Carnegie Museum of Natural History, Pittsburgh
DGM	= Departamento Nacional da Produção Mineral, Rio de Janeiro
DMNH	= Denver Museum of Natural History, Denver
FMNH	= Field Museum of Natural History, Chicago
GSI	= Geological Survey of India, Kolkata
HMN	= Humboldt Museum für Naturkunde, Berlin
ISI	= Indian Statistical Institute, Kolkata
MACN	= Museo Argentino de Ciencias Naturales, Buenos Aires
MDE	= Musée des Dinosaurés d'Esperaza, Esperaza
MLP	= Museo La Plata, La Plata
MPEF-PV	= Museo Paleontológico Egidio Feruglio, Trelew
MUCP	= Museo de la Universidad Nacional del Comahue, Neuquén
USNM	= National Museum of Natural History, Washington D.C.
YPM	= Yale Peabody Museum, New Haven
ZDM	= Zigong Dinosaur Museum, Zigong

HISTORY OF *TITANOSAURUS* DISCOVERIES AND DESCRIPTIONS

The recorded history of *Titanosaurus* discoveries stretches back to the early nineteenth century, well before the actual naming of the genus in 1877. Over the course of 50 years, the bones that would later become *Titanosaurus* were discovered and passed through several hands before reaching those of their eventual descriptor, Richard Lydekker. As was the case with other early discoveries (e.g. *Cetiosaurus*; Upchurch & Martin, 2003), original remains of the new taxon were fragmentary and detailed locality information was not collected – reports of local procurers and geological clues, such as matrix adhered to the bone, formed the basic provenance data. Consequently, little was recorded of the field relationships among the type elements of *Titanosaurus* or between them and other fossils found in the same stratum. Below we recount the early discoveries of *Titanosaurus* in central India and evaluate the validity of associations and comparisons made by its early descriptors.

Early discoveries

Recorded history of Indian sauropod discoveries begins in 1828, when a British Army officer, Captain Sleeman, collected fossil bones from Bara Simla Hill, a locality adjacent to the Gun Carriage Factory near the city of Jabalpur in central India (Fig. 1; Matley 1921:152–153; Sahni 2001). These specimens were passed to a Mr. Spilsbury, who sent them to the Indian Museum in Calcutta (hereafter Kolkata) in 1832.

Sleeman's description of his discovery (Falconer 1868) suggests that these specimens were found immediately below the basalt cap of the hill, which corresponds to the 'Upper Sands' level of the Lameta Formation (Fig. 2). Later authors disagree with this conjecture. Spilsbury's subsequent description and geological section at the locality indicate that the bones were found just above the 'Main Lameta Limestone', in the 'Ossiferous conglomerate' (Falconer 1868; Matley 1921). Matley's research at Bara Simla suggested that the 'Sauropod bed' yielded the fossils (*in* Huene & Matley 1933:4). The 'Ossiferous conglomerate' and the 'Sauropod bed' are separated by four feet, and both are found within the 'Mottled nodular beds', which are sandwiched between the 'Upper limestone' and 'Main Lameta limestone' at Bara Simla (Fig. 2). The 'Upper sands', on the other hand, are above the 'Upper limestone' and seem the least likely to have produced the fossils. Few dinosaur bones have been reported from the 'Upper Sands' at Bara Simla, although a partial left femur was discovered from 'Upper Sands' at a locality more than 100 km northeast, near Silondi (Huene & Matley 1933:30). We follow Matley in regarding the 'Sauropod bed' as being the level bearing Sleeman's fossils for two reasons. Firstly, the 'Sauropod bed' is closer to the 'Upper Sands' that Sleeman identified as having produced the remains than is the 'Ossiferous conglomerate'. Secondly and most importantly, the 'Sauropod bed' produces most of the sauropod remains, as indicated by further excavation at Bara Simla by Matley (see below).

By 1862, Sleeman's vertebrae had been passed to Hugh Falconer (Fig. 3A) by the then Superintendent of the nascent Geological Survey of India. Falconer recognised the reptilian character of the vertebrae and provided a description and principal measurements for both, as well as illustrations of the better preserved of them (Fig. 4). He did not, however, name them in his posthumous memoirs (Falconer 1868). These two vertebrae, together with a fragmentary femur collected from the same locality in 1871 by Medlicott, formed the basis of the new taxon *Titanosaurus indicus* by Lydekker (1877; Fig. 3B). Because Lydekker (1877:38) did not specify one of these elements as the holotype ('type' in former parlance), the three elements together form the type series. In his description of the new species, Lydekker (1877:40) recognised the animal as a dinosaur and noted several diagnostic features of the vertebrae but failed to identify distinctive features in the femur, remarking 'if the femur had been found alone, I should have referred it to the [British] genus *Cetiosaurus*, but the vertebrae forbid this view'. Although the femur and the caudal vertebrae came from the same locality, Matley (1921) demonstrated that they did not come from the same stratigraphic level. Whereas the vertebrae came from the 'Sauropod bed' above the 'Main Lameta Limestone', matrix adhering to the femur indicated it was from the 'Green sand' below the 'Main Lameta Limestone' (Fig. 2). On this basis, Huene & Matley (1933:29), formally excluded the femur from the type series of *T. indicus*, instead referring it to the South American genus *Antarctosaurus*.

In his original description, Lydekker (1877:41) referred to *T. indicus* two other sets of material from Pisdura, a locality 300 km south of Bara Simla (Fig. 1). These remains included '... a considerable series of caudal vertebrae ... collected by Mr. W. T. Blanford ...'; and a collection of vertebrae and a femur mentioned by Hislop (1864). Later, however, Lydekker (1879:23) identified certain differences between

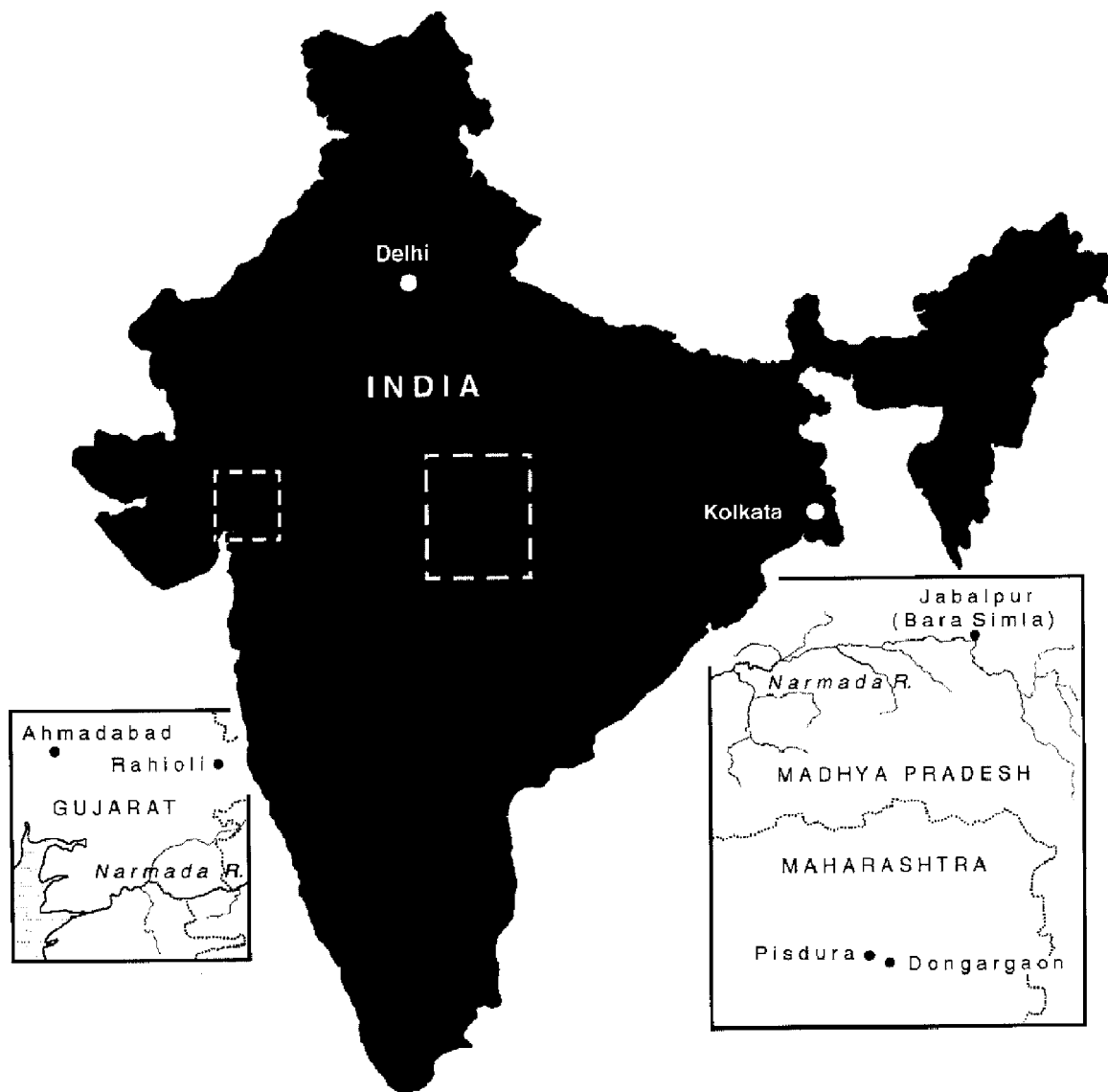


Figure 1 *Titanosaurus* localities – India. Inset at right shows three key localities in the central states of Madhya Pradesh and Maharashtra (Jabalpur, Pisdura and Dongargaon); inset at left shows the main locality (Rahioli) in the western state of Gujarat. These two important exposures of the Late Cretaceous Lameta Formation outcrop at the eastern and western edges of the Narmada River. Grey lines = rivers; dotted lines = state or country boundaries. This and other large silhouette maps are based on Shupe *et al.* (1992).

the Jabalpur and Pisdura caudal vertebrae and designated two of the latter ‘cylindrical vertebrae’ as a second species, *T. blanfordi* (see Species of *Titanosaurus*, below).

Between 1917 and 1919, Matley collected a substantial quantity of sauropod and other material from several localities on the western slope of Bara Simla. Much of the collection went to the British Museum, but the sauropod remains were kept at the Geological Survey of India (Huene & Matley 1933:1). The bulk of the sauropod material was found approximately 1.2 m above the ‘Main Lameta limestone’, in the red and green marly clay of the ‘Sauropod bed’ that yielded the original remains of *T. indicus* (Fig. 2). These new elements were not found in articulation, having been ‘washed about and somewhat damaged and broken before fossilisation’ (Matley 1921:154). Although Matley initially believed this material belonged to a single individual, morphological features present in the sample required the presence of two

taxa (*T. indicus*, *Antarctosaurus septentrionalis*) and at least three individuals (Huene & Matley 1933:4, 6–35). Indeterminate sauropod remains were found below the ‘Main Lameta Limestone’ in the ‘Carnosaur bed’, including a nearly complete maxilla (Fig. 2; Huene & Matley 1933: fig. 19). The broken head of a right humerus was found at a slightly lower level in the section, at the same level in the ‘Green sand’ as the femur Lydekker originally described as part of the type series of *T. indicus* (Table 1; Huene & Matley 1933:29–30). The authors described no new material from the ‘Ossiferous conglomerate’ above the ‘Main Lameta Limestone’ (Fig. 2).

Matley collected additional fragmentary sauropod specimens in 1920 from localities near Pisdura, the type locality of *T. blanfordi* (Figs 1 & 5). Like previous collectors, Matley picked up fossilised remains that were disinterred by the ploughing of the fields, a technique that precludes recovery of field associations. Matley’s 1920 Pisdura

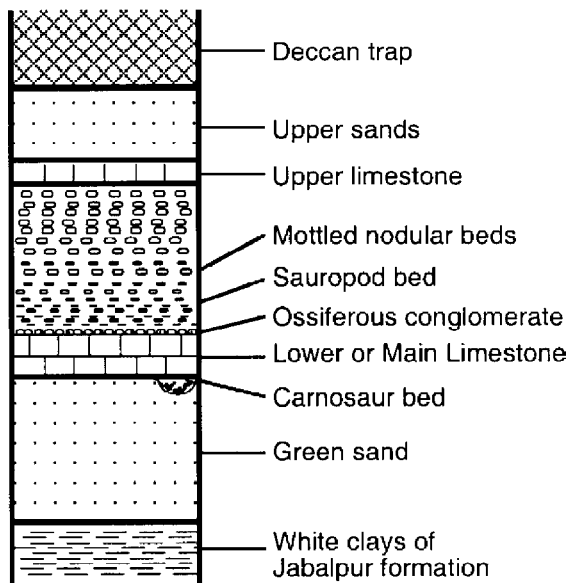


Figure 2 Matley's geological section at Bara Simla hill, Jabalpur, central India (from Huene & Matley 1933: fig. 1). Lithological key: cross-hatching indicates basalt; stipple indicates sandstone; blocks indicate limestone; dashes indicate clay; open circles indicate nodular beds.

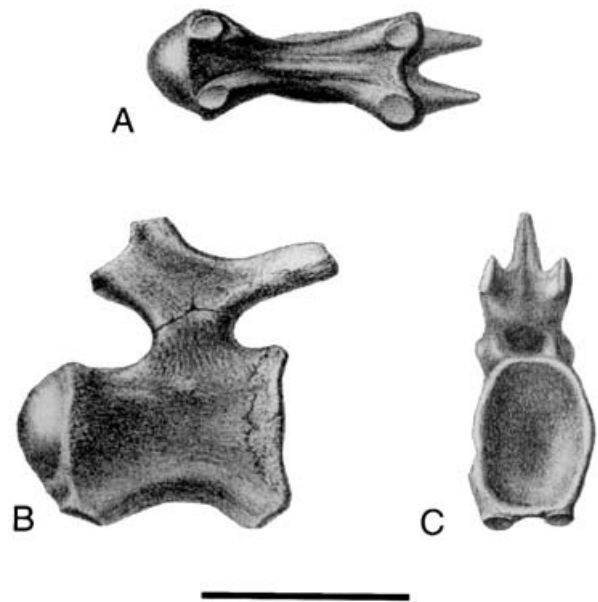


Figure 4 *Titanosaurus indicus*. Holotypic distal caudal vertebra in ventral (A), right lateral (B), and anterior (C) views. From Falconer (1868: pl. 34, figs 3–5). Scale bar = 15 cm.



Falconer



Lydekker



von Huene

Figure 3 Portraits of Hugh Falconer, Richard Lydekker and Friedrich Baron von Huene. Falconer portrait reproduced from his posthumous memoirs (Falconer 1868: frontispiece). Lydekker portrait courtesy of Archives section, Library, The Natural History Museum, London. Huene portrait reproduced from Sues 1997: fig. 2.2).

collection was later separated into four named taxa – *T. indicus*, *T. blanfordi*, *?Antarctosaurus* sp. and *Laplatasaurus madagascariensis* – and a fifth, indeterminate sauropod (Table 1; Huene & Matley 1933:35–41). In 1932–33, Matley made collections from Chota Simla, a small hill 0.5 km from Bara Simla, which, unlike the latter is not capped by the Deccan trap basalts. This expedition was funded by the Percy Sladen Trust of the BMNH and, consequently, most of the specimens were shipped to London. Matley collected titanosaur limb elements and caudal vertebrae that pertain to two individuals, based on the presence of two left femora. All

but the extraneous small left femur were considered a single, associated individual. These remains were first described by Swinton (1947), who claimed that the material was found above the 'Green sand' but below the 'Main Lameta Limestone' – a horizon approximately equivalent to the 'Carnosaur bed' at Bara Simla (Fig. 2). Unfortunately, the Chota Simla caudal vertebrae, which are the only elements that overlap the type series of *T. indicus*, were neither described nor figured by Swinton and they cannot be found in the BMNH collections at present (P.U., pers. obs.). Swinton's (1947) referral of the Chota Simla material to *T. indicus* was based on overall

Table 1 Sauropod remains described by Huene & Matley (1933).

Taxon	Locality	Material	Catalogue number	Figure
<i>Titanosaurus indicus</i>	Bara Simla ('Sauropod bed')	2 caudal vertebrae	K20/315-6	fig 2-3; pl. 1, fig 1-2
	"	Chevron (partial)	K20/318	pl. 1, fig. 3
	"	Tibia	K20/321	pl. 1, fig. 4
	"	Fibula	K27/489	fig. 4; pl. 1, fig. 5
	Silondi ('Upper sands')	Femur (partial)	K27/488	fig. 25
<i>Titanosaurus blanfordi</i>	Pisdura	3 caudal vertebrae	K27/502-4	pl. 6, fig. 1
	"	Caudal vertebra	K27/501	pl. 8, fig. 1
<i>Titanosaurus</i> sp.	"	Tibia (partial)	K27/501	pl. 7, fig. 3
	Bara Simla ('Carnosaur bed')	Femur (partial)	K27/619	fig. 22
<i>Antarctosaurus septentrionalis</i>	"	Metacarpal (partial)	K27/506	fig. 26
	Bara Simla ('Sauropod bed')	Braincase, squamosal	K27/497	figs 5-7; pl. 2, fig. 1
	"	Caudal vertebra	K20/317	fig. 9; pl. 2, fig. 2
	"	Chevron	K24/494	fig. 10
	"	Chevron	K27/492	pl. 2, fig. 3
	"	Rib shaft frags (28)	K27/495, K20/326	figs 11-15
	"	2 scapulae (?pair)	no number	fig. 9; pl. 2
	"	Humerus	no number	pl. 4, fig. 1
	"	Radius	K27/490	fig. 17
	"	Ulna	K27/491	fig. 18
<i>Antarctosaurus</i> sp.	Bara Simla (Green sand)	Sternal plate	K20/647	pl. 4, fig. 2
	"	Femur (partial)	K22/754	fig. 23; pl. 5, fig. 1
	"	Humerus (partial)	no number	fig. 24
	Pisdura	Metatarsal	K27/509	pl. 7, fig. 1
	"	Ischium	K27/510	pl. 7, fig. 2
	"	Chevron	K27/512	not figured
<i>Laplatasaurus madagascariensis</i>	"	Rib fragments	K27/513, 515-21	not figured
	Pisdura	Caudal vertebra		not figured
	"	Sacral centrum	K27/522	pl. 8, fig. 2
	"	3 caudal vertebrae	K27/498-500	pl. 8, figs 3-4
Sauropoda indet.	Bara Simla ('Carnosaur bed')	Maxilla	K27/528	fig. 19
	"	Posterior dorsal centrum	K27/704	fig. 20
	"	Dorsal neural spine	K27/706	fig. 21
	Pisdura	Radius (partial)	K27/511	pl. 6, fig. 2
	"	Metacarpal	K27/507	pl. 6, fig. 3

Plate and figure numbers refer to that work.

similarities seen in the available femora combined with the geographical and stratigraphical proximity of the Bara Simla and Chota Simla remains.

Discoveries at Bara Simla and Pisdura provided the basis for at least four titanosaur taxa, two of which were designated *Titanosaurus* species. The number of sauropod taxa at Bara Simla is an important question because it has a direct bearing on the material assigned to and, therefore, the morphology of, *Titanosaurus indicus*. This is a complex and controversial issue that has been examined using several different lines of evidence (cf. Huene & Matley 1933; Chatterjee & Rudra 1996; Jain & Bandyopadhyay 1997).

Sauropod diversity at Bara Simla

Unfortunately, no site maps for the Bara Simla quarry have ever been published and are apparently non-existent. Matley (1921) and Huene & Matley (1933) do provide some relevant descriptions of the relative positions of various skeletal elements. Of the fossils referred to *Antarctosaurus septentrionalis*, they remark that the left and right scapulae were found as a pair 'a few yards from one another', the humerus was

found 'near the right scapula and about 20 feet from the left scapula', the right radius and ulna were found in the same horizon at the same locality, as were several thoracic ribs, which were found lying parallel to each other as if still in their natural relative positions (Huene & Matley 1933:19-22). These distributions are consistent with the view that the right forelimb belonged to a single individual and that the thoracic region had not been entirely disrupted. Matley (1921) reported his initial impression that a single sauropod carcass had been preserved; probably this view was altered later because it was inconsistent with Huene's contention that the forelimb proportions suggested the presence of two individuals.

Antarctosaurus septentrionalis

Huene & Matley (1933) referred most of the material Matley collected from the 'Sauropod bed' at Bara Simla to *Antarctosaurus*, a genus first described from the Late Cretaceous of Argentina four years earlier (Huene 1929). The Indian species was named *A. septentrionalis* and comprised several elements – a partial braincase, anterior

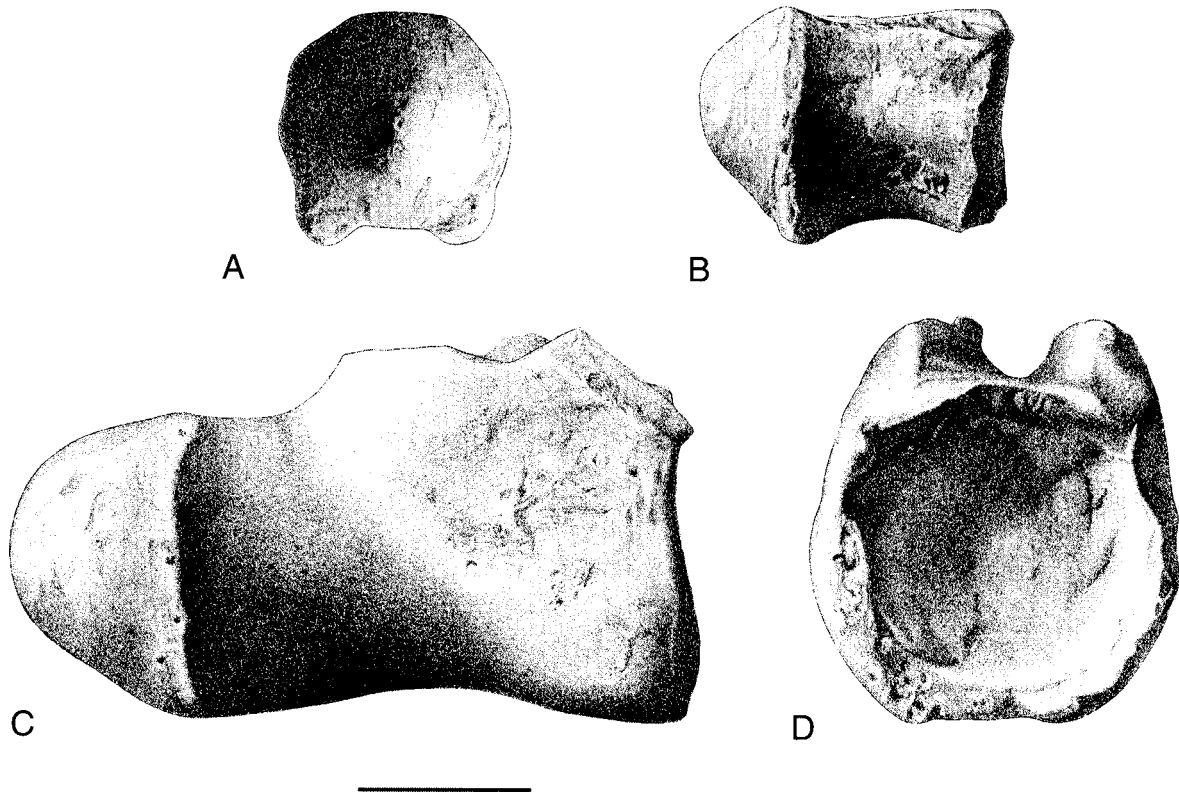


Figure 5 *Titanosaurus blanfordi*. Two distal caudal vertebrae in posterior (A), right lateral (B & C), and anterior (D) views. From Lydekker (1879: pl. 5, figs 1, 2, 4 & 5). Although both were described simultaneously and were considered types, the shorter vertebra (A & B) was formally removed from the type by Huene (1929:90–91). The longer one (C & D) now represents the holotype. A was originally published upside down; it has been inverted in this figure. Scale bar = 10 cm.

caudal vertebra, fragmentary chevrons and ribs, scapulae, partial forelimb and sternal plate fragment – none of which overlap the type *Titanosaurus* mid-caudal vertebrae. As noted above, field associations suggest that some of these elements pertain to one individual. The type species of *Antarctosaurus* is *A. wichmannianus* (Huene 1929), a controversial Argentine taxon known from a partial mandible, partial braincase and fragmentary postcranial skeleton (MACN 6904). Several authors have regarded *A. wichmannianus* as a titanosaur (Huene 1929; Powell 1986; Salgado & Calvo 1997), whereas others have suggested that at least some elements are diplodocoid (McIntosh 1990:401; Jacobs *et al.* 1993; Sereno *et al.* 1999:1344; Upchurch 1999:118). The only cladistic analysis that explicitly examined its relationships placed *A. wichmannianus* within Diplodocoidea, although it clusters within Titanosauria in suboptimal trees slightly longer than the most parsimonious tree (Upchurch 1999). This phylogenetic instability stems from an unusual combination of character states that could be a genuine aspect of sauropod evolution, but it more probably represents an incorrect association of specimens from more than one taxon (Upchurch 1999:118).

There may have been practical reasons for this seemingly impractical referral of Indian material to a South American genus rather than to the pre-existing Indian genus found in the same horizon (i.e. *Titanosaurus*) or to a new genus altogether. Firstly, *Antarctosaurus wichmannianus* was the only other titanosaur braincase known at the time and Huene had described it. None of the new Indian material could be compared with the type series of *T. indicus*,

but it shared several elements in common with *A. wichmannianus* (i.e. braincase, scapula, humerus, radius). Because of the paucity of titanosaur remains known at the time, Huene & Matley (1933) could not have known the generality or specificity of the characteristics they deemed worthy of uniting the two taxa (see ‘Obscured’ features, below). Secondly, Lydekker set a precedent for recognising common genera across Gondwana by identifying *Titanosaurus* species in Madagascar and South America. Huene (1929) had already followed suit in distinguishing the South American genus *Laplataosaurus* in Madagascar. In this context, discovery of South American taxa in India was not extraordinary. To Huene, this larger southern community of dinosaurs could be explained by a Mesozoic land bridge: ‘in Cretaceous, and especially in upper Cretaceous time, South America had a communication with south-eastern Asia [i.e., India] via Antarctica, the Australian region and the Sunda archipelago’ (Huene & Matley 1933:72).

Huene & Matley (1933:15) bolstered their grouping of the Indian and South American material in the genus *Antarctosaurus* with specific similarities between the braincases only (e.g. small supratemporal fenestra, median bulge in frontals). They identified no postcranial characteristics uniting *A. wichmannianus* and *A. septentrionalis* to the exclusion of other taxa, noting only features ‘very characteristic of all Titanosaurs’ (Huene & Matley 1933:21). Their basis for referral, then, rests solely on braincase features that were ambiguous at the time of publication. Several authors have identified differences between the South American and

Indian *Antarctosaurus* braincases, including the large, unfloored pituitary opening in *A. septentrionalis* (Berman & Jain 1982; Hunt *et al.* 1994; Chatterjee & Rudra 1996). Huene also recognised this disparity but attributed it to maturity, noting that ‘the difference between the Indian skull and that of *Antarctosaurus wichmannianus*, in reference to the hypophyseal fossa, does not mark a difference between species, because in ontogenetic evolution each tetrapod passes through a state of a hypophyseal fossa without a floor . . .’ (1929:193, translated from the Spanish). This 1929 reference to the then undescribed Indian material indicates that Huene was familiar with at least some of the Indian remains he would later describe with Matley in 1933. Other differences exist between the two *Antarctosaurus* braincases, however, including the shape of the occipital condyle and the development of the transverse parietal crest. In addition, morphological differences can be observed in the referred postcranial elements (e.g. length and shape of the scapular blade) that cast doubt on their membership in the same genus (McIntosh 1990:397).

These differences speak of more than a specific distinction between the Indian and South American form and outweigh their observed similarities, many of which appear to have a more general distribution among titanosaurs. Current evidence therefore supports McIntosh’s (1990) removal of the *A. septentrionalis* material from *Antarctosaurus*. The constituency of Indian ‘*Antarctosaurus septentrionalis*’ material requires further revision. (Here and elsewhere in this paper, formal taxa that have been determined to be invalid appear in inverted commas.)

cf. *Titanosaurus indicus*

Three additional braincases have been described from the infratrappean horizons of India since Matley’s discoveries (Berman & Jain 1982; Chatterjee & Rudra 1996). Each provenes from a separate locality: one from Dongargaon, near Pisdura, a second from Bara Simla and a third from the western state of Gujarat (Fig. 1). Of these, only the Bara Simla braincase (ISI R162) was reported to have been associated with postcranial remains; unfortunately this association was not mapped and the postcrania were not described (Chatterjee & Rudra 1996:513). Until such documentation appears, this new Bara Simla braincase will be considered an isolated discovery.

Differences observed in the four reported Indian braincases indicate at least two sauropod taxa in the Cretaceous of India, in agreement with the diversity exhibited in postcranial morphology. Consequently, Indian sauropod braincases have been informally referred to the ‘*Antarctosaurus*’ and ‘*Titanosaurus*’ morphs. The basis for this division was initiated by the informal referral of the Dongargaon braincase to *T. indicus* (Chatterjee & Rudra 1996:516), citing a personal communication from Jain. Previously, Jain (1989:100) had remarked that ‘skeletal material from the site [Dongargaon], especially the vertebrae, resembles that of *Titanosaurus indicus*’, but he did not formally refer the braincase to *Titanosaurus* nor identify an association between it and the postcranial remains found at the locality. Later, Jain & Bandyopadhyay (1997:131) claimed that ‘Our present view based on extensive excavation of the site and examination of the material from Dongargaon, has led [us] to conclude that all this material belongs to *T. colberti*’. The Dongargaon braincase, however, does not appear on the map of the

T. colberti skeleton (Jain & Bandyopadhyay 1997: fig. 2) and cannot be considered associated with the skeleton. In the absence of evidence of association, the Dongargaon braincase, as well as the related braincase from Bara Simla, cannot at this point be referred to *T. indicus*.

One titanosaur at Bara Simla?

There is no duplication of postcranial elements among the remains described by Huene & Matley (1933) from the ‘Sauropod bed’ at Bara Simla. The five caudal vertebrae pertain to slightly different regions of the tail; the only paired elements are the right and left scapulae, which are of approximately equal size and proportions; the right radius and ulna are approximately the same length; the fibula appears to have been somewhat longer than the tibia. Additionally, the forelimb proportions observed in ‘A.’ *septentrionalis* lie well within the range seen in other sauropods and most closely resemble those of titanosaurs such as *Phuwiangosaurus* and *Opisthocoelicaudia*. For example, Huene & Matley (1933) state that the radius : humerus length ratio would have to be 0.58 in ‘A.’ *septentrionalis*, although the typical value for sauropods is higher (c. 0.67). Table 2 clearly indicates that the ratios found in more primitive sauropods do not characterise titanosaurs, which have lower values as a result of relative shortening of the radius. It is noted here that Gilmore (1946:38) incorrectly reports the length of the humerus of the ‘Indian specimens’ as ‘1034’ mm, rather than its true length (1340 mm). Consequently, the values for the ulna : humerus (0.76) and radius : humerus (0.75) ratios are also incorrect and should be 0.59 and 0.58, respectively.

One of the differences between ‘A.’ *septentrionalis* and *T. indicus* noted by Huene & Matley (1933) is that the former has more slender limb proportions than the latter. The only limb elements assigned to *T. indicus* at the time were the tibia and fibula from the Bara Simla ‘Sauropod bed’. Given that the type material of *T. indicus* is two middle caudals, however, Huene & Matley’s identification of these limb elements seems arbitrary and unjustified. Furthermore, Huene & Matley only assigned forelimb elements to ‘A.’ *septentrionalis*, making direct comparisons of element robustness between this taxon and *T. indicus* impossible. Table 3 summarises estimates of limb bone robustness for a variety of well-preserved sauropod skeletons. It is clear from these data that forelimb elements of ‘A.’ *septentrionalis* and the hindlimb elements of *T. indicus* could potentially belong to a single individual.

Conclusion

The absence of detailed field records, combined with poor preservation of the elements, means the exact associations of sauropod material at Bara Simla will always remain confused and controversial. The discussion above, however, demonstrates that Huene & Matley’s (1933) decision to separate the ‘Sauropod bed’ specimens into several individuals from two taxa is not supported by the available evidence. It is possible that only one individual was present, as originally suggested by Matley (1921). Even if more than one individual is represented, two or more taxa cannot yet be reliably distinguished. However, although morphological and geological data do not argue against the presence of a single species at Bara Simla, there is simply no positive evidence supporting this hypothesis.

Table 2 Radius/humerus proportions in selected sauropod genera.

	Taxon (source)	Radius length	Humerus length	Radius/humerus
NN	<i>Shunosaurus lii</i> (ZDM T5401; Zhang 1988)	600	664	0.90
	<i>Omeisaurus tianfuensis</i> (ZDM T5701; He <i>et al.</i> 1988)	780	984	0.79
	<i>Cetiosauriscus stewarti</i> (BMNH 3078; Woodward 1905)	760	940	0.81
	<i>Tehuelchesaurus benitezii</i> (MPEF-PV 1125; Rich <i>et al.</i> 1999)	750	1140	0.66
D	<i>Apatosaurus louisae</i> (CM 3018; P.U. pers. obs.)	775	1150	0.68
	<i>Diplodocus longus</i> (AMNH 5855; P.U. pers. obs.)	537	755	0.71
	<i>Rayososaurus tessonei</i> (MUCPv-205; Calvo & Salgado 1995)	610	1017	0.60
M	<i>Brachiosaurus brancai</i> (HMN SII; PU pers. obs.)	1240	2130	0.58
	<i>Camarasaurus lentus</i> (CM 11338; PU pers. obs.)	281	408	0.69
	<i>Cedarosaurus weiskopfae</i> (DMNH 39045; Tidwell <i>et al.</i> 1999)	812	1380	0.59
T	<i>Alamosaurus sanjuanensis</i> (USNM 15560; P.U. pers. obs.)	850	1360	0.63
	' <i>Antarctosaurus</i> ' <i>septentrionalis</i> (Huene & Matley 1933)	780	1340	0.58
	* <i>Rapetosaurus krausei</i> (FMNH PR 2209; Curry Rogers & Forster 2001)	330	450	0.73
	<i>Opisthocoelicaudia skarzynskii</i> (Borsuk-Bialynicka 1977)	631	1000	0.63

All proportions are based on associated remains. All measurements are in mm. Abbreviations: **D** = diplodocoid; **M** = macronarian; **NN** = non-neosauropod; **T** = titanosaur. * indicates a juvenile individual.

Table 3 The robustness of fore and hindlimb elements for various sauropods.

	Taxon (source)	Humerus RI	Radius RI	Tibia RI	Fibula RI
NN	<i>Shunosaurus lii</i> (ZDM T5401; Zhang 1988)	0.27	—	—	—
	<i>Omeisaurus tianfuensis</i> (ZDM T5701; He <i>et al.</i> 1988)	0.30	0.18	0.30	—
	<i>Cetiosaurus oxoniensis</i> (Upchurch & Martin, in press)	0.30	—	0.28	—
	<i>Tehuelchesaurus benitezii</i> (MPEF-PV 1125; Rich <i>et al.</i> 1999)	0.31	0.14	—	—
D	<i>Amargasaurus cazaui</i> (MACN-N 15; Salgado & Bonaparte 1991)	0.31	0.25	0.26	—
	<i>Apatosaurus louisae</i> (CM 3018; Gilmore 1936)	0.36	0.25	0.31	0.20
	<i>Rayososaurus tessonei</i> (MUCPv-205; Calvo & Salgado 1995)	0.26	0.23	0.28	0.22
M	<i>Brachiosaurus brancai</i> (HMN SII; Janensch 1961)	0.22	0.19	—	—
	<i>Brachiosaurus brancai</i> (HMN St148 [tibia], St149 [fibula]; Janensch 1961)	—	—	0.29	0.20
	<i>Camarasaurus grandis</i> (YPM 1901; Ostrom & McIntosh 1966)	0.29	0.20	—	—
	<i>Camarasaurus grandis</i> (YPM 1905; Ostrom & McIntosh 1966)	—	—	0.20	0.17
	<i>Cedarosaurus weiskopfae</i> (DMNH 39045; Tidwell <i>et al.</i> 1999)	0.21	0.16	0.21	—
T	' <i>Antarctosaurus</i> ' <i>septentrionalis</i> (Huene & Matley 1933)	0.24	0.21	—	—
	<i>Opisthocoelicaudia skarzynskii</i> (Borsuk-Bialynicka 1977)	0.37	0.32	0.30	0.25
	<i>Phuwiangosaurus sirindhornae</i> (Martin <i>et al.</i> 1994, 1999)	0.25	—	—	—
	<i>Titanosaurus indicus</i> (K20/321 [tibia], K27/489 [fibula]; Huene & Matley 1933)	—	—	0.30 ^e	0.21 ^e

The Robustness Index (RI) was calculated as follows: RI = (average of the greatest widths of the proximal end, mid-shaft and distal end of the element/length of the element). ^e indicates estimated values. Abbreviations: **D** = diplodocoid; **M** = macronarian; **NN** = non-neosauropod; **T** = titanosaur.

SPECIES OF *TITANOSAURUS*

A total of 14 species of *Titanosaurus* have been named from five continental landmasses since Lydekker coined the genus in 1877. The provenance, holotypic remains and describing author for each species of *Titanosaurus* are summarised in Table 4. Below, we discuss the relationships of each species to other sauropods, the diagnostic (autapomorphic) features present in the type of each species additional remains referred to the species and the referrability of each species to the genus *Titanosaurus*, based on comparisons with its type species, *T. indicus*.

India

In his posthumous memoirs, Falconer (1868) described and illustrated the first sauropod bones from India. These

fragmentary remains later formed the basis for a new genus and species that Lydekker (1877) dubbed *Titanosaurus indicus*. Since that time, three new *Titanosaurus* species have been named from Late Cretaceous-aged horizons from central and western India (Fig. 1, Table 4).

Titanosaurus indicus

Falconer (1868) described two caudal vertebrae that can be placed in the middle third of the tail, based on the absence of transverse processes and the presence of neural arches (Fig. 4). Although he did not discuss their affinities, he recognised three diagnostic features in the two caudal vertebrae: strong procoely with the greatest convexity at the axis of the centrum, chevron facets at both ends of the centrum and a lack of prezygapophyseal facets. Later, Lydekker (1877) established the sauropod nature of the caudal vertebrae and

Table 4 Provenance, holotype and reporting author for all *Titanosaurus* species.

Area	Species	Holotype	Age	Reference
I	<i>T. indicus</i>	2 caudal vertebrae	Late Cretaceous (Maastrichtian)	Lydekker (1877)
	<i>T. blanfordi</i>	2 caudal vertebrae	Late Cretaceous (Maastrichtian)	Lydekker (1879)
	<i>T. rahioliensis</i>	Teeth	Late Cretaceous (Maastrichtian)	Mathur & Srivastava (1987)
	<i>T. colberti</i>	Partial skeleton	Late Cretaceous (Maastrichtian)	Jain & Bandyopadhyay (1997)
SA	<i>T. australis</i>	6 caudal vertebrae	Late Cretaceous (Campanian)	Lydekker (1893)
	<i>T. nanus</i>	Cervical vertebra, dorsal vertebra	Late Cretaceous (Campanian)	Lydekker (1893)
	<i>T. robustus</i>	2 ulnae, radius, femur	Late Cretaceous (Campanian)	Huene (1929)
	<i>T. araukanicus</i>	Tibia, fibula	Late Cretaceous (Campanian)	Powell (1986)
	<i>T. sp.</i>	Caudal series	Late Cretaceous (Maastrichtian)	Huene (1929), Powell (1987)
MA	<i>T. madagascariensis</i>	Caudal vertebrae	Late Cretaceous (Maastrichtian)	Depéret (1896)
AS	<i>T. falloti</i>	Femur		Hoffet (1942)
EU	<i>T. valdensis</i>	2 caudal vertebrae	Early Cretaceous (Barremian)	Huene (1929)
	<i>T. lydekkeri</i>	Caudal vertebra	Late Cretaceous (Cenomanian)	Huene (1929)
	<i>T. dacus</i>	Caudal vertebra	Late Cretaceous (Maastrichtian)	Nopcsa (1915)
	cf. <i>T. sp.</i>	Vertebrae, femur	Late Cretaceous	Depéret (1899)
	cf. <i>T. indicus</i>	Caudal vertebrae, various limb bones	Late Cretaceous (Maastrichtian)	Lapparent (1947)

Abbreviations: AS = Asia; EU = Europe; I = India; MA = Madagascar; SA = South America.

identified them and an isolated femur as the new species *T. indicus*. As mentioned above, the femur was shown to be from a different horizon than the vertebrae (Matley 1921) and was formally removed from the type series (Huene & Matley 1933). In his diagnosis, Lydekker noted that *T. indicus* could be distinguished from the English sauropods *Pelorosaurus* and *Cetiosaurus* on the basis of five features: (i) procoelous caudal vertebrae in which the neural arches were placed on the anterior half of the centrum, (ii) double chevron facets, (iii) centrum with a longitudinal ventral furrow bounded by chevron ridges, (iv) squared centrum cross-section and (v) cylindrical, elongate prezygapophyses. Shortly thereafter, Lydekker (1879:20) added a sixth diagnostic feature of *T. indicus*, 'a pair of ridges which run from near the middle of the bone to the four angles of the inferior surface, in each case running from near the centre to the periphery of this surface'. Below we discuss the current status of each of these six features.

Since the discovery of *Titanosaurus*, numerous titanosaur and non-titanosaur taxa have been described with procoelous caudal vertebrae. For example, diplodocoid sauropods have procoelous centra in the proximal portion of the tail (e.g. *Dicraeosaurus*; Janensch 1929: pl. 3, fig. 2), as does the non-neosauropod *Mamenchisaurus* (Young & Zhao 1972: figs 8–10). Procoely extending into the middle third of the tail, as is preserved in *T. indicus*, is restricted to titanosaurs. All but basal-most titanosaurs bear this type of caudal centra (*Andesaurus*: Calvo & Bonaparte 1991; *Malawisaurus*: Jacobs *et al.* 1993). Procoely extending into the middle third of the tail discriminates paraphyletic basal 'andesaurids' from derived 'titanosaurids' (Bonaparte & Coria 1993; Salgado *et al.* 1997).

Double chevron facets, the longitudinal ridges leading to them and the ventral furrow they bound are likewise known in taxa other than *T. indicus*. The diplodocids *Barosaurus* (YPM 1929; HMN dd357) and *Diplodocus* (Osborn 1899:205; AMNH 223) have quite well developed chevron ridges that parallel one another and enclose an elongate, ventral hollow. These features are synapomorph-

ies of diplodocines (Wilson 2002), although they also occur in distantly related forms such as titanosaurs. Chevron ridges of varied length and thickness bound ventral fossae of different depth in several titanosaurs, including *Ampelosaurus* (MDE C3813) *Saltasaurus* (Powell 1992: fig. 23), *Alamosaurus* (USNM 15560), and *T. colberti* (Jain & Bandyopadhyay 1997: fig. 13D). Jain & Bandyopadhyay (1997:130) specified that *T. indicus* could be recognised by caudal vertebrae with 'cross ridges on the ventral surface', re-prising Lydekker's (1879) diagnostic feature. The type caudal vertebrae, however, bear no true cross ridges (i.e. diagonally oriented, intersecting) on the ventral surface of the centrum. Rather, the chevron ridges are longitudinal and approach one another as a consequence of the constriction of the vertebra at midlength (Fig. 4A). The degree to which the centra are constricted probably varies along the length of the tail.

The squared cross-section of *T. indicus* mid-caudal centra is also a feature shared by several sauropod genera. Diplodocid caudal vertebrae have a square to rectangular cross-section with a well defined edge separating the flat ventral and lateral surfaces of the centrum (e.g. *Diplodocus*: Osborn 1899: pl. 28). This feature has also been reported in an unnamed titanosaur from Peirópolis, Brazil (see '*T. sp.*' below).

Elongate, cylindrical prezygapophyses on middle caudal neural arches are widely distributed among sauropods and do not appear to be diagnostic of any major lineage.

In summary, all six features forwarded by Lydekker in his diagnosis of *T. indicus* are now broadly distributed within Titanosauria. Of these, some are unique to Titanosauria or its subgroups, whereas others are found in other sauropod lineages as well. Because no diagnostic characters could be identified, *T. indicus* must be regarded as a *nomen dubium*.

Titanosaurus blanfordi

Lydekker (1879) named a second *Titanosaurus* species from two caudal vertebrae from Pisaura (Fig. 1) that were collected by their namesake, W. T. Blandford. Lydekker did not designate either vertebra the holotype, so together these two

vertebrae represent the type series of *T. blanfordi* (Fig. 5). Most of Lydekker's comparisons focused on the larger, better preserved vertebra (Figs 5C & D), which he allied with *Titanosaurus* by virtue of 'being extremely procœlous, and in having the neural arch confined to the anterior half of the centrum' (1879:22). He considered it a species apart from '*T. indicus*' by the lack of a median ventral furrow and the cylindrical (rather than square) cross-section of its centrum (Figs 5C & D). It is unlikely that either of these features can be ascribed to variation along the length of the tail, but this cannot be assessed in the absence of more complete remains. Although these features may differentiate the two taxa, both are variable among sauropods and cannot stand alone as diagnostic features for a genus or species.

The second, smaller vertebra (Figs 5A & B) has considerably different proportions than the first – its length-to-height ratio is much less than that of the larger vertebra (L:H = 1.3 versus 2.4). These differences were noted by Huene (1929) and formed the basis for his referral of the shorter vertebra (Figs 5A & B) to the species *Laplataosaurus madagascariensis*, leaving only the larger vertebra as the holotype (by monotypy) of *T. blanfordi*. The justification for this decision is reproduced below (Huene 1929:90–91, translated from the Spanish):

The other Indian species, *Titanosaurus Blanfordi* of Pisdura, originates from the same beds as the former [*T. indicus*] and is characterised by vertebrae lacking compression, being somewhat wider than tall. I found that the two vertebrae carefully reproduced and described [by Lydekker] not only can be distinguished from *Titanosaurus indicus*, but also from each other – in spite of pertaining to a similar caudal region – so that they cannot be considered as pertaining to the same species either. The vertebra from plate V, figures 4 and 5 [Figs 5C & D] is very similar to *Titanosaurus indicus*, only not displaying the compression and being relatively more elongate; to this I would like to limit the determination of Lydekker: *Titanosaurus Blanfordi*. The considerably smaller vertebra (pl. V, figs 1 and 2; [Figs 5A & B]) has in common with the latter the subcylindrical cross-section, but is relatively shorter, although pertaining to a similar caudal region . . . it can be differentiated even more from the former (*Blanfordi*) and from the *indicus*, than can these two from each other. Its construction is like that of the caudals of *Laplataosaurus*. Following the plate, the similarity with cf. *Laplataosaurus madagascariensis* is very great . . . I regard the vertebra reproduced by Lydekker (loc. cit., pl. V, figs 1–2) as «probably pertaining to cf. *Laplataosaurus madagascariensis* (Depéret)». [original italics]

Huene & Matley (1933:37, 39) accepted Huene's (1929) taxonomic rearrangement in their description of new remains from India. Nevertheless, they repeat Lydekker's mistake by referring to *T. blanfordi* additional caudal centra that have short proportions and a median ventral furrow (Huene & Matley 1933: pl. 8, fig. 1). Huene & Matley (1933:38) explain away these obvious discrepancies between holotype and referred remains as the result of their different positions in the series, which they ascribed to caudal 18–20 and caudal 8–10, respectively. Position and variation in the caudal series, however, cannot be discerned from two isolated caudal vertebrae. In addition, they referred a metacarpal fragment, a partial tibia and possible scapular fragment to *T. blanfordi*, none of which overlap the holotype caudal vertebra (Table 1; Huene & Matley 1933: pl. 7, fig. 3;

fig. 26). Of these, only the distal tibia, which is broadly expanded transversely, bears features allying it to titanosaurs in general, although not to *Titanosaurus* in particular. Referral of the tibia to *T. blanfordi* was based on 'a size which might possibly be in agreement with' the referred caudal vertebra 8–10 discussed above (Huene & Matley 1933:38). This cannot be justified. As neither the caudal nor the appendicular remains are here regarded as appropriately referred to *T. blanfordi*, the validity of the species will be judged solely on the basis of the holotype caudal vertebra (Figs 5C & D).

The holotype *T. blanfordi* caudal centrum lacks transverse processes but has neural arch pedicles, suggesting it was positioned somewhere in the middle third of the tail. It is more than twice as long as it is tall and strongly procœlous. The posterior convexity is hemispherical, with its main axis located just dorsal to the midline. The transverse and dorsoventral diameters of the anterior centrum face are subequal, in contrast to the taller proportions of '*T. indicus*' (Fig. 4C). The neural arches are shifted to the anterior extreme of the dorsal aspect of the centrum and there are no chevron facets on the ventral aspect of the centrum. The proportions and morphology of this caudal vertebra closely resemble those of other titanosaurs, including *Pellegrinisaurus* (Salgado 1996: fig. 7), *Titanosaurus australis* (Huene 1929: pl. 8, fig. 1; see below) and *Gondwanatitan* (Kellner & Azevedo 1999: fig. 15). Although its proportions are identical to none of these, the differences between *T. blanfordi* and other titanosaurs are within the expected range of variation along the tail in a single individual. Because no autapomorphies are displayed in the holotypic caudal vertebra of *T. blanfordi*, it cannot be considered a valid taxon.

Titanosaurus rahioliensis

India's first dinosaur eggs and egg clutches were discovered by the Geological Survey of India (GSI) near the village of Rahioli in Gujarat, adjacent to the mouth of the Narmada River (Fig. 1; Mohabey 1984; Srivastava *et al.* 1986). The egg-bearing limestone horizon at Rahioli corresponds to the 'Main Lameta Limestone' at Bara Simla (Fig. 2; Khosla & Sahni 1995). Palaeohistological studies of eggshell microstructure have recognised several different parataxa in the Lameta Formation, indicated that the Indian eggshells are dinosaurian and suggested that they are derived from a titanosaur (Mohabey 1996, 2001). Recent discoveries of associated titanosaur bones and eggshells in Patagonia have supported this hypothesis (Chiappe *et al.* 1998). Further GSI investigation in the Rahioli area led to the discovery of a rich pocket of sauropod bones (Mathur & Pant 1986; Mohabey 1987, 1989) and sauropod and theropod teeth (Mathur & Srivastava 1987) in the conglomeratic and calcareous sandstone above the 'Main Lameta Limestone'. The Rahioli area was made a National Park by the Geological Survey of India in 1983 (Sahni 2001).

Few of the dinosaur bones from Rahioli have been described and only the teeth have been named so far. These include several narrow-crowned sauropod teeth that were designated (?) *T. rahioliensis* (GSI 19,997–20,007; Mathur & Srivastava 1987:564). These teeth were 'tentatively placed in the sauropod genus *Titanosaurus* – the characteristic Upper Cretaceous sauropod genus from Madhya Pradesh and the study area', but no claim was made for any association with postcranial remains (Mathur & Srivastava 1987:564).

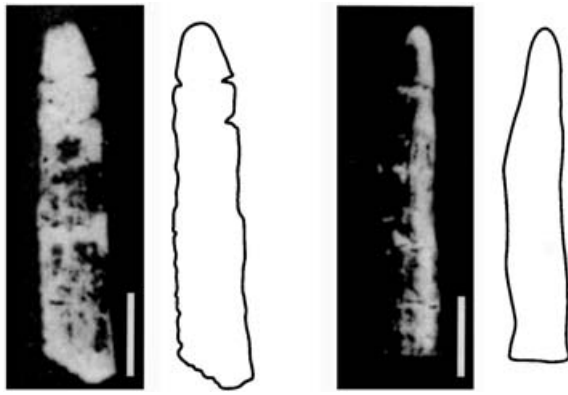


Figure 6 (?)*Titanosaurus raholiensis*. Two views of an isolated tooth (GSI 20,006), designated one of holotypic series by Mathur & Srivastava (1987: pl. 3, fig. 6a, b). Scale bar = 5 mm. This is the only published image of this species; the original materials are no longer available. Interpretive line drawings accompanying the photos indicate the approximate outline of the tooth.

Currently there is no basis for referral of these teeth to *Titanosaurus* in particular, although their distinctive morphology may allow future discoveries to link them to a particular Indian sauropod genus.

Mathur & Srivastava (1987: pl. 3, figs 3–8) provided photographs for each different tooth of (?)*T. raholiensis*, which can no longer be located in the type collection of the GSI in Kolkata (A. Banerji, pers. comm.). One photograph is reproduced here along with a coarse outline drawing (Fig. 6). Although this image is not the ideal means by which to recognise the detailed features described below, it is the best image available. The teeth are slender and slightly arched along their length, attaining a D-shaped cross-section towards their apex. The crown bears faint longitudinal ridges and reduced enamel on one side. It is unclear whether the labial or the lingual surface has reduced enamel because the authors specify the 'labial side with reduced enamel' in one instance, but later refer to '... the lingual side where the enamel is thin' and '... the inherent character of having reduced enamel on the lingual face of the crown' (Mathur & Srivastava 1987:564). S. Srivastava (pers. comm.) has confirmed that the enamel is reduced on the lingual surface of the tooth. The only other occurrence of asymmetrical enamel among sauropods is in *Nigersaurus* (also reduced lingually), the slender-crowned rebbachisaurid diplodocoid from the Early Cretaceous of Niger (Serenó *et al.* 1999: fig. 2).

Lacking any connection to postcranial elements, (?)*T. raholiensis* cannot be referred to *Titanosaurus*. Its similarities to the diplodocoid *Nigersaurus* indicate that referral of the Indian teeth to a particular sauropod subgroup awaits further discoveries. (?)*T. raholiensis* is here considered an indeterminate neosauropod on the basis of its slender crowns lacking denticles.

Titanosaurus colberti

The recently described partial skeleton of *T. colberti* from Dongargaon (Figs 1 & 7) represents one of the few Indian dinosaurs known from associated remains (Jain & Bandyopadhyay 1997). Based on a partial axial column, pectoral and pelvic girdles and a forelimb lacking the manus

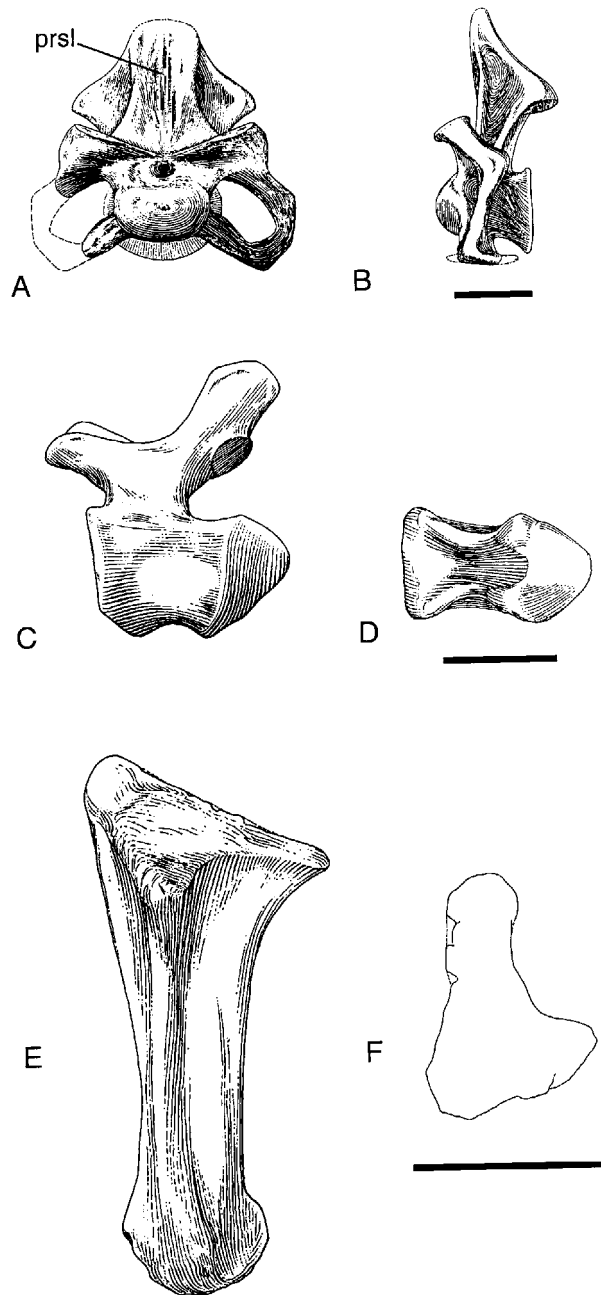


Figure 7 *Titanosaurus colberti*. Elements of the holotypic partial skeleton ISI R335. Middle cervical vertebra in anterior (A) and left lateral (B) views; middle caudal vertebra in left lateral (C) and ventral (D) views; right ulna in lateral (E) and proximal (F) views. prsl = prespinal lamina. Scale bar = 20 cm for A and B, 10 cm for C and D and 25 cm for E and F. From Jain & Bandyopadhyay (1997: figs. 4A, 4C, 12C, 12D, 22A).

(ISI R335/1-65) whose association is mapped, *T. colberti* can be distinguished from all other sauropods on the basis of several autapomorphic features (see Implications for Titanosaur Systematics, below).

In addition to describing this excellent specimen, Jain & Bandyopadhyay (1997) reviewed the history of titanosaur discoveries in India and discussed the relationship of *T. colberti* to other titanosaur species. Their revision of Indian

titanosaur systematics makes three important points that we discuss below.

Firstly, they designated '*Antarctosaurus septentrionalis*' a junior synonym of '*Titanosaurus indicus*' '[b]ecause of the absence of any significant differences between these two forms' (Jain & Bandyopadhyay 1997:128). It is true that there is little disagreement between the preserved elements at Bara Simla, both in terms of duplicate elements and elements that articulate with one another, as discussed above (see One Titanosaur at Bara Simla?, above). However, this is a poor sample from which to determine variation – the skeletal elements that have been recovered (long bones, caudal vertebrae) generally display less morphological variation than more complex elements such as presacral vertebrae, which have not yet been described from Bara Simla. However compelling the lack of morphological conflict among the elements recovered from Bara Simla, it cannot form the basis for their incorporation as a single species. Ascribing all remains from Bara Simla to a single species not only will create a potentially unnatural assemblage, it also forces future discoveries of presently unknown elements to be referred to it.

Secondly, Jain & Bandyopadhyay (1997:131) claimed four valid Indian sauropod species – '*T. indicus*', '*T. blanfordi*', '*T. madagascariensis*' and '*T. colberti*'. This tally differs with that of Chatterjee & Rudra (1996), who recognise only one species, '*T. indicus*'. Diagnostic features for '*T. indicus*', '*T. blanfordi*' and '*T. madagascariensis*' 'rest mainly on the shape of the midcaudal centra (flat-sided, cylindrical, or squarish)', respectively (Jain & Bandyopadhyay 1997:129). '*T. colberti*' was distinguished from other *Titanosaurus* species by the lack of these and other distinguishing features and its prominent caudal prezygapophyses. As discussed above (see *T. indicus*, above) these features indicate the presence of multiple taxa, but they cannot function as diagnoses for these species because their distribution is too general within Neosauropoda.

Thirdly, in the final section of their paper, Jain & Bandyopadhyay (1997:134) present a revised diagnosis of the genus *Titanosaurus* that employs 20 characters:

Large advanced sauropods with strongly procoelous caudals throughout the series; cervicals and dorsals opisthocoelous with well-marked pleurocoels; transverse processes of cervicals robust, directed laterally, very wide posteriorly in shoulder region; transverse process in dorsals narrow and directed outward and a little upward; neural spine not bifid, directed posteriorly; sacrum with six co-ossified vertebrae and ribs; first and sixth sacral centra convex anteriorly and posteriorly respectively; midcaudal and part of distal caudals with prominent variable chevron facets; robust prezygapophyses extending to the anterior margin of the caudals; first sacral rib extended outward below the iliac blade; preacetabular process of the ilium projecting outward becoming almost horizontal; bladelike ischium transversely expanded in the middle; shaft of slender radius perpendicular to the axis of the expanded distal ends; ulna robust and triangular in cross section; humero-femoral ratio 0.74; tibio-femoral ratio 0.65; femur without any lateral prominence; moderate development of nuchal crest of braincase; transverse ridge on parietal; high buttress ridge below the paroccipital process.

Of these, only two features can be scored in all four taxa; the majority of features apply only to *T. colberti*. More

importantly, however, only one of these characters, 'transverse processes of cervicals robust . . . very wide posteriorly in shoulder region', could be useful as a diagnostic feature of a genus or species, but this feature is known only from referred remains. The 19 other characters have generalised distributions that apply to Titanosauria, Macronaria, Neosauropoda and Eusauropoda. Single spines, for example, are widely distributed among sauropods.

The associated remains of *T. colberti* overlap with the type caudal vertebrae of '*T. indicus*'. As Jain & Bandyopadhyay (1997:130) indicate, these differ in important ways (e.g. shape of centrum, prominence of chevron facets). These authors do not, however, give their reasoning for considering them congeneric. In fact, there is little evidence on which to base this referral. Although we consider *T. colberti* to be a valid species (see below), it cannot be placed in the genus *Titanosaurus*.

South America

Constructed in 1884, the provincial museum in La Plata, Argentina housed 'unrivalled treasures . . . collected within the last few years by the untiring energy of its Director [Dr. F. P. Moreno]' (Lydekker 1894:2–3). Twice between 1893 and 1894, Lydekker visited the La Plata Museum to study these fossils, which included Cretaceous-aged dinosaur bones from Neuquén, Chubut and Santa Cruz districts (Anonymous 1896; Fig. 8). Lydekker (1893) referred some of these remains to two new species of *Titanosaurus*, a genus he had recognised from India only 16 years earlier. Lydekker identified several features that the new species (*T. australis*, *T. nanus*) and new genera (*Argyrosaurus*, *Microcoelus*) shared with sauropods from India. On the basis of these features, Lydekker (1893:3) provisionally defined Titanosauridae as 'Sauropodous Dinosaurs in which the caudal vertebrae, with the exception [*sic*] of the first, are procoelous, the presacrals opisthocoelous, and the lumbar without lateral cavities; the superior extremities of the chevron-bones being open'. Of these features, only procoelous caudal vertebrae appear to have been unique to '*T. indicus*' and the South American forms. However, the presence of this feature in *Argyrosaurus* was based on referral of 'two enormous posterior caudal vertebrae from Santa Cruz, which agree in colour and mineral composition with the foregoing femur [from the Río Senguerr]' (Lydekker 1893:11). This referral, however, is problematical because both specimens were found quite far from the sediments of Río Chubut that produced the articulated forelimb upon which Lydekker based the genus (Fig. 8). The observation that 'lumbar' (i.e. posterior dorsal) vertebrae lack pleurocoels resulted from a misidentification of two caudal vertebrae, which lack lateral cavities (Lydekker 1893:6, plate 2, figs 1–2). A correctly identified 'lumbar' bears a small lateral opening, or pleurocoel, confirming their presence in this region of the dorsal column (Lydekker 1893: pl. 2, fig. 3; 6). It is surprising that Lydekker regarded open chevrons as unique to Titanosauridae, because this character had already been described in the British genus *Cetiosaurus* (e.g. Phillips 1871: fig. 59). Similarly, presacral opisthocoely was known in other sauropods described prior to the time of his writing, such as *Camarasaurus* (Cope 1878: fig. 9).

In 1921, after a more than 30-year hiatus, the director of the Museo La Plata (Dr. L. M. Torres) resumed exploration



Figure 8 *Titanosaurus* localities – South America. Inset map of Argentine Patagonia identifies *Titanosaurus*-bearing sites in Neuquén, Río Negro, Chubut and Santa Cruz Provinces. White dots within rectangle on large map refer to Cinco Saltos and Santa Cruz. Grey lines = rivers; dotted lines = state or country boundaries. Large silhouette map based on Shupe *et al.* (1992).

of dinosaur-bearing sediments in Patagonia (Huene 1929:1). Between 1923 and 1926, Friedrich von Huene (Fig. 3C) travelled to La Plata to study these new specimens, Lydekker's collection and MACN material collected earlier by Wichmann (1916). Huene (1929) produced a monograph that described new sauropod taxa based solely on new material (*Antarctosaurus*, *Campylodoniscus* [= '*Campylodon*', Steel 1970]), as well as two new taxa (*Laplatasaurus*

araukanicus, *Titanosaurus robustus*) based on revision of specimens allocated to *T. australis* by Lydekker (1893).

The taxonomy of Cretaceous sauropods of Argentina received little attention for 50 years, until it was taken up again by Bonaparte & Gasparini (1979). In addition to better constraining the stratigraphic distribution of South American Cretaceous sauropods, they specified lectotypes for those species in which either none was specified in or none

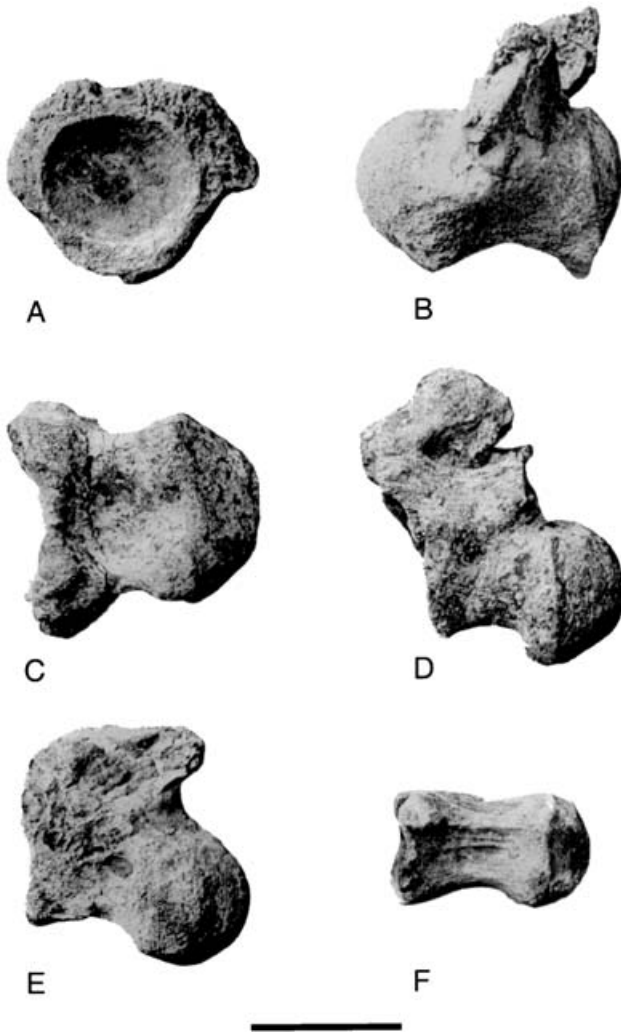


Figure 9 *Titanosaurus australis*. Holotypic series of six caudal vertebrae (MLP 77-V-28-1). **A**, anterior caudal centrum in anterior view; **B**, caudal vertebra 1 in right lateral view; **C**, anterior caudal vertebra in ventral view; **D**, anterior or middle caudal vertebra in left lateral view; **E**, anterior or middle caudal vertebra in left lateral view; **F**, distal caudal vertebra in ventral view. From Lydekker (1893: pl. 1). Scale bar = 10 cm.

was obvious from the works of Lydekker (1893) and Huene (1929).

Powell's (1986) unpublished thesis remains the most recent treatment of South American titanosaurs. Like that of Huene (1929), Powell's work included description of new taxa based on recent discoveries (*Aeolosaurus*, *Epachthosaurus*) and revision of the taxonomy of his predecessors – transferring *T. australis* and *T. robustus* to a new genus (*Neuquensaurus*) and referring Huene's *Laplatasaurus araukanicus* back to *Titanosaurus*.

Lydekker, Huene and Powell's shifting navigation through the morass of titanosaur taxonomy includes confusing switchbacks and dead ends. In the following sections, we introduce and discuss each of the four *Titanosaurus* species in the order in which they were named, reserving judgement on the species for the end of each of these sub-sections. We carry these nomenclatorial decisions into the remaining sub-

Table 5 Holotype and referred remains of *T. australis*, from Lydekker (1893).

Element	Figure	Remarks
Anterior caudal vertebrae	pl. 1 figs 1–3, 5	Holotype
Middle caudal vertebra	pl. 1 fig. 4	Holotype
Posterior caudal vertebra	pl. 1 fig. 6	Holotype
Posterior 'lumbar' vertebrae	pl. 2, figs 1, 2	Referred
Anterior 'lumbar' vertebrae	pl. 2, fig. 3	Referred
Dorsal vertebra	pl. 2, fig. 4	Referred*
Sacrum	pl. 2, fig. 5	Referred
Dorsal vertebra	pl. 3, fig. 4	Referred*
Coracoid	pl. 3, fig. 7	Referred
Ilium fragment	pl. 3, fig. 8	Referred
Humerus	pl. 4, fig. 1	Referred*
Femur	pl. 4, fig. 3	Referred*
Dorsal rib fragment	pl. 4, fig. 4	Referred
Femur	not figured	Referred
Scapula	not figured	Referred
Fragmentary pelvis	not figured	Referred

Plates and figures refer to that work. * indicates elements later referred to *Laplatasaurus araukanicus* by Huene (1929).

sections, where possible including parenthetical reference to earlier terminology.

Titanosaurus australis

Lydekker (1893:4) based *T. australis* on 'a large series of associated vertebrae from Neuquén mostly belonging to a single individual, together with bones of the fore and hind limbs, and some fragments of the pectoral and pelvic girdles. The caudal vertebrae in plate i may, however, be taken as the actual types' (Fig. 9). Other vertebrae referred to the species include an 'anterior lumbar', two (misidentified) 'posterior lumbar', and a sacrum; appendicular remains include a coracoid, scapula, humerus, fragmentary pelvis and two femora (see Table 5). In addition to the figured and described specimens were several that were mentioned but not described. From the above quotation, it is not clear how many individuals were referred to the species – even the series of caudal vertebrae that Lydekker considered the type were only 'mostly' belonging to one individual. If so, referral of appendicular remains is problematical if the 'fragments of the pectoral and pelvic girdles' were not associated with the type caudal vertebrae.

Lydekker noted that the caudal vertebrae of the Patagonian species differed from '*T. indicus*' in their less laterally compressed cross-section and only weakly marked posterior chevron facets. These differences, added to the geographical distance separating the two forms, justified their specific separation. Of the six holotypic vertebrae, only one (Fig. 9F) is from a similar region of the tail as the '*T. indicus*' type vertebra. As shown in ventral view, it lacks the ridges present in '*T. indicus*'. The generic identity of *T. australis*, then, was based on procoelous caudal centra. Although he does not identify any substantial points of difference between the Indian and Patagonian caudal vertebrae, Lydekker (1893:5) acknowledged the tenuity of their congenity:

But it must be borne in mind that the other parts of the skeleton might display points of distinction which would render it

necessary to refer the South American species to a genus apart. Accordingly, the reference of the latter to *Titanosaurus* must be regarded as a more or less provisional measure, rendered necessary by our very incomplete knowledge of the type species; although it is certain that, in any cases the two forms are very closely allied.

Huene (1929:23) regarded *T. australis* as the species 'represented in most abundance in the material of Lydekker and in the discoveries of Cinco Saltos [Fig. 8] in March 1922' (translated from the Spanish). Huene was in part responsible for this abundance, referring four partial vertebral series and numerous limb elements to the species, which formed the basis for the first reconstruction of a titanosaur (Huene 1929: fig. 10). Of the process of referring remains to various species, Huene (1929:23, translated from the Spanish) remarked that:

The numerous bones at Cinco Saltos had been discovered in a way that does not allow determination of which bones pertain to each individual, with the exception of the few series of caudal vertebrae. Various species and various genera are completely intermixed. The separation, sadly, I had to do by examination, and in these cases errors could not be excluded . . . All the material had to be ordered by me in such a way that consideration of its shape, preservation, and comparison resulted in the most natural correlation possible.

Bonaparte & Gasparini (1979) accepted these referrals but noted that only new discoveries could confirm their validity. Additionally, they formally specified the six caudal vertebrae figured by Lydekker (1893: pl. 1), which pertain to MLP 77-V-28-1, as the holotype of *T. australis*.

Likewise, Powell (1986:160) accepted 'the materials referred to this species with little variation from the way they were arranged by Huene (1929)' (translated from the Spanish). However, Powell (1986:81) considered that *T. australis* 'clearly pertains to a genus totally distinct from *Titanosaurus* and more similar in all respects to *Saltasaurus loricatus*, but with differential characteristics that permit proposal of a new genus: *Neuquensaurus*' (translated from the Spanish). Powell (1986) identified several features that distinguish *Neuquensaurus* from *Titanosaurus*, in particular the presence of somphospondylous caudal centra. Powell (1986:162) identified a holotype and provided a diagnosis for *Neuquensaurus*, but nomenclatorial acts in dissertations are not recognised by the International Code of Zoological Nomenclature (ICZN Articles 8 and 9, 1999). *Neuquensaurus* first appeared in published form a year later (Powell 1987), but without explicit reference to its former status as a *Titanosaurus* species. Five years later, Powell (1992:199) referred to *Neuquensaurus* as a replacement for *Titanosaurus* and indicated the two relevant species names elsewhere in that same publication. Because *Neuquensaurus* is a replacement name for an available name (*nomen novum*) rather than a name for new material, Powell (1992) suffices as valid publication for the referral of *T. australis* and *T. robustus* to the replacement genus *Neuquensaurus* as *N. australis* and *N. robustus* (ICZN Article 13.1.3; 1999).

Although he refrained from employing Powell's nomenclature, McIntosh (1990:394) was clearly aware of his work. Unlike Powell (1986) however, McIntosh (1990) found no generic-level differences separating materials assigned to *T. australis*, *T. robustus* and *Saltasaurus loricatus*, but he did consider them distinct species of *Saltasaurus* (i.e. *S. australis*, *S. robustus*, *S. loricatus*). We follow Powell (1992) in recognising genus-level differences amongst these species

(e.g. Wilson 2002: appendix 4), and recommend retaining both *Saltasaurus* and *Neuquensaurus*, with the caveat that further studies investigate whether the lectotype specified by Bonaparte & Gasparini (1979) pertains to a single individual and whether the Cinco Saltos material can be confidently referred to *Neuquensaurus* (= '*Titanosaurus*') *australis*. A review of this species is currently being undertaken by L. Salgado (pers. comm.).

Titanosaurus nanus

Lydekker founded this new species on two articulated presacals (a cervical and a dorsal; MLP. Ly. 18/19), provisionally assigning it to *Titanosaurus* (1893:9). Other than their small size, there is little that distinguishes these vertebrae from others. Powell (1986:91) designated *T. nanus* a *nomen dubium*, remarking that '[T]hese materials are poorly preserved and do not present morphological details that permit their clear differentiation at a generic or specific level' (translated from the Spanish). We accept this determination here and regard *T. nanus* as a *nomen dubium*.

Titanosaurus robustus

Huene (1929:48) recognised *T. robustus* from a subset of elements that Lydekker (1893) assigned to *Neuquensaurus* (= '*Titanosaurus*') *australis* but did not describe, as well as remains collected more recently from Cinco Saltos. The difference between *T. robustus* and *T. australis* ' . . . is based in the first place on the extremities, thigh and leg, arm and forearm . . . represented in Cinco Saltos alongside *Titanosaurus australis*' (Huene 1929:48, translated from the Spanish). Because Huene did not identify a holotype, Bonaparte & Gasparini (1979:397, translated from the Spanish) specified as the lectotype four limb elements that 'apparently pertain to the same individual': a right ulna (MLP 26-250), left ulna (MLP 26-251), left radius (MLP 26-254) and left femur (MLP 26-259). The three forearm elements are of appropriate size and shape to pertain the same individual (Fig. 10). Whether the femur belongs to the same individual cannot be determined (Fig. 11). Because the lectotype does not include caudal vertebrae, comparisons to '*T. indicus*' could not be made.

As mentioned above, Powell (1992) referred both Argentine *Titanosaurus* species to the new genus *Neuquensaurus* (*N. australis* and *N. robustus*). The features Huene (1929) listed as distinguishing the two species were attributed by Powell (1986:179) to either breakage or to comparisons between elements incorrectly referred to the latter species. This and the lack of differences between the two species led Powell (1986:180, 1992:199) to consider *N. robustus* (= '*T. robustus*') a *nomen dubium*.

Like Powell, McIntosh (1990) did not consider *T. robustus* to be generically allied with the Indian *Titanosaurus*, but he did regard it as a distinct species. As mentioned above, McIntosh (1990:395) referred *T. australis* and *T. robustus* to the genus *Saltasaurus*, noting that '[t]he differences between *Saltasaurus* and *Titanosaurus australis* and *T. robustus* . . . are not here deemed of taxonomic importance'.

Based on the uncertainty surrounding elements assigned to *T. robustus*, comparisons to either *Neuquensaurus australis* or *Saltasaurus loricatus* remain tentative. Specifically, further studies are needed to determine whether the lectotype

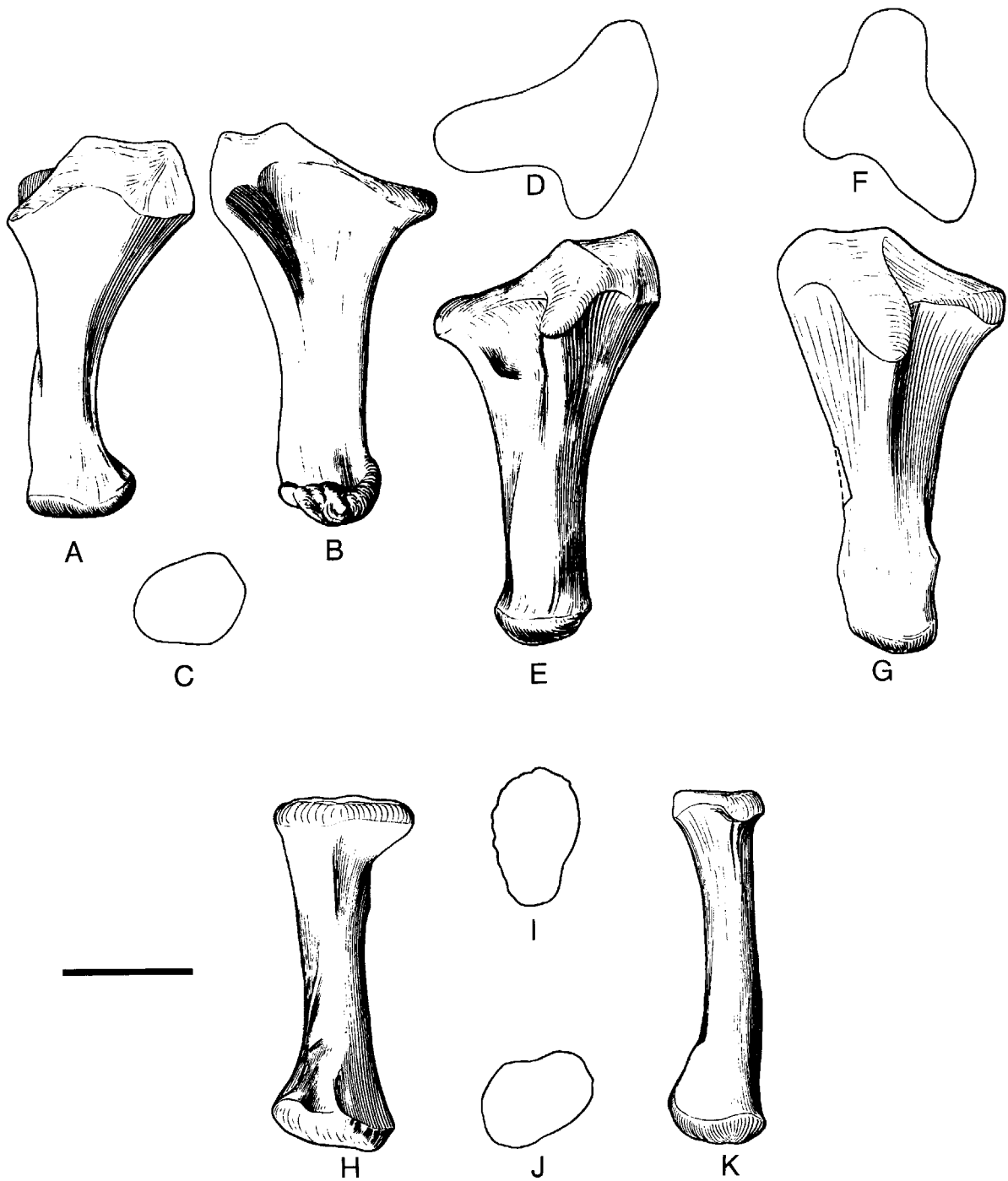


Figure 10 *Titanosaurus robustus*. Lectotype, as specified by Bonaparte & Gasparini (1979:397). Left ulna (MLP 26-251) in posterior (A), medial (B), distal (C), proximal (D) and lateral (E) views. Right ulna (MLP 26-250) in lateral (G) and proximal (F) views. Left radius (MLP 26-259) in medial (H), proximal (I), distal (J) and anterior (K) views. Posterior is towards the top of the page for all proximal and distal views. Note that both Huene (1929) and Bonaparte & Gasparini (1979) regarded these elements as pertaining to the opposite side of the body as indicated here. This difference may relate to interpretation of the relative positions of the forearm elements (see Huene 1929: fig. 1). From Huene (1929: pl. 18, figs 3–5). Scale bar = 10 cm.

elements comprise a single individual, and if so, what features distinguish it from other genera. We tentatively agree with Powell (1986, 1992) that the material originally referred to as *T. robustus* by Huene (1929) (= '*S. robustus*' of McIntosh [1990]) is a *nomen dubium*, pending further investigation.

Titanosaurus araukanicus

Huene (1929:53) noted that Lydekker 'erroneously had united some and separated others' in his (1893) description of *Titanosaurus* remains from Argentina (translated from the Spanish). Accordingly, Huene (1929:53–66) described a subset of those remains (see Table 5, asterisks) and new material

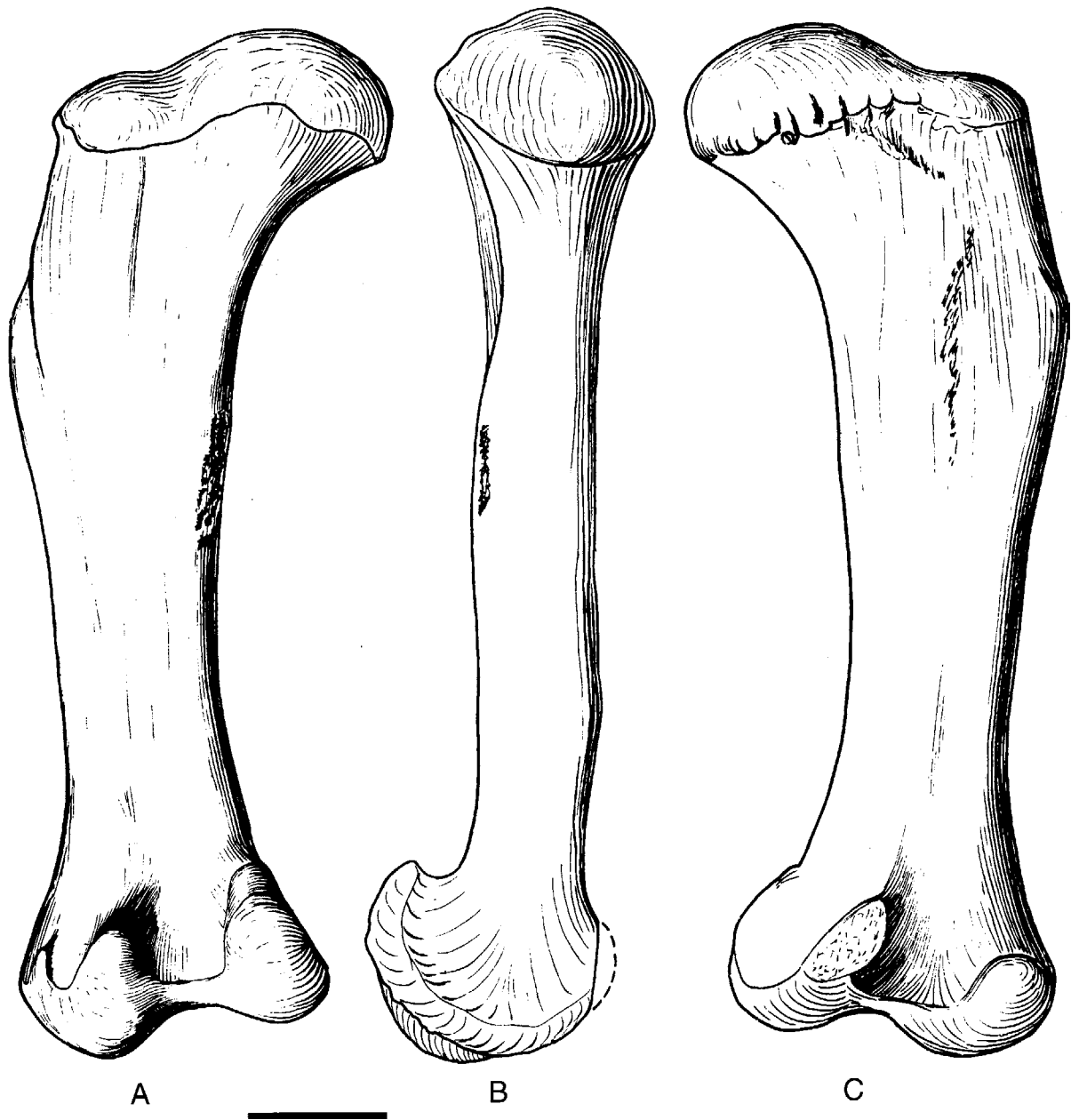


Figure 11 *Titanosaurus robustus*, continued. Lectotype, as specified by Bonaparte & Gasparini (1979:397). Left femur (MLP 26-259) in posterior (A), medial (B) and anterior (C) views. From Huene (1929: pl. 20, fig. 1). Scale bar = 10 cm.

from Cinco Saltos as a new genus and species, *Laplataosaurus araukanicus*, which was distinguished from *Titanosaurus* by its larger size and more slender proportions (1929:84). No holotype was specified, and support was not given for associations between the various elements. Bonaparte & Gasparini (1979:399–400) later specified as the lectotype a right tibia and fibula (MLP 26-306; Fig. 12) that ‘are characterised by being gracile and slender, traits that differentiate them clearly from those of *Titanosaurus* and partially from *Antarctosaurus*’ (translated from the Spanish). Although relative lengths of these two elements are within the expected range, there is no evidence that they belong to the same individual. Again, the lectotype does not include caudal vertebrae, so comparisons to ‘*T. indicus*’ cannot be made.

Powell (1979) referred to *Laplataosaurus araukanicus* additional remains collected from Salta Province that included material described by Bonaparte & Bossi (1967) as *Antarctosaurus* sp. and additional remains collected from the same locality (Fig. 8). According to Powell (1979:193), these included ‘an accumulation of disarticulated elements pertaining to three individuals’ (translated from the Spanish by M. Carrano). The remains included a premaxilla, poorly preserved cervical and caudal vertebrae, a humerus, ulna, radius, ilium, pubis, femur, tibia and fibula. The fibula bears similar proportions as the lectotype of *L. araukanicus*, but the diagnostic tuberosity on the lateral aspect of the shaft could not be identified because of preservation. For this reason, the elements from Salta Province described by Powell (1979)

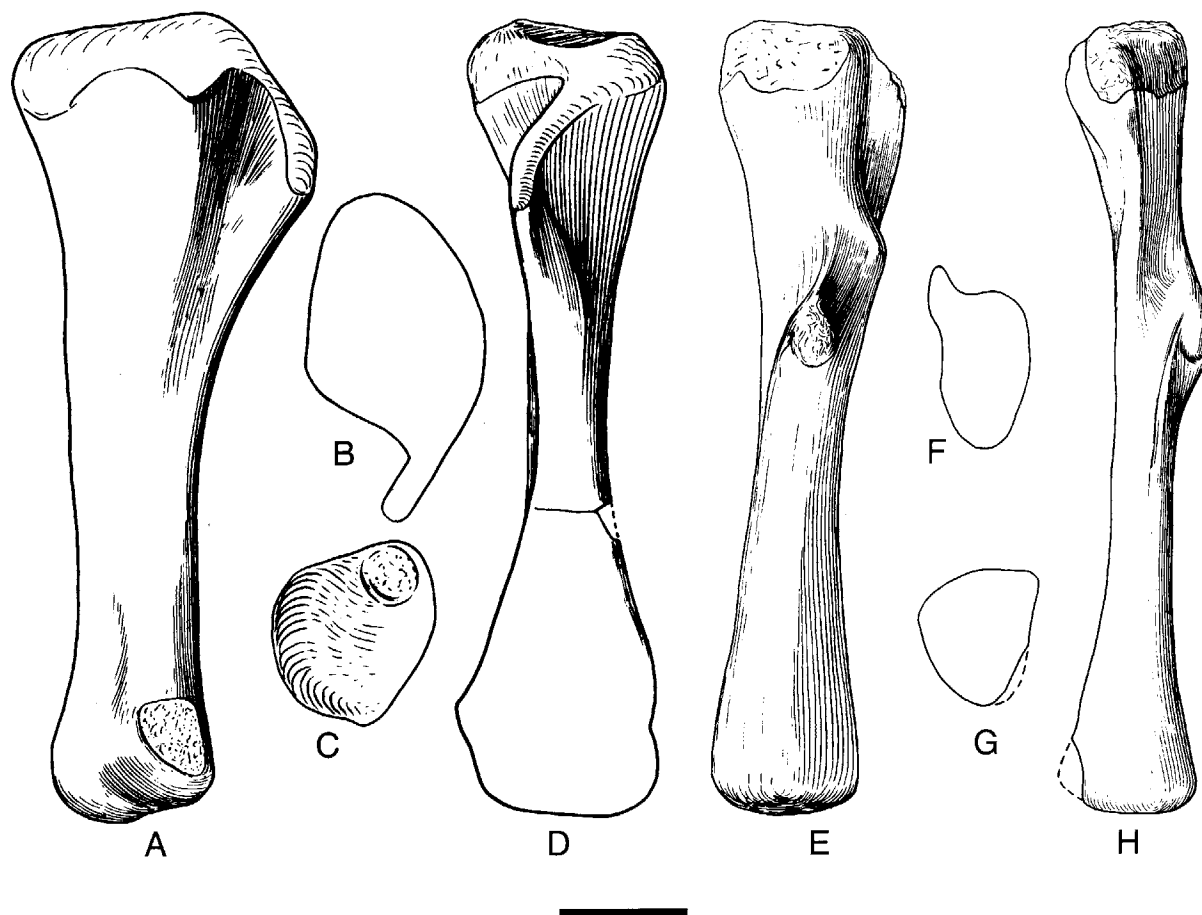


Figure 12 *Titanosaurus araukanicus*. Lectotype (MLP 26-306), as specified by Bonaparte & Gasparini (1979:399). Right tibia in lateral (A), proximal (B), distal (C) and anterior (D) views; right fibula in lateral (E), proximal (F), distal (G) and posterior (H) views. From Huene (1929: pl. 27, figs 1–2). Scale bar = 10 cm.

cannot be referred to *L. araukanicus*. It is worth noting that a premaxillary fragment resembling that described by Powell (1979) as *Laplata-saurus* was recently described by Coria & Chiappe (2001). These authors also hypothesised titanosaur affinities for the element. Although this possibility exists, a second possibility is that they pertain to a rebbachisaurid diplodocoid, which are known to have stacked, comb-like dentition (Serenó *et al.* 1999; Wilson 2002). Although the rebbachisaurid *Rayososaurus* comes from Cretaceous deposits in Patagonia (Calvo & Salgado 1995; Calvo 1999), it is not yet known from jaw elements.

In his revision of South American titanosaur, Powell (1986) referred remains assigned to *Laplata-saurus* to the genus *Titanosaurus* as *T. araukanicus*. This decision was based on similarities to '*Titanosaurus indicus* Lydekker, particularly with the remains of an incomplete but associated specimen discovered in India that was reported by Swinton (1947)' (Powell 1986:88, translated from the Spanish). As mentioned above, remains described by Swinton (1947) were not explicitly compared with the holotype of '*T. indicus*' and the relevant remains are no longer available to make such comparisons. Accordingly, because these remains cannot be reliably referred to '*T. indicus*', they cannot form the basis of referral of remains from Patagonia to the genus. Moreover, the name *Titanosaurus araukanicus*, although mentioned in

Powell (1992), was not described as a replacement name for *Laplata-saurus*.

McIntosh (1990) retained Huene's genus *Laplata-saurus*, identifying the limb elements as gracile but stressing that its position among other titanosaur was contingent on the association between the lectotype limb elements and the caudal vertebrae. Although we agree that more associations need to be established, we consider the hypertrophied fibular lateral trochanter to be diagnostic for a subgroup of Titanosauria (e.g. Wilson 2002; Upchurch *et al.* in press) and consider aspects of the proportions and double lateral tuberosity of the fibula to be diagnostic at the generic level. We suggest that *Laplata-saurus* Huene (1929) be retained for MLP 26-306, *Laplata-saurus araukanicus*.

Titanosaurus sp.

Powell (1987) described three series of vertebrae collected by L. I. Price from the Upper Cretaceous sediments of the Baurú Group near Peirópolis in Minas Gerais State, Brazil (Fig. 8). Campos & Kellner (1999) have more recently specified the material as coming from Price's Quarry 1 ('Caiera'), but did not specify a formation or age. The material described by Powell (1987) pertains to a complete cervical series (lacking the atlas) and three dorsal vertebrae (DGM 'Series A'), five

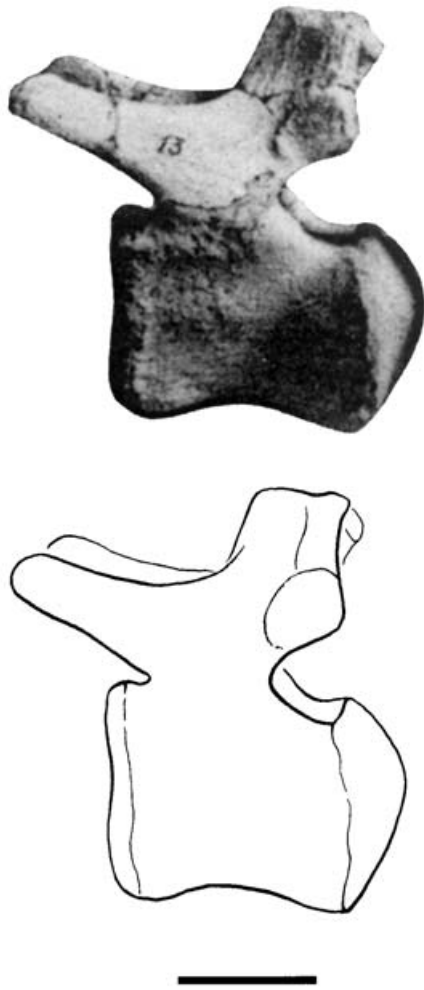


Figure 13 *Titanosaurus* sp. Representative distal caudal vertebra in left lateral view. From Powell (1987: pl. 3, fig. 5). Scale bar = 10 cm.

cervical and 10 dorsal vertebrae, an articulated sacrum and ilium and 10 caudal vertebrae (DGM 'Series B'), and the last sacral vertebrae and 18 articulated anterior caudal vertebrae (DGM 'Series C').

Powell considered most of the material to be 'Titanosaurinae indet.' (e.g. Powell 1987:157), but referred DGM 'Series C' to *Titanosaurus* sp., on the basis of resemblance 'to those of the type of *Titanosaurus indicus* Lydekker 1877 in their morphology and proportions' (Powell 1987:162, translated from the Spanish). Noting that the 'Indian species differs by having more laterally compressed centra and more prominent chevron facets', Powell (1987:162) did not consider them conspecific. No comparisons to the Patagonian species *Neuquensaurus australis*, '*Titanosaurus robustus*', or *Laplatasaurus araukanicus* were mentioned.

The middle caudal vertebrae described by Powell (1987) do resemble those of '*T. indicus*' in their slender, transversely compressed proportions (Fig. 13). However, these similarities are shared by other titanosaurs, including *Andesaurus* (Calvo & Bonaparte 1991: fig. 4c) and *Aeolosaurus* (Salgado & Coria 1993b: fig. 4a). These proportions may eventually be shown to be confined to a titanosaur subgroup, but not to one particular genus. The excellent material

of DGM 'Series C' described by Powell (1987) cannot be referred to *Titanosaurus*, but it is diagnostic and deserves restudy.

Madagascar

Soon after the initial discoveries of *Titanosaurus* in India and Patagonia, exploration in Cretaceous rocks near Mahajanga, Madagascar (Fig. 14) produced large bones that were referred to the genus, including the first record of dermal armour in a sauropod (Depéret 1896). Additional remains were collected in the decade that followed (Thevenin 1907), but it was not until recently that well preserved sauropod skeletons have been reported from the Cretaceous of Madagascar (*Rapetosaurus*: Curry & Forster 1999; Curry Rogers & Forster 2001).

Titanosaurus madagascariensis

Depéret (1896) based the Malagasy species of *Titanosaurus* on two caudal vertebrae, a partial humerus and a dermal ossification. He did not designate any or all of these elements as the holotype of *T. madagascariensis*. The dermal ossification can be safely excluded from the holotype, however, as Depéret notes '... I refer to the same animal, but without absolute certainty, a large dermal ossification' (1896:183, translated from the French by M. Carrano). The humerus came from a different locality than the caudal vertebrae, which were attributed to the same individual (Depéret 1896; Fig. 14, sites 1 and 3). The humerus and caudal vertebrae are syntypes of the species. Curry Rogers & Forster (2001:530) and Curry Rogers (2002) recognised two titanosaur morphs in the Maevarano Formation that could be distinguished by their caudal vertebrae. They considered *T. madagascariensis* to be a *nomen dubium* because its syntype vertebrae display both morphologies. They did not comment on resemblances between these vertebrae and those of their new taxon *Rapetosaurus*, a titanosaur based on associated remains. Below we investigate the affinities of these syntype vertebrae with those of '*T. indicus*'.

The caudal vertebrae of *T. madagascariensis* (Figs 15A & B), although fragmentary, preserve several features that Lydekker (1877, 1879, 1893) listed as diagnosing *Titanosaurus*: procoelous caudal centra, anteriorly placed neural arches, double chevron articulation and a median ventral groove bounded by divergent crests (Depéret 1896:183–184). The shape of the Malagasy centra, however, were considered specifically distinct from those of *Titanosaurus* remains known at the time, which were either rectangular or subcircular in cross-section (Depéret 1896:186–188). No other distinctive features were mentioned. Later, Thevenin (1907) described from the same locality additional remains that he referred to *T. madagascariensis*. Thevenin's material includes nearly complete anterior and mid-caudal vertebrae and fragmentary limb elements that he neither figured nor described. Although his description of the anterior caudal vertebra is brief, he drew attention to its broad, back-swept transverse processes, a feature that Huene regarded as unlike *Titanosaurus*. Huene (1929) referred the Malagasy species to *Laplatasaurus*, a genus he described previously from Upper Cretaceous sediments in South America. His basis for this decision is provided here (Huene 1929:91, translated from the Spanish):

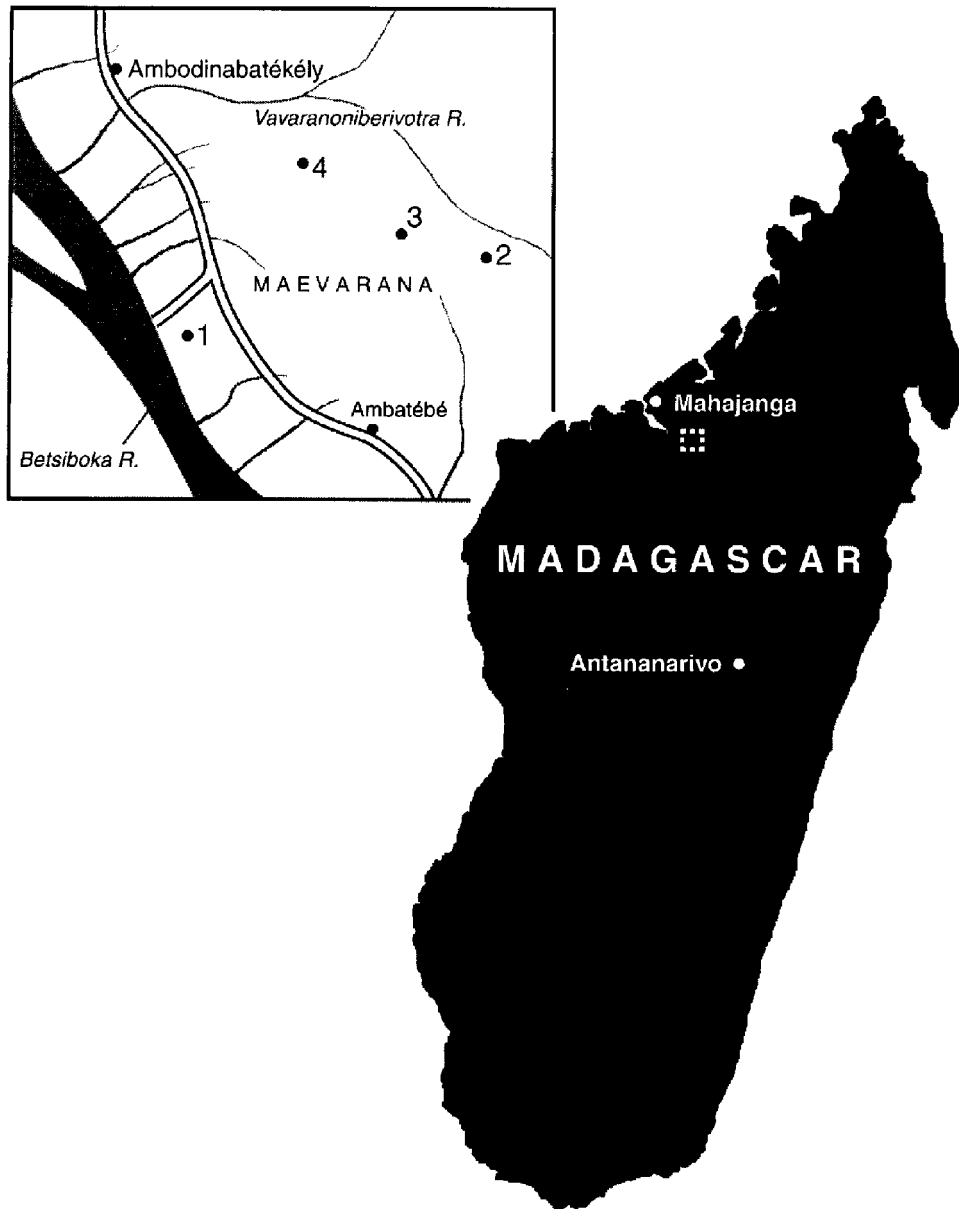


Figure 14 *Titanosaurus* localities – Madagascar. Inset map indicates fossil localities near village of Maevarana, adjacent to the Betsiboka River. The parallel lines adjacent to the river indicate an undeveloped *piste* road. Sites 1–4 represent dinosaur localities identified by Depéret (1896: fig. 1). Site 1 yielded the *Titanosaurus* caudal vertebrae and osteoderm; site 2 yielded ‘*Megalosaurus*’ teeth; site 3 yielded the *Titanosaurus* humerus; site 4 yielded unspecified dinosaurian remains (probably postcranial material of ‘*Megalosaurus*’). Depéret provided no scale for this map and did not locate it within the context of Madagascar. Comparisons to other maps indicate that the inset map reproduced here represents a relatively small area just west of the ‘Begidro’ locality identified by Rogers *et al.* (2000: fig. 2; M. Carrano, pers. comm.). However, both placement and scale of the dashed inset on the larger map of Madagascar are approximate. We have modified the inset map to read ‘Maevarana’ where Depéret (1896) has written ‘Meravana’ (M. Carrano, pers. comm.). Grey lines = rivers. Large silhouette map based on Shupe *et al.* (1992).

The species *Titanosaurus madagascariensis* from the Upper Cretaceous of Madagascar, following the descriptions of Depéret and Thevenin, differs considerably from the Indian and Patagonian species. The titanosaurid characters are certainly well expressed by way of the procoelous centrum, the tall cone of articulation, and the forward insertion of the neural arch. But the heaviness and shortness of the caudal vertebrae is much greater than in *Titanosaurus australis* (and [*T.*] *robustus*) and *Titanosaurus indicus*. The vertebrae are wide, like the Patagonian ones, and at the same time shorter. The broad groove on the ventral surface is not as profound, but of the same width as in *Titanosaurus australis*. One notable

difference between these two species is the strong and massive transverse processes of the Malagasy form. In all details in which this *Titanosaurus* species is differentiated from others, it seems to resemble the caudal vertebrae of *Laplataosaurus*, principally from the Rancho de Avila in Patagonia, only that the zygapophyseal facets are much more marked. Of the figured vertebrae, both the smaller of Depéret (loc. cit., pl. 6, 2) and the last of Thevenin (loc. cit., pl. 1, 16) call attention even more vigorously for their caudal ribs. As this removes these species from the type of *Titanosaurus*, it brings them nearer to *Laplataosaurus*. For these reasons, I would like to directly designate the Malagasy form as cf. *Laplataosaurus*

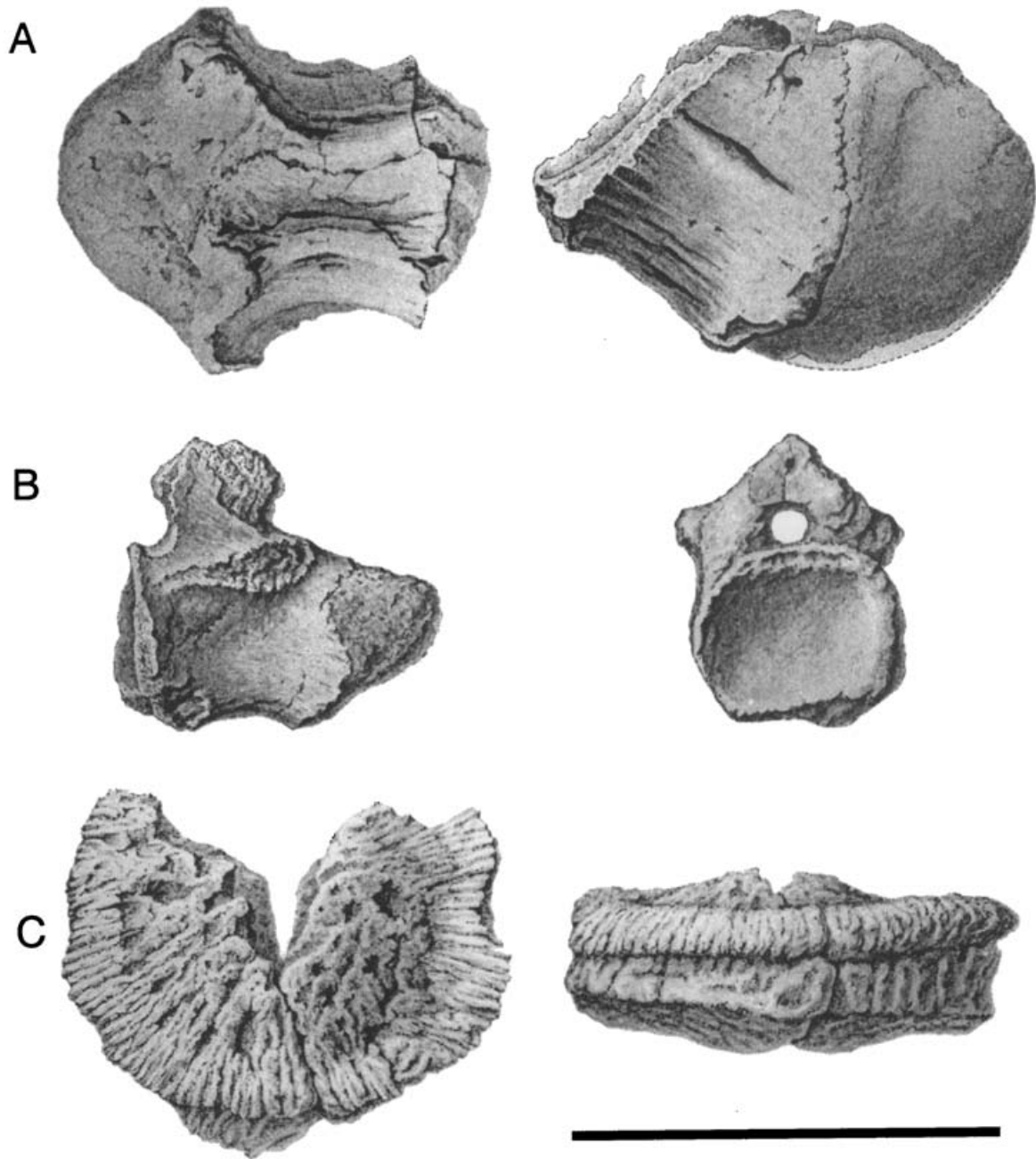


Figure 15 *Titanosaurus madagascariensis*. Holotypic caudal vertebrae and referred osteoderm. **A**, anterior caudal centrum in ventral and left lateral views; **B**, middle caudal centrum and partial neural arch in left lateral and anterior views. **C**, referred osteoderm in two views. From Depéret (1896: pl. 6, figs 1–3). Scale bar = 15 cm for **A** and **B**, 20 cm for **C**.

madagascariensis (Depéret), and compare it with the vertebrae reproduced by Lydekker (loc. cit., 1879, pl. 5, figs 1–2), to which I give the same name.

Importantly, Huene identified procoely and anteriorly positioned neural arches as diagnostic for the Family Titanosauridae, rather than for the genus *Titanosaurus*, as had been suggested by Lydekker (1877), Depéret (1896) and Thevenin (1907). Referral of Malagasy titanosaur material to *Laplata-saurus* awaits revision of the original materials and description of ‘Malagasy Taxon B’ (Curry Rogers 2002). However, as the lectotype of *Laplata-saurus araukanicus* is a tibia and fibula (Bonaparte & Bossi 1967), comparisons are limited to

these elements, which are currently unknown amongst the materials of Depéret, Thevenin and Curry Rogers. We regard *Titanosaurus* (=‘*Laplata-saurus*’ Huene 1929) *madagascariensis* as a *nomen dubium* pending further study.

Asia

Sauropods are well known from Asia during the Jurassic, but are represented by comparably fewer genera during the Cretaceous (Weishampel 1990; Hunt *et al.* 1994; G. Olshevsky, pers. comm.). Early Cretaceous Chinese sauropods include the titanosauriforms *Euhelopus* (Wiman 1929; Wilson 2002) and *Huabeisaurus* (Pang & Cheng 2000), the neosauropod



Figure 16 *Titanosaurus* localities – Asia. Inset map indicates two localities in Laos discussed in the text. The inset map is redrawn from Taquet (1998: fig.29), which was based in part on the map of Hoffet (1942). Grey lines = rivers; dotted lines = state or country borders. Large silhouette map based on Shupe *et al.* (1992).

Mongolosaurus (Gilmore 1933; Barrett *et al.* 2002; Wilson 2002), and the indeterminate eusauropod ‘*Asiatosaurus*’ (Osborn 1924; McIntosh 1990; Barrett *et al.* 2002). Early Cretaceous sediments from Thailand have produced the titanosaur *Phuwiangosaurus* (Martin *et al.* 1994; Upchurch 1998). Three sauropod taxa are known from the Late Cretaceous of Mongolia: the well-preserved remains of the titanosaur *Opisthocoelicaudia* (Borsuk-Bialynicka 1977), as well as the isolated skulls of *Nemegtosaurus* (Nowinski 1971) and *Quaesitosaurus* (Kurzanov & Bannikov 1983), which have been regarded as closely related to either diplodocoids (McIntosh 1990; Upchurch 1999) or titanosaurs (Calvo 1994; Salgado & Calvo 1997; Wilson 1997, 2002; Curry Rogers &

Forster 2001). *T. falloti* (Hoffet 1942), from the Early Cretaceous of Laos, represents the sole species of *Titanosaurus* recorded from Asia.

Titanosaurus falloti

The holotypic remains of *T. falloti* (Hoffet 1942), were discovered in Muong Phalane, Laos (Fig. 16) and include a complete femur and fragments of three others (Taquet 1994). The femur (Fig. 17) bears the deflected shaft diagnostic of Titanosauriformes (Salgado 1993; Salgado *et al.* 1997), but furnishes no features to further resolve the relationships of *T. falloti* within that group. In fact, Allain *et al.* (1999:610) could identify no autapomorphies in the holotypic remains

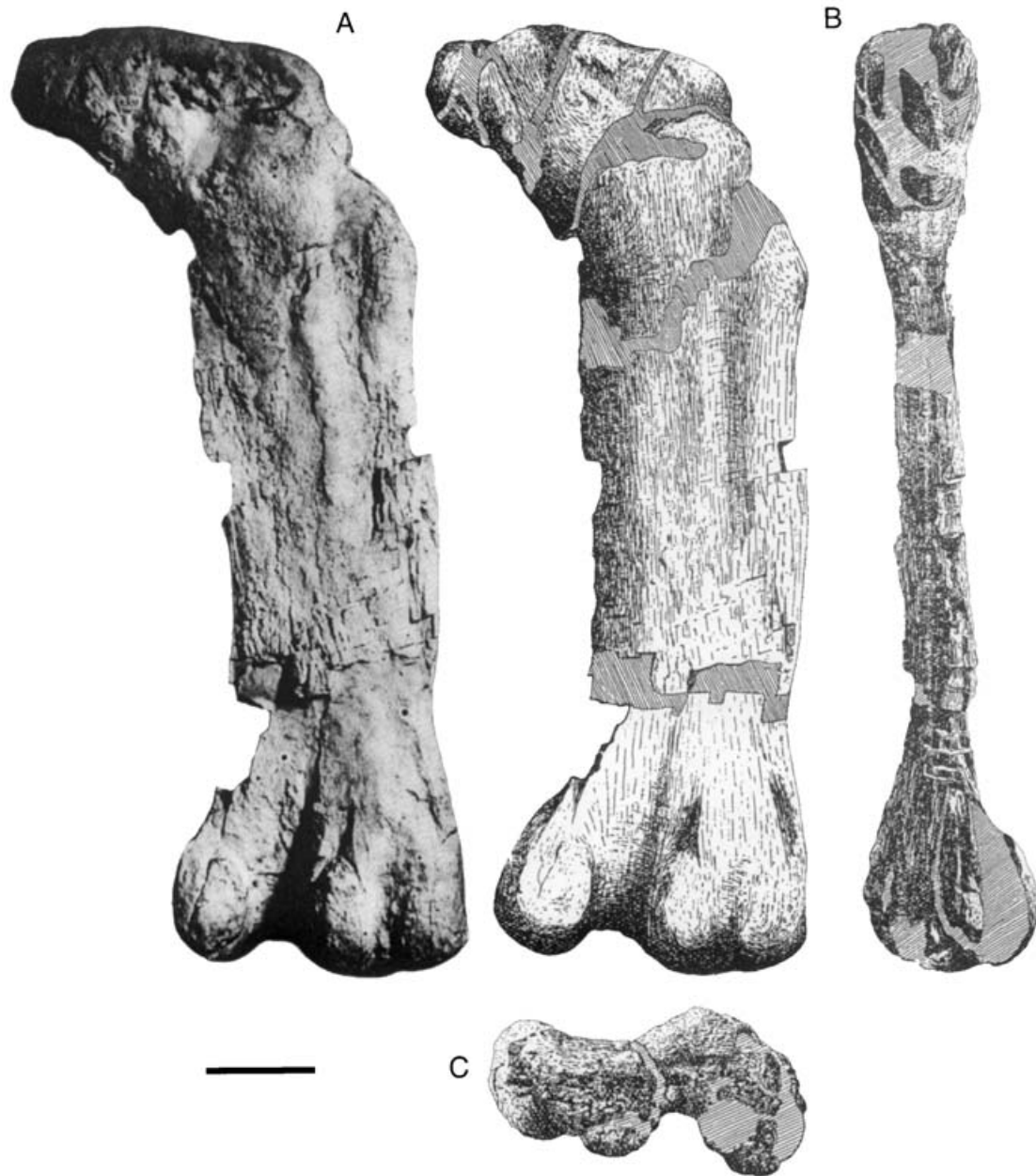


Figure 17 *Titanosaurus falloti*. Holotype femur in posterior (A), medial (B) and distal (C) views. Photograph from Taquet (1994:51), line drawings from Hoffet (1942: fig. 1). Scale bar = 20 cm.

and regarded *T. falloti* to be a *nomen dubium*. Subsequent discoveries at Tang Vay (Fig. 16) have produced partially articulated remains of two individuals that comprise the holotype of the new taxon *Tangvayosaurus hoffeti* (Allain *et al.* 1999). Hoffet's original material, though non-diagnostic, was referred to this new genus (Allain *et al.* 1999), a judgement we regard as premature. *Tangvayosaurus* is regarded as *Titanosauria incertae sedis* on the basis of its short ischium (Wilson 2002; Upchurch *et al.* in press).

Europe

Titanosaurus species have been registered at several European localities. These include two from the Isle of Wight, England, two from southern France, and one from

Romania (Fig. 18). Since their original description, nearly all of these *Titanosaurus* species have been redescribed and given new generic names.

Titanosaurus valdensis

Lydekker (1887:158) described from the 'Wealden' of the Isle of Wight two sauropod mid-caudal vertebrae (BMNH R146a, R151) that appeared to be 'intermediate in character between the figured vertebrae of *T. Blanfordi* and *T. indicus*' (Figs 18 & 19A). 'Wealden' sediments on the Isle of Wight are now referred to the Wessex Formation, which is Early Cretaceous (Barremian) in age (e.g. Martill & Naish 2001). Despite the similarities recognised with Indian forms, Lydekker (1887:158) chose to refer the Wessex Formation material to the British genus *Ornithopsis*, for which 'we find



Figure 18 *Titanosaurus* localities – Europe. Materials referred to *Titanosaurus* have been recorded from four localities in Europe. Map based on Shupe *et al.* (1992).

that the caudal vertebrae have not been hitherto known, and there is accordingly a strong *prima facie* presumption that the specimens under consideration may belong to that genus'. Lydekker regarded *Ornithopsis* and *Titanosaurus* as more similar to one another than to other known sauropods (e.g. *Camarasaurus*) and placed them in the Family Ornithosidae. In the discussion following the reading of Lydekker's (1887) paper to the Geological Society of London, Seeley questioned the identification of the vertebrae as well as their assignment to *Ornithopsis*, while Hulke considered the Isle of Wight and Indian forms to be of specific identity.

A year later, Lydekker (1888) referred to *Titanosaurus* 'sp. a' the Wessex Formation vertebrae (BMNH R146a, R151) and referred to *Titanosaurus* 'sp. b' a vertebra from younger, Upper Greensand sediments of the Isle of Wight (see *T. lydekkeri*, below). Huene (1929) created species names for both. Referring to *Titanosaurus* 'sp. a', Huene (1929:92) remarked:

The two vertebrae of the Wealden of the Isle of Wight were described by Lydekker (*op. cit.*) as morphologically intermediate between *Titanosaurus indicus* and *Titanosaurus Blanfordi*. This species could be designated *Titanosaurus Valdensis* n. sp. Without doubt, it is the oldest species known. In view of the scarce material, there is no reason to assign this specimen to a genus other than that indicated by Lydekker in the *Cat. Foss. Rept. B. M.*, 1888. (translated from the Spanish)

Salgado & Calvo (1997:45) echoed Huene's observation that *Titanosaurus valdensis* represents the oldest titanosaur and suggested that the early titanosaur diversity at the Isle of Wight (e.g. *T. valdensis*, *Pelorosaurus*, *T. lydekkeri* [see below]) provided evidence for 'a probable European origin for the Titanosauridae'.

McIntosh (1990:352) considered *T. valdensis* to be an indeterminate titanosaurid, a decision that would be challenged later by Le Loeuff (1993:107, fig. 1), who redescribed

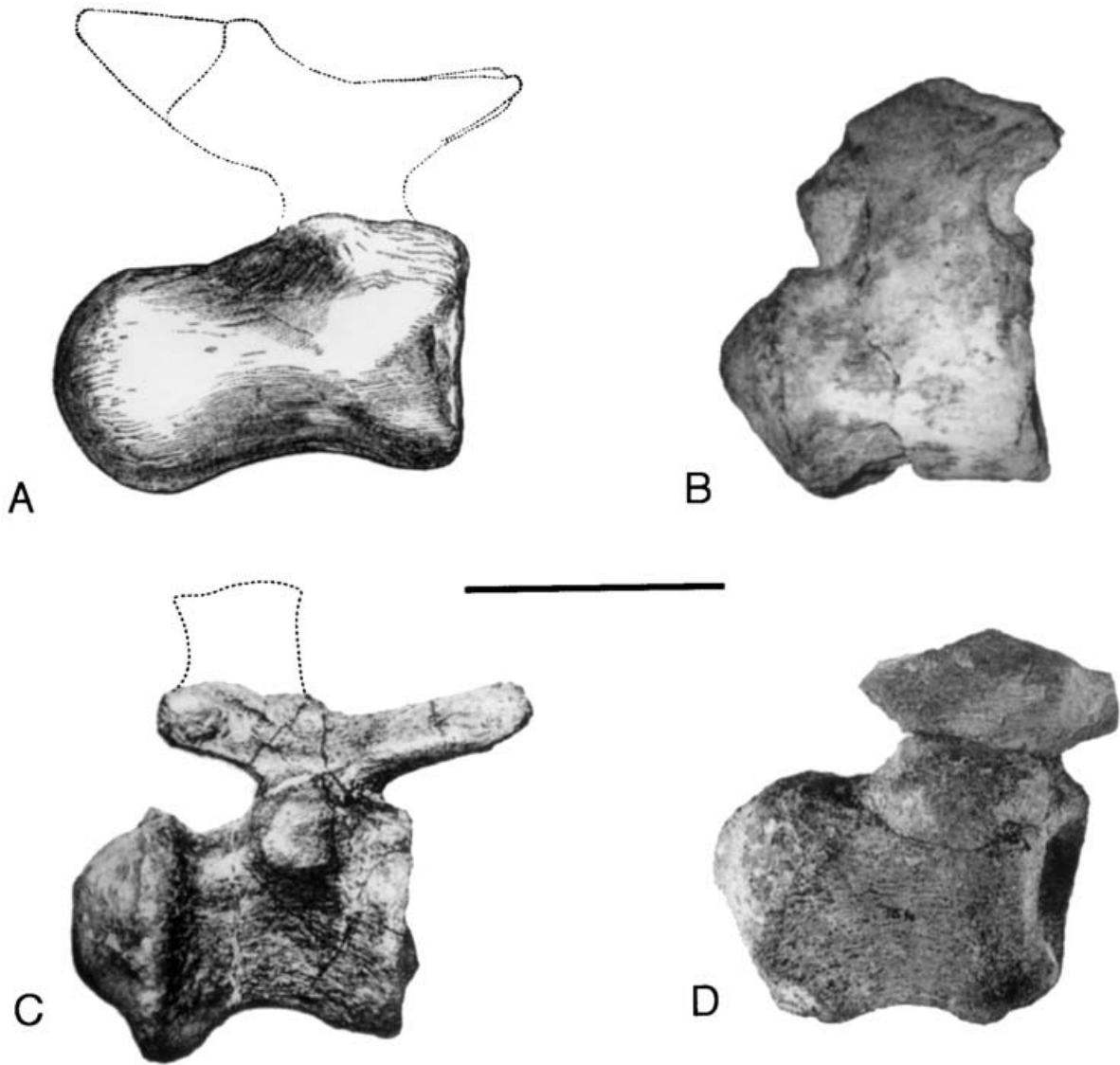


Figure 19 European *Titanosaurus* species. **A**, caudal vertebrae in right lateral view of *T. valdensis* (BMNH R151, lectotype) reproduced from Lydekker (1888: fig. 22). **B**, *T. lydekkeri* (holotype: BMNH 32390). **C**, *T. dacus* from Nopcsa (1915: pl. 3, fig. 4), dashed line added. **D**, cf. *T. indicus* reproduced from Lapparent (1947: pl. 1, fig. 18). Scale bar = 10 cm for **A**, **C** and **D**; 5 cm for **B**.

the *T. valdensis* material and referred to it a third, better preserved specimen from the Beckles collection (BMNH R1886). The referred specimen also came from the 'Wealden' of the Isle of Wight, although its precise locality is not known. Le Loeuff identified in these specimens autapomorphies that he considered evidence of a generic distinction from *Titanosaurus*. As a result, Le Loeuff (1993) coined the new genus *Iuticosaurus* to accommodate them. He designated the better vertebra of Lydekker's material (BMNH R151) as lectotype and the vertebra from the Beckles collection (BMNH R1886) as the paralectotype. Naish & Martill (2001:226) did not regard the defining characteristics of *Iuticosaurus valdensis* to be valid and considered it to be *Titanosauria indet.*

Remains of *Iuticosaurus valdensis* have been re-examined and are briefly described below. The lectotype (BMNH R151; Fig. 19A) is a waterworn mid-caudal centrum that is moderately elongate, with a length-to-height ratio (excluding the length of the posterior convexity) of 1.34. The

centrum is strongly procoelous and appears to be laterally compressed, a feature that may be an artefact caused by wear of the lateral surfaces (Le Loeuff 1993). Although the ventral and lateral surfaces merge smoothly into each other, they are oriented at approximately 90° in cross-section. No chevron facets or ventrolateral ridges can be observed, although this may be because of wear. No transverse processes or ridges are present at the neurocentral junction. The neural arch is missing, but its base is situated on the anterior half of the centrum.

BMNH R146a displays no character states that indicate that it belonged to a titanosaur. It is a moderately elongate (length : height = 1.45) amphicoelous centrum with the arch occupying the middle part of the centrum. We therefore exclude BMNH R146a from further consideration and regard it as an indeterminate sauropod.

The paralectotype (BMNH R1886) is well preserved and retains the base of the neural arch and postzygapophyses.

This centrum is strongly procoelous, subcircular in cross-section, and slightly more elongate (length:height = 1.71) than the lectotype (BMNH R151). Chevron facets are not well preserved and ventrolateral ridges are absent. The dorsoventrally convex lateral surface merges smoothly into the transversely convex ventral surface. There is a low, rounded horizontal ridge located at the neurocentral junction. The neural arch is low and surrounds a small, subcircular neural canal. The neural arch is situated towards the anterior end of the centrum, but less so than in the lectotype (BMNH R151). The base of the neural spine suggests that it was directed strongly backwards, with its tip lying above or even beyond the posterior articulation of the centrum. The ventral margin of the posterior part of the spine is slightly expanded laterally. This forms a faint ledge that may have underlain the postzygapophyseal articular facets. This ledge extends forwards and is continuous with the horizontal ridge at the neurocentral junction.

No satisfactory diagnostic features for *T. valdensis* were provided by Huene (1929), but Le Loeuff (1993:107) identified two autapomorphies: (i) the presence of a 'promontory' on the lateral surface, formed by a ridge that extends along the ventral edge of the neural spine and onto the neurocentral junction; and (ii) the neural spine terminates level with, or beyond, the posterior tip of the centrum. There are, however, several difficulties with these autapomorphies. Firstly, the presence of the lateral promontory is questionable in the lectotype (BMNH R151), and the posterior extent of the neural spine cannot be scored because the neural arch is not preserved. Secondly, the lateral promontory and ridge are quite subtle features in the paralectotype (BMNH R1886), despite the apparent lack of weathering. Finally, both autapomorphies are present in other titanosaurs. For example, Salgado *et al.* (1997:31, character 35) score the presence of a '[p]rominent lateral ridge on base of neural arch in mid-caudals' in several titanosaurs (e.g. *Alamosaurus*, *Epachthosaurus*, *Neuquensaurus* and *Saltasaurus*). In addition, the neural spines of the middle caudal vertebrae of *Pellegrinisaurus* (Salgado 1996: figs 6, 7) also terminate above or beyond the posterior tip of the centrum. These concerns, coupled with the inadvisability of naming a new taxon on very incomplete material, suggests that the validity of *Iuticosaurus* (= *Titanosaurus*) *valdensis* cannot be sustained at present. We therefore agree with Naish & Martill (2001) in regarding it as *nomen dubium*.

Titanosaurus lydekkeri

Lydekker (1888) described a caudal vertebra from the Upper Green sand (Cenomanian) of the Isle of Wight as *Titanosaurus* 'sp. b' (Figs 18 & 19B). As mentioned above, Huene created a new species name, *T. lydekkeri*, for this element, noting that '[i]t is doubtful whether the genus *Titanosaurus* fits for this somewhat coarse caudal vertebra; this assertion can be checked as soon as more complete discoveries permit more exact studies' (1929:91, translated from the Spanish). McIntosh (1990:351) considered *T. lydekkeri* specifically identical to *Macrurosaurus semnus*, but Le Loeuff (1993:108) considered *T. lydekkeri* to referable *Iuticosaurus* (as *I. lydekkeri*) but regarded it as a *nomen dubium*, as did Naish & Martill (2001).

The type, and only, specimen of *T. lydekkeri* (BMNH 32390) is a single anterior caudal centrum and partial neural

arch (Fig. 19B). The centrum length-to-height ratio (excluding the length of the posterior articular convexity) is 1.07. The centrum is slightly compressed transversely, but the lateral surfaces are convex dorsoventrally and merge smoothly into the ventral surface. There is no ventral excavation and ventrolateral ridges are absent. The centrum is strongly procoelous and may have had transverse processes, indicated by broken ridge-like areas close to the top of the centrum. There is no horizontal ridge at the neurocentral junction. The base of each prezygapophysis is preserved, but little detail can be seen.

Although the type caudal of *T. lydekkeri* appears to pertain to a titanosaur, there are no autapomorphic features to distinguish it from others. We therefore agree with Le Loeuff (1993) and Naish & Martill (2001) that *T. lydekkeri* (= *Iuticosaurus lydekkeri*) represents a *nomen dubium*.

Titanosaurus dacus

Nopcsa (1915) described as *Titanosaurus dacus* two vertebrae from the Maastrichtian of Romania (Figs 18 & 19C). These elements are procoelous, but do not share any close resemblance to the Indian species. Many more elements were added to Nopcsa's original collection, which Huene (1932) later broke up into four species of the new genus *Magyarosaurus* (*M. dacus*, *M. hungaricus*, *M. transylvanicus*, *M. sp.*). Both McIntosh (1990) and Le Loeuff (1993) regarded only one species, *M. dacus*, as valid. Certain of the referred limb elements appear to be diagnostic, but it is not yet clear whether all are appropriately assigned. *Magyarosaurus* requires revision (e.g. Jianu & Weishampel 1999:336).

cf. *Titanosaurus* sp.

Depéret (1899:692) made brief mention of limb bones and procoelous vertebrae from Maastrichtian deposits of Saint-Chinian, southeastern France (Fig. 18) that he referred to *Titanosaurus*. This designation was followed by Huene (1929:88) without discussion. Lapparent (1947:27, footnote) mentions that 'there exist in the Museum of Paris vertebrae from Saint-Chinian' that 'may pertain to *T. indicus*' (translated from the French). Le Loeuff (1993:109), however, notes that the holotypic materials, which include caudal vertebrae, a humerus and femur, are now housed in the Université de Lyon. These elements have not yet been figured or described, although Lapparent (1947) listed cervical vertebrae that are 5 cm long, and Huene (1929) listed the femur as 1 m long. Comparisons between this specimen and the '*Titanosaurus indicus*' caudals have not yet been made.

cf. *Titanosaurus indicus*

Lapparent (1947) described a second *Titanosaurus* species from several vertebrae and limb elements collected from the Maastrichtian of Fox-Amphoux, Provence (Figs 18 & 19D). There is no information that suggests that these elements pertain to a single individual. The specific referral was based on caudal vertebrae 'with short body, flattened laterally and not as tall at the bottom, resembling very exactly *Titanosaurus indicus*' (Lapparent 1947:27, translated from the French). Included among these remains is an amphicoelous anterior caudal vertebra that bears 'the special form of the neurapophysis, forked anteriorly with two very divergent branches that rise posteriorly as single and broad blade, which characterises *T. indicus*' (Lapparent 1947: 27, pl. 1, fig. 15, translated from the French). This feature, however, has a very

general distribution among sauropods and is not restricted to any titanosaur genus. The caudal vertebrae share neither general nor specific features with the Indian material; the limb elements do not preserve any features allying them to titanosaurs. This material should be regarded as *Sauropoda indet.* pending revision.

VALIDITY OF THE GENUS *TITANOSAURUS*

Titanosaurs are a diverse and widespread clade that, along with rebbachisaurids, were the latest surviving sauropods. The validity of the eponymous *Titanosaurus* and its referred species has broad implications in terms of systematics, palaeobiogeography and taxonomy. Below we discuss the effects of history on character distribution, the validity of the genus *Titanosaurus* and its individual species and implications for both higher-level titanosaur systematics and geographical distributions.

'Obsolescent' features

At the time of his writing, the species-defining characters listed by Lydekker (1877) were unique to '*Titanosaurus indicus*' among dinosaurs (e.g. presence of procoelous distal caudal vertebrae). These features now obtain a broad distribution among titanosaurs. Thus, species-defining characters (autapomorphies) have obsolesced into characters defining larger groups (synapomorphies) over time, through the discovery of new and better skeletons. As Sues (1998:241) has noted, 'For paleontologists the problem is unfortunately a very common one: in the course of time incomplete but once distinctive type material has become inadequate for identifying the taxon under discussion'. Because new discoveries can only broaden existing character distributions over time, early taxa diagnosed by relatively few characters are the most strongly impacted by character obsolescence. History has stripped *Titanosaurus* of its uniqueness through obsolescence of the characters originally used to define it.

At one level, obsolescent features are a manifestation of equivalence taxa. The features Lydekker originally used to diagnose '*Titanosaurus indicus*' remain diagnostic today at higher levels, but not at the generic or specific levels. This would not be problematical if the features were originally diagnostic at a higher taxonomic rank – features commonly shift between suprageneric hierarchical levels of diagnosticity with no effects on taxonomy. When these same changes are played out at generic or specific level, however, the effects can be important taxonomically, especially in taxa with few defining features. At another level, however, 'obsolescent' features stem from missing data. If a complete skeleton were available to Lydekker, he would have identified diagnostic features spanning several hierarchical levels, tempering lower-level referrals of newly discovered material. Lydekker (1893:5) stressed the tenuity of his referral of the South American form to the Indian genus, noting that better preserved skeletons might preserve details that suggest that the South American species is 'a genus apart' (see *T. australis*, above). However, this admonishment went unheeded and specimens from around the world were considered identifiable as *Titanosaurus*; later these better preserved remains would serve as proxy holotypes. These

proxies permitted additional referrals to the genus, turning the chain of evidence linking holotype and referred remains onto itself full circle. What is to be done with taxa characterised only by such 'obsolescent' features?

Comparable situations are presented by the dinosaur genera *Iguanodon* and *Coelophysis*, as well as the phytosaur *Parasuchus*, whose type species (*I. anglicus*, *C. bauri*, *P. hislopi*) were described over a century ago on the basis of fragmentary remains that are no longer diagnostic. Recently, revisors have petitioned to preserve these generic names by replacing the non-diagnostic holotypes with more complete neotypes (Colbert *et al.* 1992; Charig & Chapman 1998; Chatterjee 2001). Support for these petitions has relied on the observations that the holotypic and neotypic remains pertain to the same taxon (or do not differ noticeably from one another) and have similar provenance, that the generic names are entrenched in the literature and have given rise to suprageneric taxa and that the proposed neotype material effectively has supplanted the holotype as representative of the genus.

Although *Titanosaurus* has provided the basis for several suprageneric taxa and a fairly complete skeleton has been referred to it ('*T.* colberti'), it does not represent a parallel to *Iguanodon*, *Coelophysis* and *Parasuchus*. Unlike these genera, *Titanosaurus* is not the only sauropod known from the Lameta Formation. Its taxonomic 'meaning' is ambiguous and not tied to the Lameta Formation or even to India, and no one specimen has come to represent it – indeed many have. Most importantly, the potential neotype ('*T.* colberti') differs from the holotype species ('*T. indicus*') in even the limited comparisons that can be made between the distal caudal vertebrae (Jain & Bandyopadhyay 1997). It is clear from the preceding that the holotypic remains of '*Titanosaurus indicus*' preserve morphological features no longer diagnostic at lower levels, and no neotype can be established for it. Because '*T. indicus*' is the type species of the genus, *Titanosaurus* must likewise be considered a *nomen dubium*.

Of the 14 referred '*Titanosaurus*' species evaluated here, only five can be considered valid: *Neuquensaurus* (= '*Titanosaurus*') *australis*, *Magyarosaurus* (= '*Titanosaurus*') *dacus*, *Laplatasaurus* (= '*Titanosaurus*') *araukanicus*, the Peirópolis '*Titanosaurus*' sp. and '*Titanosaurus*' *colberti* (Table 6). All but the lattermost species require extensive revision of the original remains, as well as assessment of relevant referred remains. Some of these are currently under study and will not be discussed further here. '*T.* colberti', however, is a well preserved, well described, associated individual for which a new generic name and revised diagnosis are presented below.

SYSTEMATIC PALAEOLOGY

SAUROPODA Marsh, 1878

TITANOSAURIA Bonaparte & Coria, 1993

ISISAURUS new genus

TYPE SPECIES. *Isisaurus colberti* (Jain & Bandyopadhyay, 1997).

DIAGNOSIS AND OCCURRENCE. As for the species.

ETYMOLOGY. *Isi*, honoring the Indian Statistical Institute (ISI), which houses India's foremost collection of Mesozoic

Table 6 Summary of age, distribution and taxonomic determination of the 14 *Titanosaurus* species discussed in the text.

Species	Age	Distribution	Determination
<i>Titanosaurus indicus</i> Lydekker, 1877	Maastrichtian	India, France	Nomen dubium
<i>T. blanfordi</i> Lydekker, 1879	Maastrichtian	India	Nomen dubium
<i>T. australis</i> Lydekker, 1893	Maastrichtian	Argentina, Uruguay	<i>Neuquensaurus</i>
<i>T. nanus</i> Lydekker, 1893	Maastrichtian	Argentina	Nomen dubium
<i>T. madagascariensis</i> Depéret, 1896	Campanian	Madagascar	Nomen dubium
cf. <i>T. sp.</i> Depéret, 1899	Late Cretaceous	France	Nomen dubium
<i>T. dacus</i> Nopcsa, 1915	Maastrichtian	Romania	<i>Magyarosaurus</i>
<i>T. araukanicus</i> Huene, 1929	Campanian Maastrichtian	Argentina, Uruguay	<i>Laplatasaurus</i>
<i>T. lydekkeri</i> Huene, 1929	Barremian	United Kingdom	Nomen dubium
<i>T. robustus</i> Huene, 1929	Maastrichtian	Argentina	Nomen dubium?
<i>T. valdensis</i> Huene, 1929	Barremian	United Kingdom	Nomen dubium
<i>T. falloti</i> Hoffet, 1942	Late Cretaceous	Laos	Nomen dubium
<i>T. rahioliensis</i> Mathur & Srivastava, 1987	Maastrichtian	India	Nomen dubium?
<i>T. sp.</i> Powell, 1987	Maastrichtian	Brazil	Sp. et gen. indet.
<i>T. colberti</i> Jain & Bandyopadhyay, 1997	Maastrichtian	India	<i>Isisaurus</i>

fossil vertebrates and whose scholars discovered and described the holotype skeleton; *saurus*, Greek for reptile.

Isisaurus colberti (Jain & Bandyopadhyay, 1997) (Fig. 7)

HOLOTYPE. Based on a partial skeleton of a single individual comprising a partial axial column, shoulder and pelvic girdles, and a forelimb lacking the radius and manus (ISI R335/1-65).

OCCURRENCE. The skeleton was excavated from a locality near Dongargaon Hill, in Chandrapur district, Maharashtra, central India (Fig. 1). The specimen was preserved in infratrappean horizons of the Lameta Formation, which have been dated as Late Cretaceous (Maastrichtian) (Jain & Bandyopadhyay 1997).

DIAGNOSIS. Medium-sized sauropod sharing with titanosaurs posterior dorsal vertebrae lacking hyposphene–hypantrum articulations, procoelous anterior caudal vertebrae, deep haemal canal, prominent olecranon process and platelike ischia (Wilson 2002; Upchurch *et al.* in press). With more derived forms, it shares broad anterior caudal neural spines, anterior and middle caudal centra with a ventral longitudinal hollow, procoelous (cone-shaped) middle and posterior caudal centra, scapular blade deflected dorsally, stout ulnar proportions, iliac blades oriented perpendicular to the body axis and an ischium shorter than the pubis (Wilson 2002). *Isisaurus colberti* is diagnosed by the following autapomorphies: anteroposteriorly elongate cervical parapophyses (Jain & Bandyopadhyay 1997), cervical neural arches with prespinal and postspinal laminae, anteriormost dorsal vertebra with pronounced coel between prezygodiapophyseal, centroprezygapophyseal and anterior centrodiapophyseal laminae, posterior dorsal neural arches with parapophyses positioned above the level of the prezygapophyses and anteroposteriorly compressed distal caudal chevron blades (from Wilson 2002).

REMARKS. Two recent cladistic analysis have investigated the relationships of *Isisaurus colberti*. Both position *I. colberti* as sister-group to Saltasauridae (Wilson 2002; Upchurch *et al.* in press).

IMPLICATIONS FOR TITANOSAUR SYSTEMATICS

Confusion has surrounded the definition of the Family Titanosauridae since its inception. Gilmore (1946:29) remarked that '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'. Problematic assignments of new taxa to Titanosauridae are the result of the fragmentary remains of its type genus. Although not diagnostic as a genus, '*Titanosaurus*' is diagnostic as a member of Titanosauria by virtue of procoelous distal caudal centra, which are present in all but the most basal, *Andesaurus*-like titanosaurs. A more specific designation is not possible.

Traditional taxonomy

Titanosauria was coined by Bonaparte & Coria (1993), who recognised the need for a higher taxon to include the two families of the group they recognised as closely related – Andesauridae and Titanosauridae. Their definition is provided below (Bonaparte & Coria 1993:280, translated from the Spanish):

The recognition of a new family of Titanosauria [Andesauridae] has posed to us the question of whether it is opportune to recognize a larger entity uniting Andesauridae, with hyposphene-hypantrum and amphiplatyan caudals, together with Titanosauridae, lacking hyposphene and with procoelous caudals. The recognition of Titanosauria, of suprafamilial hierarchy, is a response to the increasing diversity of titanosaur taxa discovered in recent years that cannot be placed within Titanosauridae . . .

Andesauridae integrates the titanosaurs with normal (*Andesaurus*) or hypertrophied (*Argentinosaurus*, *Epachthosaurus*) hyposphene-hypantrum, with amphiplatyan caudals as registered in *Andesaurus* (Calvo & Bonaparte 1991), and originating from infra-Senonian levels.

Titanosauridae includes the typical titanosaurs of the Senonian, which lack the hyposphene and possess procoelous caudals,

including the subfamilies recognised by Powell (1986): Saltasaurinae, Argurosaurinae, Antarctosaurinae, and Titanosaurinae.

Whereas Titanosauridae is defined on the basis of derived characters, Andesauridae is based on primitive characters that by definition specify a paraphyletic group. Until taxa are found sharing synapomorphies with *Andesaurus*, 'Andesauridae' will remain an informal name. It is also noted here that the derived characters of Bonaparte & Coria's (1993) Titanosauridae (i.e. procoelous caudal vertebrae, absence of hyposphene-hypantrum articulations in dorsal vertebrae) appear at different nodes in the analysis of Wilson (2002).

Titanosaur inter-relationships

Six analyses have evaluated the evolutionary history of titanosaurs (Salgado *et al.* 1997; Upchurch 1998; Sanz *et al.* 1999; Curry Rogers & Forster 2001; Wilson 2002; Upchurch *et al.* in press). Although each employed a different array of taxa, a core of well-known titanosaur genera were common to all of them (Table 7). Simplified cladograms representing the relationships of these core titanosaur taxa are presented in Fig. 20; a consensus of those hypotheses is provided in Fig. 21. All agree that *Andesaurus*, *Malawisaurus* and *Isisaurus* (= '*Titanosaurus*') *colberti* are basalmost titanosaurs, sequential outgroups to a clade including *Opisthocoelicaudia*, *Alamosaurus*, *Neuquensaurus* (= *Titanosaurus*) *australis* and *Saltasaurus*. These latter two are unanimously considered sister taxa, but their immediate outgroup is not yet agreed upon (Fig. 20). These preliminary analyses are the first step towards establishing a framework for titanosaur evolutionary history. However, at least a dozen valid titanosaur genera have yet to be accommodated by a phylogenetic analysis, in addition to the many undescribed specimens uncovered in recent years.

Based on the evidence given above, the genus *Titanosaurus* is invalid and co-ordinate suprageneric Linnean taxa must likewise be abandoned. As observed by Gilmore 50 years ago, 'Titanosauridae' has served as little more than a receptacle for indeterminate Cretaceous sauropods. It is this broad, featureless definition of 'Titanosauridae' combined with partially and non-overlapping taxa referred to the ill-defined genus '*Titanosaurus*' that has abetted the inertial state of titanosaur systematics over the last century. Based on the limited consensus that has already been achieved, we propose and define a standard nomenclature for Titanosauria and its subgroups that will facilitate future exploration within the group.

Phylogenetic taxonomy

The six analyses listed above employed taxon names inconsistently to nodes on the titanosaur cladogram. Whereas some used different names to refer to the same clade (e.g. Titanosauridae *versus* Saltasauridae, Figs 20B & E), others employed different definitions for the same taxon name (e.g. Saltasaurinae in Figs 20D *versus* E). All but one analysis employed Titanosauria; of those, all but Sanz *et al.* (1999) used it in the same sense. The constituency of Titanosauria matched that implied by its original definition, which in-

Table 7 Included genera and taxon names employed for six analyses of titanosaur inter-relationships.

Analysis	Titanosaur genera	Named nodes
Salgado <i>et al.</i> (1997)	<i>Aeolosaurus</i> <i>Alamosaurus</i> <i>Andesaurus</i> <i>Argentinosaurus</i> <i>Epachthosaurus</i> <i>Malawisaurus</i> <i>Neuquensaurus</i> <i>Opisthocoelicaudia</i> <i>Saltasaurus</i> 'Titanosaurinae indet.'	Titanosauria Titanosauridae Titanosaurinae Saltasaurinae
Upchurch (1998)	<i>Alamosaurus</i> <i>Andesaurus</i> <i>Malawisaurus</i> <i>Opisthocoelicaudia</i> <i>Phuwiangosaurus</i> <i>Saltasaurus</i>	Titanosauroidae Titanosauridea [sic]
Sanz <i>et al.</i> (1999)	<i>Andesaurus</i> <i>Argurosaurus</i> <i>Epachthosaurus</i> <i>Lirainosaurus</i> <i>Opisthocoelicaudia</i> Peirópolis form <i>Saltasaurus</i>	Titanosauriidea [sic] Titanosauria Eutitanosauria
Curry Rogers & Forster (2001)	<i>Alamosaurus</i> <i>Antarctosaurus</i> <i>Malawisaurus</i> <i>Nemegtosaurus</i> <i>Neuquensaurus</i> <i>Opisthocoelicaudia</i> <i>Quaesitosaurus</i> <i>Rapetosaurus</i> <i>Saltasaurus</i> ' <i>Titanosaurus</i> '	Titanosauria Saltasaurinae
Wilson (2002)	<i>Alamosaurus</i> <i>Malawisaurus</i> <i>Nemegtosaurus</i> <i>Neuquensaurus</i> <i>Opisthocoelicaudia</i> <i>Rapetosaurus</i> <i>Saltasaurus</i> ' <i>Titanosaurus</i> ' <i>colberti</i>	Titanosauria Saltasauridae Saltasaurinae Opisthocoelicaudiinae
Upchurch <i>et al.</i> (in press)	<i>Alamosaurus</i> <i>Andesaurus</i> <i>Argentinosaurus</i> <i>Austrosaurus</i> <i>Gondwanatitan</i> <i>Lirainosaurus</i> <i>Malawisaurus</i> <i>Opisthocoelicaudia</i> <i>Pellegrinisaurus</i> <i>Phuwiangosaurus</i> <i>Saltasaurus</i> ' <i>Titanosaurus</i> ' <i>colberti</i>	Titanosauria Lithostrotia Saltasauridae

Boldface type indicates genera or clade names not used in other analyses.

cludes *Andesaurus* and all other titanosaurs (Bonaparte & Coria 1993). The phylogenetic definition of Titanosauria, however, varied among analyses. Salgado *et al.* (1997:18) proposed a node-based grouping of 'the most recent common

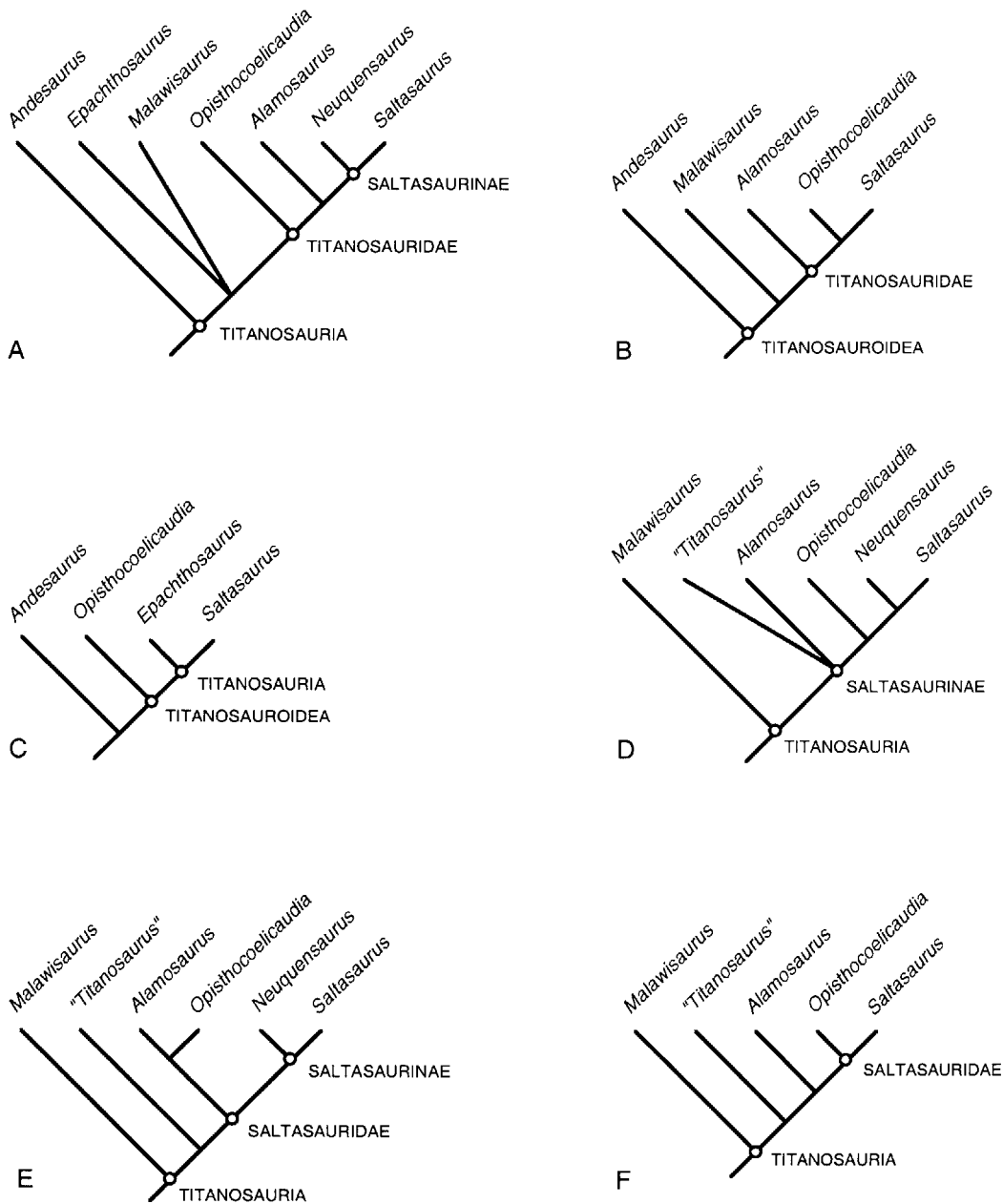


Figure 20 Titanosaur inter-relationships. **A**, Salgado *et al.* (1997); **B**, Upchurch (1998); **C**, Sanz *et al.* (1999); **D**, Curry Rogers & Forster (2001); **E**, Wilson (2002); **F**, Upchurch *et al.* (in press). Topologies have been simplified to include genera scored in more than one analysis (see Table 7). For Curry Rogers & Forster (2001), '*Titanosaurus*' includes '*T. indicus*' (including the Berman & Jain (1982) braincase) and *Isisaurus* (= '*Titanosaurus*' *colberti*), whereas for Wilson (2002) and Upchurch *et al.* (in press) it refers specifically to *Isisaurus* (= '*Titanosaurus*' *colberti*).

ancestor of *Andesaurus delgadoi* and Titanosauridae and all of its descendants', whereas Wilson (2002) used the existing stem-based definition for Titanosauria presented by Wilson & Sereno (1998:22) as, 'Titanosauriforms more closely related to *Saltasaurus* than to either *Brachiosaurus* or *Euhelopus*'. Because the Salgado *et al.* (1997) definition has priority and most closely represents Bonaparte & Coria's (1993) traditional definition, it will be adopted here (see below). Upchurch (1998: table 4) did not use Titanosauria, but 'Titanosauroidae', noting that it is 'preferred to the earlier equivalent term 'Titanosauria' because a set of taxonomic categories of superfamily rank will bring greater consistency and stability to sauropod classification'. Both Salgado

et al. (1997) and Upchurch (1998) used Titanosauridae but applied the name to different nodes – the former to *Malawisaurus* and all more derived titanosaurs, the latter to taxa more derived than *Malawisaurus* (compare Figs 20A & B). Wilson (2002) used Saltosauridae to refer to the clade equivalent to Upchurch's Titanosauridae, whereas Curry Rogers & Forster (2001) called this node Saltosaurinae (Figs 20D & E). Sanz *et al.* (1999:252) proposed a new clade name, 'Eutitanosauria', for 'the most recent common ancestor of *Saltasaurus*, *Argyrosaurus*, *Lirainosaurus*, plus the Peirópolis titanosaur and all its descendants'. As defined, 'Eutitanosauria' could be synonymous with Saltosauridae or Saltosaurinae. Upchurch *et al.* (in press) created

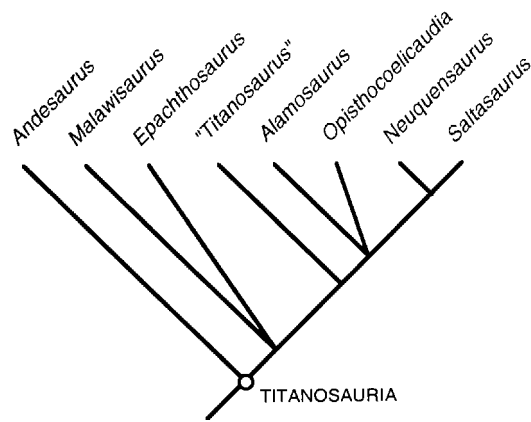


Figure 21 Adams consensus tree of titanosaur relationships based on the six analyses depicted in Fig. 20.

‘Lithostrotia’ as a node-based group including *Malawisaurus* and more derived titanosaurs, which share the presence of dermal armour (as implied by the clade name). Sereno (1998: table 4) also created a node-stem triplet definition for Saltasauridae and its constituent subclades, Saltasaurinae and Opisthocoelicaudiinae, which Wilson (2002) followed.

Phylogenetic definitions for Titanosauria and its subclades are provided below (node-based definitions in bold-face type, stem-based definitions in regular type). Species are used as reference taxa. These phylogenetic definitions anchor traditional and new taxon names to stable nodes, preserving priority and reflecting traditional usage where possible.

Titanosauria (Bonaparte & Coria 1993) – *Andesaurus delgadoi* (Calvo & Bonaparte 1991), *Saltasaurus loricatus* (Bonaparte & Powell 1980), their most recent common ancestor and all descendants.

Lithostrotia (Upchurch *et al.* in press) – *Malawisaurus dixeyi* (Haughton 1928), *Saltasaurus loricatus* (Bonaparte & Powell 1980), their most recent common ancestor and all descendants.

Saltasauridae (Bonaparte & Powell 1980) – *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka 1977), *Saltasaurus loricatus* (Bonaparte & Powell 1980), their most recent common ancestor and all descendants.

Saltasaurinae (Bonaparte & Powell 1980) – All saltasaurids more closely related to *Saltasaurus loricatus* (Bonaparte & Powell 1980) than to *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka 1977).

Opisthocoelicaudiinae (McIntosh 1990) – All saltasaurids more closely related to *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka 1977) than to *Saltasaurus loricatus* (Bonaparte & Powell 1980).

Titanosauria is here recognised as a node-based group, as originally conceived by Bonaparte & Coria (1993) and following the original phylogenetic definition provided by Salgado *et al.* (1997). In addition, this node-based definition better partitions diversity within the Somphospondyli, a stem-based group (Wilson & Sereno 1998; Wilson 2002). Lithostrotia (Upchurch *et al.* in press) has been adopted to help discriminate between basal members of the titanosaur

radiation. The node-stem triplet at Saltasauridae has likewise been adopted, as suggested by Sereno (1998).

TITANOSAUR DISTRIBUTIONS: GONDWANAN OR GLOBAL?

The taxonomic license with which remains were referred to *Titanosaurus* has resulted in the genus forming the basis for the first group of endemic ‘Gondwanan’ dinosaurs. As Lydekker (1895:329) noted, ‘while several of its [Sauropoda] North American representatives appear inseparable from their European allies, the Indian and Argentine forms are likewise referable to one and the same genus’. With acceptance of a tectonic model of palaeogeography, Gondwanan faunas (e.g. titanosaurs – *Titanosaurus* and related forms) were envisioned as having been produced by the separation of northern and southern landmasses at the close of the Jurassic (e.g. Bonaparte 1999). The vicariant origin of *Titanosaurus* and related forms can be rejected on two counts.

Firstly and most important, the vicariant scenario requires that the divergence of Titanosauria from their sister-taxa was fueled by the breakup of Pangaea into Laurasia and Gondwana, a Late Jurassic event (Smith *et al.* 1994). Titanosaur body fossils and ichnofossils, however, first appear in the Middle Jurassic and thus could not have been produced by the initial breakup of Pangaea. This does not exclude the possibility of a vicariant signal at lower levels, which may be expected based on titanosaur distributions on southern continents during the Cretaceous, when Gondwana separated into individual continental landmasses. Detailed palaeobiogeographical studies await a generic-level phylogeny for Titanosauria.

Secondly, titanosaurs are not restricted to southern landmasses. Until quite recently, however, this was not appreciated. Few titanosaurs had been recovered from northern landmasses, among them *Alamosaurus* from North America (Gilmore 1922, 1946), *Titanosaurus falloti* from Laos (Hoffet 1942), *Titanosaurus* (Lapparent 1947) and ‘*Hypselsaurus*’ (Matheron 1869) from France, *Macrurosaurus* from England (Seeley 1869), and *Magyarosaurus* (= *Titanosaurus*) from Romania (Nopcsa 1915; Huene 1932). In a palaeobiogeographical context, these taxa were treated as exceptions that evidenced independent dispersal events from south to north sometime during the Cretaceous (e.g. Lucas & Hunt 1989; Le Loeuff 1993, 1995; Sullivan & Lucas 2000). This ‘austral immigrant’ hypothesis has been challenged, however, by recent discoveries of Early Cretaceous North American titanosaurs (Britt *et al.* 1998) and cladistic reinterpretation of known sauropod taxa such as ‘*Pelorosaurus becklesii*’ (Upchurch 1995), *Phuwiangosaurus* (Upchurch 1998), *Opisthocoelicaudia* (Gimenez 1992; Salgado & Coria 1993a), and *Nemegtosaurus* (Calvo 1994; Salgado *et al.* 1997; Wilson 1997; Curry Rogers & Forster 2001; but see Upchurch 1999 and Upchurch *et al.* in press for a dissenting view). Currently, titanosaur distributions and predicted origin prior to the breakup of Pangaea (Wilson & Sereno 1998; Hunn *et al.* 2002) support the hypothesis that soon after their origin, titanosaurs dispersed across the substantial continental connections that still existed.

The apparent absence of titanosaurs in Europe and North America from the Cenomanian to the early Campanian has been interpreted as regional extinction followed by

reinvasion (Lucas & Hunt 1989; Le Loeuff 1995). Although these hypotheses remain plausible, it can no longer be assumed that titanosaurs must have migrated from southern continents; nor can we rule out the possibility that the absence of mid-Cretaceous titanosaurs reflects sampling bias in the areas concerned.

CONCLUSIONS

The historical, taxonomic and distributional consequences of the naming of 14 '*Titanosaurus*' species has impacted understanding of Cretaceous sauropods. Re-evaluation of the type species, '*Titanosaurus indicus*', indicates that it has no diagnostic features and must be considered a *nomen dubium*. Co-ordinated suprageneric Linnean taxa (i.e. Titanosauroidae, Titanosauridae, Titanosaurinae) are likewise abandoned. Only five of the species referred to *Titanosaurus* are based on diagnostic materials; the remainder are non-diagnostic. Although some non-diagnostic species have been discarded with the discovery of new material (e.g. *T. madagascariensis*, *T. falloti*), many are still in use. We recognise as diagnostic one Indian species (*Isisaurus* [= '*Titanosaurus*'] *colberti*), one European species (*Magyarosaurus* [= '*Titanosaurus*'] *dacus*) and three South American species (*Neuquensaurus* [= '*Titanosaurus*'] *australis*, *Laplatasaurus* [= '*Titanosaurus*'] *araukanicus*, '*T.*' sp.).

Revision of the genus *Titanosaurus* has important implications on the taxonomy applied to titanosaurs. Taxonomic names have been applied variously in the few cladistic analyses of titanosaurs compared. In an effort to standardise what has seemed a confusing taxonomy, we propose phylogenetic definitions for Titanosauria, Lithostrotia (Upchurch *et al.* in press), Saltasauridae, Saltasaurinae and Opisthocoelicaudiinae. It is our hope that the basic definitions here outlined will provide a stable framework for the description of new taxa and the cladistic analyses that follow.

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