Asociación Paleontológica Argentina. Publicación Especial 7 ISSN 0328-347X
VII International Symposium on Mesozoic Terrestrial Ecosystems: 139-144. Buenos Aires, 30-6-2001

A reassessment of the phylogenetic position of Cretaceous sauropod dinosaurs from Queensland, Australia

Ralph E. MOLNAR[1]

Abstract. The Cretaceous sauropod material from Queensland, Australia, has been regarded as pertaining to a persistently primitive sauropod lineage (*e.g.*, Coombs and Molnar). The specimens derive from the Toolebuc and Allaru (Albian marine) and Winton (Cenomanian continental) Formations. Recent phylogenetic analyses carried out by workers in Argentina, the USA and England permit a reassessment of this fragmentary material. As far as can be ascertained from the material, there is no indication from the character states that more than a single taxon is represented. Character states diagnostic of the Titanosauriformes, the Titanosauria, the Somphospondyli and the Titanosauridae are present. Thus the Queensland material does not pertain to cetiosaurids but belongs to titanosaurs, extending their range into Australia

Key words. Sauropods. Austrosaurus. Titanosaurs. Cretaceous. Paleozoogeography.

Introduction

By the 1950's titanosaurs were widely recognized both as the latest sauropod group to diversify and as pre-eminently the sauropods of Gondwanaland. Both conclusions had been foreshadowed by von Huene (1929). With titanosaurs prominent in South America, Africa and India - as well as a few occurrences in North America and Europe - it seemed anomalous that there was no evidence whatever that they had inhabited Australia. Titanosaurs were chiefly recognized by their possession of procoelous caudal vertebrae. Although Australian sauropod material was sparse and fragmentary, the tail was arguably the best known part of the anatomy, and procoelous caudals were clearly lacking. Salgado (1993) departed from the usual interpretation of *Austrosaurus* as a plesiomorphic sauropod and suggested titanosaurian affinities, specifically that it was the member of a clade also including the titanosaurids. Study of new titanosaur material from Argentina, supplemented by recently discovered specimens from Malawi, has shown that procoelous caudals are neither necessary nor sufficient to recognize titanosaurs (Calvo and Bonaparte, 1991; Salgado and Coria, 1993; Jacobs *et al.*, 1993). The recent interest in the morphology of titanosaurs, and the phylogenetic relationships of sauropods, exemplified by Giménez (1992), Upchurch (1995), Salgado *et al.* (1997), Wilson and Sereno (1998) and Upchurch (1998), has made it possible to reassess the phylogenetic affinities of the Australian Cretaceous sauropod material and address the anomalous absence of titanosaurs. This paper looks specifically at *Austrosaurus mckillopi* Longman (1933) and the material from the Winton Formation, much of which has been referred to *Austrosaurus* sp.

The first sauropod material recorded from Queensland (Queensland Museum {= QM} F311) was collected in 1913 from Blackall, east-central Queensland, probably from the Winton Formation. Identified as a femur of *Diprotodon*, it was not correctly recognized as from a sauropod until 1980. In 1932, large but incomplete presacral vertebrae were discovered in the Allaru Mudstone near Maxwelton, north-central Queensland. Studied by Longman (1933), they were made the holotype of *Austrosaurus mckillopi* (QM F2316). Vertebrae (QM F2470) acquired in 1935 were identified as a cervical series of the pliosaur *Kronosaurus*. Only in 1980 was it realized they were sauropod caudals. Sauropod vertebrae, correctly identified, were acquired in 1952 from Chorregon, central Queensland (QM F10916) also probably from the Winton Formation. Thus, fragmentary Cretaceous sauropod material had slowly accumulated at the Queensland Museum from several sites in central Queensland. But, with the exception of Longman's work on *Austrosaurus*, it was not until the early 1970's - with the collection of several specimens from the Winton Formation in the vicinity of Winton, central Queensland - that research interest was shown in this material, resulting in Coombs and Molnar (1981). All of this material de-

[1]Museum of Northern Arizona, 3101 North Fort Valley Road, Flagstaff, Arizona, 86001, USA.

 0328-347X/01$00.00+50

rives from the "middle Cretaceous" Albian (marine Allaru or Toolebuc Formations) and Cenomanian stages (continental Winton Formation). The few other Cretaceous sauropod specimens from Queensland will be treated elsewhere.

Longman (1933) tentatively attributed *A. mckillopi* to the Cetiosauridae. Likewise Coombs and Molnar (1981) concluded that the material from near Winton probably derived from a cetiosaurid, then considered a clade rather than a grade. Because of the fragmentary nature of these specimens, resulting in a large number of unknown character states, analyzing the sauropods as a whole with the inclusion of the character states for the Queensland material is less likely to illuminate the position of that material than to destabilize the results of the analysis. Thus the results of the analyses of Salgado *et al.* (1997), Wilson and Sereno (1998) and Upchurch (1998) (which are basically similar) are here accepted, and the likely phylogenetic position of the Queensland material established in relation to them.

Coombs and Molnar (1981) described five individual specimens, but were uncertain whether all of them represented the same taxon. Here nine specimens (including the previously studied five) are examined, and will be treated individually to avoid assumptions regarding their taxonomic uniformity.

Character states present

The vertebrae of these specimens are more abundant and generally better preserved than the appendicular material, thus they are emphasized here. Seven vertebral apomorphies used by Salgado *et al.* (1997) are present in the Queensland material (the nodes are those of Salgado *et al.*, 1997, fig. 19): 1 (node 2) opisthocoelous cervical and anterior trunk vertebrae; 8 (node 4) presence of pleurocoels on presacral vertebrae; 9 (node 5) opisthocoelous posterior trunk and sacral centra; 15 (node 6) neural arches positioned anteriorly in mid- and posterior caudal centra; 20 (node 8) eye-shaped pleurocoels in trunk vertebrae, and 22 (node 8) presence of centro-parapophyseal lamina in posterior trunk vertebrae. Character 34 (node 14) depressed mid- and posterior caudal centra with dorsoventrally convex lateral faces is present in the mid-caudal of QM F2470, but absent in the other caudals and other specimens. Characters 1 and 9 are assumed to be present because opisthocoelous anterior and posterior trunk vertebrae are clearly present. Cervicals are possibly, but not certainly, known in the Winton material and *Austrosaurus mckillopi*, and sacral centra have not been recovered. Character 15 is also assumed to be present (in QM F2470). The neural arches are represented only by their bases, thus anterior cannot be determined for these elements, however posteriorly-positioned caudal neural arches have never been reported in sauropods, so the arches must have been anteriorly-positioned. One character, 19 (node 6), presence of prominent lateral bulge in femur below greater trochanter, is present in QM F3390 (Coombs and Molnar, 1981).

Four of the characters used for vertebrae by Wilson and Sereno (1998) are present in both QM F2316 and QM F6737. These are characters: 59, anterior dorsal centra opisthocoelous; 68, presacral pleurocoels deep and invaginated; 92, posterior dorsal centra opisthocoelous, with convexity present on anterior face of centrum; and 102, presacral vertebrae composed of spongy bone. However characters 59 and 92 are uncertain for QM F6737 in that the incompleteness of the vertebrae makes the identification of their position uncertain: they may be anterior rather than posterior dorsals. At least one of these characters is present, but if only one is present it is unclear which one. Two derived features are present in the femur of QM F3390: 10, femoral shaft with elliptical cross-section, long axis oriented mediolaterally; and 100, femur with proximal one-third of shaft deflected medially (which is taken to be equivalent to state 19 of Salgado *et al.*, 1997). Character 3, deltopectoral crest of humerus low, is present in QM F311.

The following apomorphic vertebral states of Upchurch (1998) are present in the Queensland material: B5 (C97), pleurocoels in dorsal centra; C27 (C132), centrum length divided by centrum height (in most craniad caudals) is approximately 0.5-0.6; H7 (C145) middle and distal chevrons are 'open' at their proximal ends; K4 (C138), neural arches of middle caudals are situated on the cranial half of the centrum; K9 (C205), osseous tissue structure of presacral vertebrae is composed of a small number of very large 'cancellar' spaces separated by thin bony lamellae; M1 (C96), pleurocoels in cranial dorsal centra have tapering acute, caudal margins; P1 (C137), centra of middle caudals display a dorsoventrally compressed transverse cross-section, and; Q5 (C136), ventral surfaces of cranial caudal centra are mildly or deeply excavated, with the excavation bounded by a ventrolateral ridge on each side (convergent in *Barosaurus* and *Diplodocus*). One state, 12 (node 7), of Upchurch (1995) is present in QM F3390 and QM F7291, femoral distal condyles extend prominently anteriorly as well as posteriorly.

Character assessment by specimen

QM F311: This incomplete humerus presents no useful characters beyond one - deltopectoral crest low - indicating that it pertains to a sauropod.

QM F2316: Holotype of *Austrosaurus mckillopi*: QM F2316 consists largely of a series of incomplete dorsal vertebrae, with the neural arches and much of the surficial bone often partially or entirely missing. Longman (1933) described three individual pieces but in June 1933, after his publication, a further five large and more than ten small pieces were acquired. One of these, a dorsal lacking the transverse processes and neural spine but with the neural arch and its laminae preserved, adds substantially to the understanding of the anatomy of *Austrosaurus*. In almost all pieces, the articulations between adjacent centra are usually maintained, but the middle portions of the centra are broken (figure 1). In spite of the preservation, several character states can be confidently determined. The material shows that posterior trunk vertebrae possessed centro-parapophyseal laminae and that eye-shaped pleurocoels were present in these vertebrae (figure 1). The posterior dorsal centra were opisthocoelous, with a convexity present on the anterior face of the centrum (figure 1) and the presacral vertebrae were composed of spongy bone. These character states indicate that *A. mckillopi* is a member of the Titanosauria of Salgado *et al.* (1997).

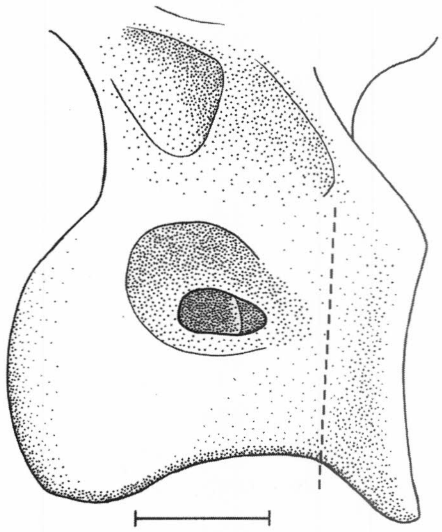

Figure 1. Reconstructed dorsal vertebra of *Austrosaurus mckillopi* Longman (1933) based on block A of QM F2316. The dashed line marks the region at which the vertebrae are broken. The part behind it has been reconstructed from the adjacent preceding vertebra. Scale bar 5 cm

QM F2470: This consists of six proximal caudals preserved as three articulated pairs, one pair retaining both neural arches and one chevron, plus one middle and one distal caudal. Although unfortunately lacking locality data, it is the best-preserved of the Australian sauropod material. The neural arches are positioned anteriorly on the middle and posterior caudal centra and the middle caudal centrum is depressed with dorsoventrally convex lateral faces. Both characters indicate titanosauriform affinities (Salgado *et al.*, 1997). The ventral surfaces of the cranial caudal centra are mildly or deeply excavated, with the excavation bounded by a ventrolateral ridge on each side: this character indicates titanosaurid affinities, although also appearing convergently in other taxa as mentioned above. The lengths of the proximal caudal centra increase backwards, thus suggesting a match with part of Upchurch's state W14 (lengths of caudal centra gradually increase from Cd1-Cd20). This state is characteristic of the Diplodocidæ. However, in view of the indication of titanosauriform affinities by the other characters, this is considered here to be a reversal.

QM F3390: The specimen includes a well-preserved proximal portion of femur (no longer as complete as figured by Coombs and Molnar, 1981) and the distal end of presumably the same femur, as well as the proximal and distal ends of a humerus. The distal femur shows the condyles extending prominently anteriorly as well as posteriorly and the proximal femur displays a prominent lateral bulge below the greater trochanter. Femoral distal condyles that project anteriorly as well as posteriorly simply indicates membership in the Neosauropoda, but the lateral bulge is found in the Titanosauriformes.

QM F6737: This material consists of incomplete dorsals, pieces of ribs, proximal and middle caudals, a partial scapula, a coracoid (incorrectly referred to QM F7880 by Coombs and Molnar, 1981), metacarpals, and the proximal end of an ischium. It shows the characters given in Table 1, in other words characters 1, 8, 9 and 15 of Salgado *et al.* (1997), 59, 68, 92 and 102 of Wilson and Sereno (1998), and B5, C27, K9, P1 and Q5 of Upchurch (1998). Several of these merely support its identification as eusauropod. Mid- and posterior caudal neural arches positioned anteriorly (15 of Salgado *et al.*, 1997) and posterior dorsal centra opisthocoelous, with convexity present on anterior face of centrum (92 of Wilson and Sereno, 1998) indicate Titanosauriformes; presacral vertebrae composed of spongy bone indicates Somphospondyli; and centra of middle caudals displaying dorsoventrally compressed transverse cross-sections (102 of Wilson and Sereno, 1998) indicates Titanosauridæ.

QM F7291: This specimen consists of a metacarpal, the distal end of a femur and unidentified fragments. These are apparently the remains of a more complete specimen that had long been exposed. The femoral piece shows that the distal condyles extend prominently anteriorly as well as posteriorly, indicating only that it is neosauropod.

QM F7292: Caudals, two partial ulnae, two partial radii, two partial humeri, a partial scapula (substantially more complete than realized by Coombs and Molnar, 1981), four metacarpals and pieces of ribs

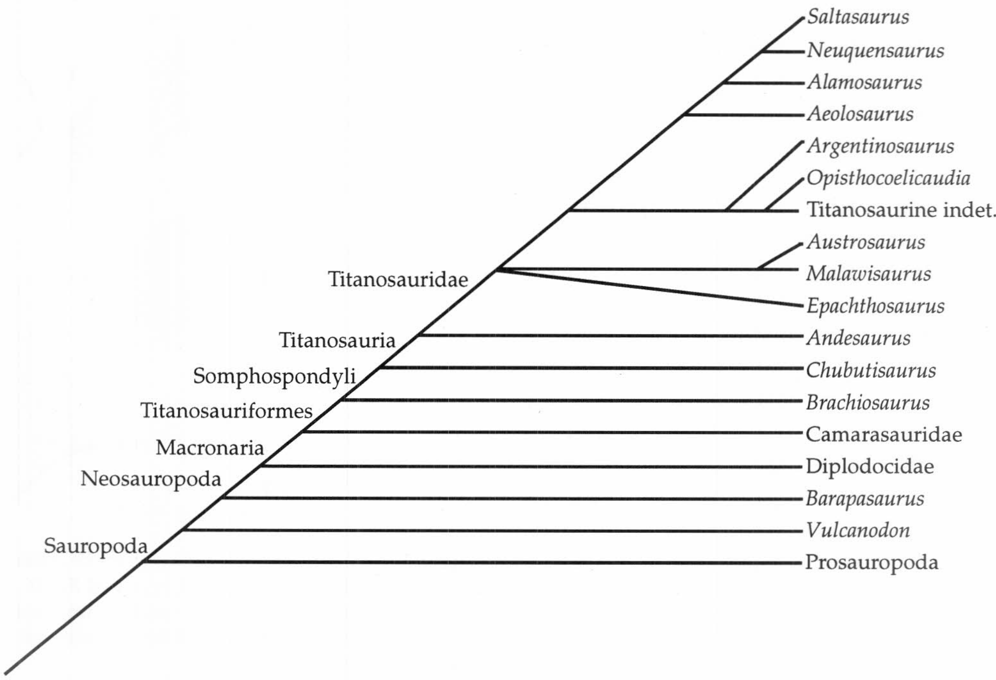

Figure 2. Suggested phylogenetic position of *Austrosaurus* shown on the cladogram of Salgado *et al.* (1997).

make up this specimen. Although this material includes more than ten middle and distal caudals, these exhibit none of the derived states of Salgado *et al.* (1997) or Wilson and Sereno (1998), however the neural arches of the middle caudals are situated on the cranial half of the centra. This character indicates little more than that the material pertains to a macronarian sauropod. The metacarpals have subtriangular proximal ends, thus matching (part of) state 81 (metacarpal proximal ends subtriangular, composite proximal articular surface U-shaped) of Wilson and Sereno (1998), supporting neosauropod affinities.

QM F7880: This incomplete femoral head presents no characters beyond those indicating that it probably pertains to a sauropod.

QM F10916: Three incomplete proximal caudals and one distal caudal make up this specimen. All retain the bases of the neural arches and transverse processes. The largest is substantially more worn and abraded than the others, and lacks much of the surficial lamellar bone: the others are among the better-preserved of the Queensland sauropod material. This material also affords none of the derived states used by Salgado *et al.* (1997) or Wilson and Sereno (1998), but does show that the ventral surfaces of proximal caudal centra are mildly or deeply excavated, the excavation bounded by a ventrolateral ridge on each side (character Q5 of Upchurch, 1998). This state indicates titanosaurid affinities.

Phylogenetic implications of the character states present

Vertebral characters 1 and 8 of Salgado *et al.* (1997) - opisthocoelous cervical and anterior trunk vertebrae and presence of pleurocoels on presacral vertebrae - define sauropods and neosauropods respectively and character 9, opisthocoelous cervical and anterior trunk vertebrae, defines camarasauromorphs: these characters are seen in both QM F2316 and QM F6737. Character 15, neural arches positioned anteriorly in mid- and posterior caudal centra, defines the Titanosauriformes, and is seen in both QM F2470 and QM F6737, and characters 20 and 22 - eye-shaped pleurocoels in trunk vertebrae and centro-parapophyseal lamina in posterior trunk vertebrae - define the Titanosauria and are seen in QM F2316 (*Austrosaurus mckillopi*). Depressed middle and posterior caudal centra with dorsoventrally convex lateral faces (character 34), at least partly present in QM F2470, defines an unnamed node within the titanosaurians. Characters 92 and 102 of Wilson and Sereno (1998) - posterior dorsal centra opisthocoelous, with anterior face of centrum convex, and presacral vertebrae composed of spongy bone - (seen in QM F2316 and QM F6737) are, respectively, diagnostic of the nodes Titanosauriformes and Somphospondyli. Upchurch's (1998) characters M1 (pleurocoels in cranial dorsal centra have tapering acute, caudal margins), P1 (centra of middle caudals

Table 1. Characters and taxonomic assignments of Cretaceous Queensland sauropods.

Specimen	Taxon indicated	Characters present
QM F31	Sauropoda	Deltopectoral crest of humerus low.
QM F2316, holotype of Austrosaurus mckillop	Titanosauria	Opisthocoelous cervical and anterior trunk vertebrae (presumed). Posterior dorsal centra opisthocoelous, convexity present on anterior face of centrum. Presacral vertebrae composed of spongy bone. Presence of pleurocoels on presacral vertebrae. Presacral pleurocoels deep and invaginated. Eye-shaped pleurocoels in trunk vertebrae. Presence of centro-parapophyseal lamina in posterior trunk vertebrae.
QM F2470	Titanosauridae	Ventral surfaces of cranial caudal centra: are mildly or deeply excavated, with the excavation bounded by a ventrolateral ridge on each side. Centra of middle caudals display a dorsoventrally compressed transverse cross-section. Neural arches positioned anteriorly in mid- and posterior caudal centra. Depressed mid- and posterior caudal centra with dorsoventrally convex lateral faces.
QM F3390	Titanosauriformes	Femoral shaft with elliptical cross-section, long axis oriented mediolaterally. Femur with proximal one-third of shaft deflected medially. Femoral distal condyles extend prominently anteriorly as well as posteriorly.
QM F6737	Titanosauridae	Opisthocoelous cervical and anterior trunk vertebrae. Opisthocoelous posterior trunk and sacral centra. Neural arches positioned anteriorly in mid- and posterior caudal centra. Presence of pleurocoels on presacral vertebrae. Presacral pleurocoels deep and invaginated. Presacral vertebrae composed of spongy bone. Centrum length divided by centrum height (in the most craniad caudals) is approximately 0.5-0.6. Ventral surfaces of cranial caudal centra are mildly excavated, with the excavation bounded by a ventrolateral ridge on each side. Centra of middle caudals display a dorsoventrally compressed transverse cross-section.
QM F7291	Neosauropoda	Femoral distal condyles extend prominently anteriorly as well as posteriorly.
QM F7292	Titanosauriformes	Neural arches of middle caudals are situated on the cranial half of the centrum.
QM F7880	None	None
QM F10916	Titanosauridae	Centrum length divided by centrum height (in the most craniad caudals) is approximately 0.5-0.6. Ventral surfaces of cranial caudal centra are mildly excavated, with the excavation bounded by a ventrolateral ridge on each side.

display a dorsoventrally compressed transverse cross-section), and Q5 (ventral surfaces of cranial caudal centra are mildly or deeply excavated, with the excavation bounded by a ventrolateral ridge on each side) define the Titanosauroidea, the Titanosauridæ and *Opisthocoelicaudia* + *Saltasaurus* respectively. M1 is seen in QM F2316, P1 and Q5 are both found in QM F2740, and Q5 alone in QM F6737 and QM F10916.

Femoral character state 10 (of Wilson and Sereno, 1998), shaft with elliptical cross-section with long axis oriented mediolaterally, indicates sauropods, character 12 (node 7) (of Upchurch, 1995), femoral distal condyles extend prominently anteriorly as well as posteriorly, indicates neosauropods, and characters 100 (of Wilson and Sereno, 1998), femur with proximal one-third of shaft deflected medially, and 19 (of Salgado *et al.*, 1997), opisthocoelous cervical and anterior trunk vertebrae, indicate Titanosauriformes: all are seen in QM F3390.

In summary, the presence of anteriorly placed neural arches in mid- and posterior caudals (character 15 of Salgado *et al.*, 1997) in QM F2470 and QM F6737 indicates that this material derives from a member of the Titanosauriformes, and eye-shaped pleurocoels in the trunk vertebrae, and centro-parapophyseal lamina in the posterior trunk vertebrae (characters 20 and 22 of Salgado *et al.*, 1997) in QM

F2316 (*Austrosaurus mckillopi*) indicates that it belongs to the Titanosauria. Depressed mid- and posterior caudal centra with dorsoventrally convex lateral faces (character 34) defines an unnamed node within the Titanosauria, indicating that QM F2470 is a member of this group. Opisthocoelous posterior dorsal centra, with anterior face of centrum convex, and presacral vertebrae composed of spongy bone (characters 92 and 102 of Wilson and Sereno, 1998) in QM F2316 and QM F6737 show that theses specimens derive from members of the Somphospondyli. Centra of middle caudals that display a dorsoventrally compressed transverse cross-section, and ventral surfaces of cranial caudal centra excavated, with the excavation bounded by a ventrolateral ridge on each side, (characters P1 and Q5 of Upchurch, 1998) – one or both characters seen in QM F2740, QM F6737 and QM F10916-respectively diagnose the Titanosauridæ and *Opisthocoelicaudia* + *Saltasaurus*, indicating that this material is titanosaurid. The medial deflection of the proximal third of the femoral shaft (character 100 of Wilson and Sereno, 1998, and 19 of Salgado *et al.*, 1997) found in QM F3390 indicates that it is a titanosauriform.

Conclusions

QM F311 and QM F7880 can be assigned only to the Sauropoda. QM F7291 and QM F7292 pertain to the Neosauropoda. QM F2316 (the holotype of *Austrosaurus mckillopi*) belongs to the Titanosauria (Salgado *et al.*, 1997). QM F3390 also belongs to the Titanosauriformes. QM F6737, QM F2470 and QM F10916 all show characters of the Titanosauridæ.

Thus five specimens - QM F2316 (*A. mckillopi*), QM F2470, QM F3390, QM F6737, QM F10916 - have character states clearly indicating their membership in the Titanosauriformes and three of these - all but QM F2316 and QM F3390 - in lower level taxa within the Somphospondyli. In other words, they are more closely related to *Saltasaurus* than to *Brachiosaurus*. The remaining specimens from this region (QM F311, QM F7291, QM F7292, QM F7880) lack character states showing their lower-level affinities. Only a single character state found in a single specimen - Upchurch's W14 in QM F2740 - contraindicates titanosauriform affinities: but this specimen also has three states indicating titanosauriform affinities.

This analysis provides no support for the existence of more than a single taxon of sauropods, although admittedly the material is incomplete. However, preliminary inspection of material not discussed here suggests that a second taxon may have been present.

The conclusion that the Cretaceous sauropods of central Queensland represented a persistently primitive lineage (Coombs and Molnar, 1981) is incorrect. They represent a lineage (Figure 2) at least as advanced as *Malawisaurus* (Jacobs *et al.*, 1993), and show that titanosaurids did, after all, inhabit Australia. If, as seems plausible, all the specimens discussed here do pertain to a single genus, it must have been a titanosaurid; if not, a titanosaurid and at least one less advanced taxon, such as *Andesaurus* (Calvo and Bonaparte, 1991), were present. The suggestions of Salgado (1993) and Salgado and Calvo (1997) that *Austrosaurus* was a titanosauriform are correct.

The presence of one or more titanosaurians in the "Middle Cretaceous" indicates that this lineage arrived in what is now Australia by the Early Cretaceous, possibly during the Late Jurassic. The absence of strongly procoelous caudals in the Australian form, an absence also seen in *Malawisaurus* (Jacobs *et al.*, 1993), suggests that these forms may be related, and may have formed part of an eastern Gondwanan clade of titanosaurs distinct from the better-known titanosaurids of South America.

References

Calvo, J. O. and Bonaparte, J. F. 1991. *Andesaurus delgadoi* gen. et sp. nov. (Saurischia-Sauropoda), dinosaurio Titanosauridæ de la Formación Río Limay (Albiano-Cenomaniano), Neuquén, Argentina. *Ameghiniana* 28: 303-310.

Coombs, W. P., Jr. and Molnar, R. E. 1981. Sauropoda (Reptilia, Saurischia) from the Cretaceous of Queensland. *Memoirs of the Queensland Museum* 20: 351-373.

Giménez, O. 1992. Estudio preliminar del miembro anterior de los saurópodos, Titanosauridæ. Programa y Resúmenes *9° Jornadas Argentinas de Paleontología de Vertebrados* p. 43 (abstract).

Huene, F. R. von 1929. Los Saurisquios y Ornitisquios del Cretáceo Argentino. *Anales del Museo de La Plata* (ser. 2), 3: 1-196.

Jacobs, L. L., Winkler, D. A., Downs, W. R. and Gomani, E. M. 1993. New material of an Early Cretaceous titanosaurid sauropod dinosaur from Malawi. *Palaeontology*, 36: 523-534.

Longman, H. A. 1933. A new dinosaur from the Queensland Cretaceous. *Memoirs of the Queensland Museum* 10: 131-144.

Salgado, L. 1993. Comments of *Chubutisaurus insignis* Del Corro (Saurischia, Sauropoda). *Ameghiniana* 30: 265-270.

Salgado, L. and Coria, R. A. 1993. Consideraciones sobre las relaciones filogenéticas de *Opisthocoelicaudia skarzynskii* (Sauropoda) del Cretácico superior de Mongolia. Programa y Resúmenes *10° Jornadas Argentinas de Paleontología de Vertebrados* p. 60 (abstract).

Salgado, L. and Calvo, J. O. 1997. Evolution of titanosaurid sauropods. II: The cranial evidence. *Ameghiniana* 34: 33-48.

Salgado, L., Coria, R. A. and Calvo, J. O. 1997. Evolution of titanosaurid sauropods. I: Phylogenetic analysis based on the postcranial evidence. *Ameghiniana* 34: 3-32.

Upchurch, P. 1995. The evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society of London* (B) 349: 365-390.

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

Wilson, J. A. and Sereno, P. C. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Society of Vertebrate Paleontology Memoir* 5: 1-68.

Accepted: December 27th, 2000.