

The end of the sauropod dinosaur hiatus in North America

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ABSTRACT

Sauropod dinosaurs reached their acme in abundance and diversity in North America during the Late Jurassic. Persisting in lesser numbers into the Early Cretaceous, sauropods disappeared from the North American fossil record from the Cenomanian until the Campanian or Maastrichtian stage of the Late Cretaceous. This ca. 25–30 million-year long sauropod hiatus has been attributed to either a true extinction, perhaps due to competition with ornithischian dinosaurs, or a false extinction, due to non-preservation of sediments bearing sauropods. The duration of the sauropod hiatus remains in question due to uncertainty in the ages and affinities of the specimens bounding the observed gap. In this paper, we re-examine the phylogenetic affinity of materials from Campanian-aged sediments of Adobe Canyon, Arizona that currently mark the end of the sauropod hiatus. Based on the original description of those remains and new specimens from the same formation, we conclude that the Adobe Canyon vertebrae do not pertain to titanosaurs, but to hadrosaurid dinosaurs. Other reports of Campanian North American titanosaurs are imprecisely or erroneously dated and/or identified. Based on this reassessment, the sauropod hiatus extended until the last 5 million years of the Cretaceous. Reintroduction of sauropods into North America in the Maastrichtian is first registered ca. 30 million years after the first recorded dispersals of dinosaur taxa between the continent and Asia (e.g., ceratopsians, pachycephalosaurids, theropods), but is nearly coincident with the dispersal of derived hadrosaurids to South America.

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1. Introduction

Sauropod dinosaurs were the most diverse and abundant herbivores in Late Jurassic North American faunas, but they declined in diversity in the Early Cretaceous, being comprised only of basal members of the clade Titanosauriformes (Wedel et al., 2000; Wilson, 2002; Rose, 2007; Chure et al., 2010). Near the middle of the Cretaceous (ca. 100 Ma), sauropods disappeared from the North American body fossil and ichnofossil records and reappeared in the body fossil record near the end of the Cretaceous. All Maastrichtian North American sauropods have been referred to a single species, *Alamosaurus sanjuanensis*, which belongs to the sauropod clade Titanosauria and is found throughout the southwestern United States (Sullivan and Lucas, 2000; Williamson and Weil, 2008). In contrast, Campanian North American sauropod remains have not been assigned to a particular genus or species, but all have been referred to Titanosauria (McCord, 1997; Montellano-Ballesteros, 2003).

The period between the disappearance and reappearance of sauropods in North America has been termed the “sauropod hiatus” by Lucas and Hunt (1989:75) who provided two explanatory hypotheses. The first, termed the “austral immigrant” hypothesis,

recognizes a true sauropod regional extinction in North America at ca. 100 Ma followed by dispersal of *Alamosaurus* from South America ca. 25–30 Ma later. This hypothesis can be generalized to an “immigrant” hypothesis because derived titanosaurs are known from other landmasses adjacent to North America (Le Loeuff, 1993; Wilson and Sereno, 1998). The second, termed the “inland herbivore” scenario, attributes the absence of titanosaurs during most of the Late Cretaceous in North America to a lack of preservation of sediments representing appropriate titanosaur-supporting environments at that time, specifically the inland paleoenvironments that are the setting for the relatively few titanosaur body fossils that are preserved (Lucas and Hunt, 1989).

Choosing between these hypotheses depends on the lower-level relationships of *Alamosaurus*, and thus far all phylogenetic studies including *Alamosaurus* posit that it has its closest relatives outside of North America (e.g., Salgado et al., 1997; Wilson, 2002; Upchurch et al., 2004; Calvo et al., 2008), favoring the immigrant hypothesis but not the inland herbivore scenario. However, if the indeterminate Campanian titanosaur remains cannot be referred to *Alamosaurus* (see below), they raise the possibility that there is a second Late Cretaceous titanosaur taxon present in North America. Herein, new materials resembling elements previously considered to pertain to titanosaurs are described and their taxonomic identity and implications for latest Cretaceous North American paleobiogeography are discussed.

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Institutional abbreviations: AMNH, American Museum of Natural History, New York, USA; ASDM, Arizona-Sonora Desert Museum, Tucson, USA; IGM, Instituto de Geología, Universidad Nacional Autónoma de México; MLP, Museo de La Plata, La Plata, Argentina; UALP, University of Arizona Laboratory of Paleontology, Tucson, USA.

2. Systematic palaeontology

DINOSAURIA Owen, 1842

ORNITHISCHIA Seeley, 1888

ORNITHOPODA Marsh, 1881

HADROSAURIDAE Cope, 1869

gen. et sp. indet.

Material: two posterior cervical vertebrae (ASDM 482, 552) and one partial middle dorsal vertebra (ASDM 485) belonging to one individual.

Locality, horizon, and age: Adobe Canyon, Santa Rita Mountains, Arizona, USA (Fig. 1). Shale member of the Fort Crittenden Formation. The Fort Crittenden Formation and its correlatives in other regions are thought to be Campanian in age because they are conformably overlain by volcanic rocks that are 70–75 Ma old (Heckert et al., 2003; Riley, 2004).

2.1. Description

All three vertebrae were found within 2 m of one another (along with numerous other fragmentary bones) and are regarded as belonging to one individual. They were embedded in a hard, reddish–purple calcareous mudstone matrix that was removed with a pneumatic drill after periodic submergence in weak formic acid (7%, buffered with calcium phosphate). The bone surface is incomplete in some places due to pre-burial erosion and cracking of the bone. The vertebrae were preserved in direct contact with fragments of several gastropod shells, which were partially embedded in the matrix surrounding the bone. Most of these gastropods are broken, but one, embedded on the posterior lip of the neural canal of ASDM 552, is relatively complete. As preserved, it is 1.4 cm in diameter and 0.9 cm

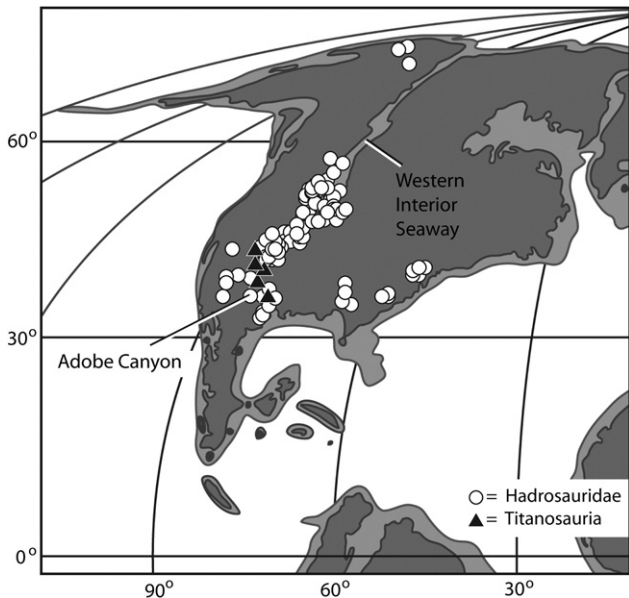


Fig. 1. Map of Campanian and Maastrichtian titanosaurs (triangles) and hadrosaurids (circles) localities in North America, with the location of the Adobe Canyon vertebrae indicated. Data amalgamated and modified from the Paleobiology database (www.pdb.org); data were downloaded on 2/02/10 with the parameters “Campanian”, “Maastrichtian”, “Titanosauria”, and “Hadrosauridae”, plotted on a 65 Ma Mollweide paleogeographic reconstruction, downloaded from Blakey, 2006.

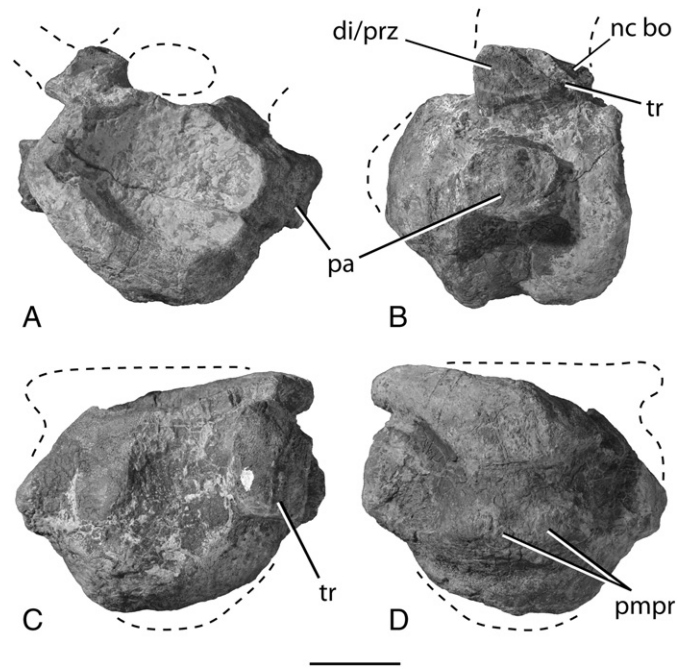


Fig. 2. Posterior cervical vertebra ASDM 552 in A. anterior, B. left lateral, C. dorsal and D. ventral views. Abbreviations: di/prz, broken base of diapophysis and prezygapophysis; nc bo, neural canal border; pa, parapophysis; pmpr, paramedian processes; tr, trough. Dashed lines indicate missing bone. Scale bar equals 5 cm.

in height, and probably pertains to the river snail *Viviparus*, which is common in the shale member of the Fort Crittenden Formation, where it is often preserved in close association with vertebrate bones (Miller, 1964; Heckert et al., 2003).

Two of these vertebrae are cervical vertebrae based on the presence of parapophyses on the centrum (ASDM 582, 482; Figs. 2 and 3). They are similar to one another in size, shape, and completeness. The centra are strongly opisthocelous and wider than tall. The centrum of the more complete cervical vertebra measures 13.2 cm long and 11.8 cm tall posteriorly (Fig. 2). We estimate that it was 15.8 cm wide. The other cervical centrum has lateral faces that are angled inwards dorsally and ventrally, giving it a hexagonal appearance in anterior and posterior views (Figs. 2 and 3). On the ventral aspect of the centrum, near the rim of the condyle, there are two subtle paramedian processes whose function is unknown. The diapophyses, parapophyses, and neural arches of both cervical vertebrae are broken off near their bases, but a trough of finished bone delineates the broken base of the neural arch pedicle from that of the diapophysis on the left side (Fig. 2). The neural canal is about 5.2 cm wide, or about 30% the width of the centrum. The parapophyses extend from the mid-length of the vertebra to the edge of the condyle, and are large, stalk-like, and oval, with their long axis directed anteroposteriorly. They are set off from the base of the diapophyses by a dorsolateral embayment (Figs. 2 and 3).

The third vertebra is a dorsal vertebra based on the presence of a dorsoventrally elongate parapophysis positioned on the neural arch and prominent, dorsolaterally projecting diapophyses (ASDM 485; Fig. 4). The dorsal vertebra is broken asymmetrically just above its neural canal. A ca. 20 cm long fragment of a rib was preserved in contact with this break. Exposed surfaces among the broken pieces of the centrum (now glued together) reveal its apneumatic structure. The centrum is slightly opisthocelous and wider posteriorly than anteriorly, measuring 11.7 cm long, 13.4 cm wide, and 12.4 cm tall posteriorly. The ventral surface is weakly keeled. The parapophyses are posterodorsally oriented, low-relief, oval structures that are tucked anterior and ventral to the diapophyses. The right diapophysis is broken and the articular surface for the tuberculum of the dorsal rib

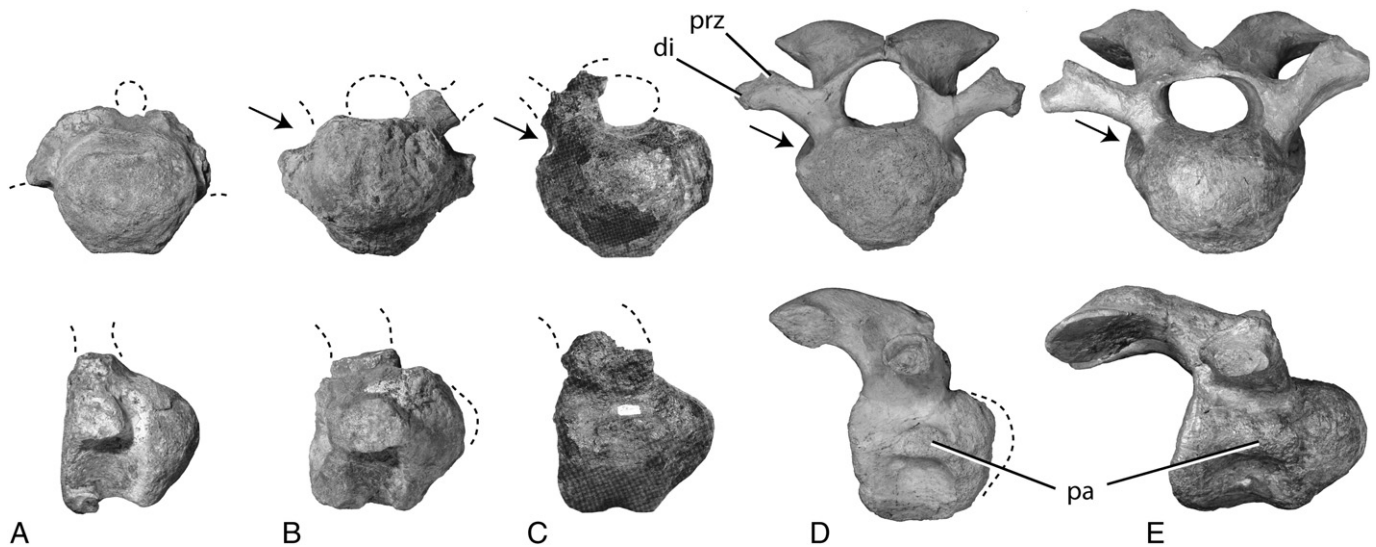


Fig. 3. Comparison of Adobe Canyon vertebrae, titanosaur caudal vertebrae, and hadrosaurid cervical vertebrae. A. anterior caudal vertebra of *Neuquensaurus australis* (MLP Ly 2) in posterior (top) and left lateral (bottom) views, B. cervical vertebra of an indeterminate hadrosaurid from Adobe Canyon (ASDM 552) in anterior (top) and right lateral (bottom) views, C. cervical vertebra of an indeterminate hadrosaurid (UALP 4005) in anterior (top) and right lateral (bottom) views, D. cervical vertebra of *G. mongoliensis* (AMNH 6551) in anterior (top) and right lateral (bottom) views, E. cervical vertebra of *H. altispinus* (AMNH 5272) in anterior (top) and right lateral (bottom) views. Vertebrae are scaled to the same centrum length. Dashed lines indicate missing bone. Arrows indicate an “embayment” between the parapophysis and diapophysis, which is absent in the caudal vertebra of *Neuquensaurus australis*. Abbreviations: di, diapophysis; pa, parapophysis; prz, prezygapophysis. Image of UALP 4005 © Copyright 1997. The Society of Vertebrate Paleontology. Reprinted and distributed with permission of the Society of Vertebrate Paleontology.

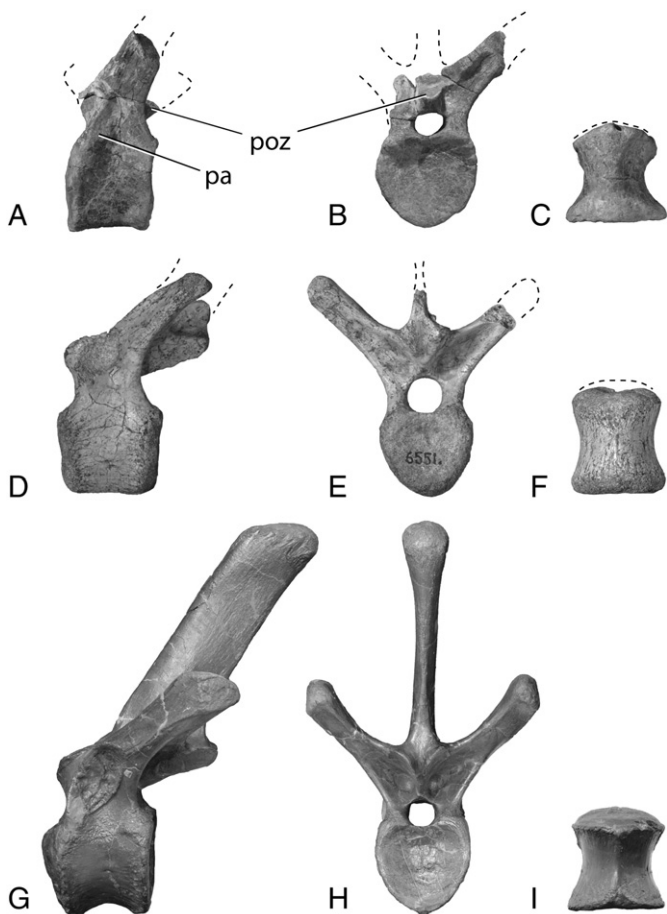


Fig. 4. Dorsal vertebrae of hadrosaurid dinosaurs, scaled to centrum length. A–C. Dorsal vertebra of an indeterminate hadrosaurid from Adobe Canyon (ASDM 485). D–F. Dorsal vertebra of *G. mongoliensis* (AMNH 6551). G–I. Dorsal vertebra of *G. notabilis*. A, D, G. Left lateral view, B, E, H. Posterior view, C, F, I. Ventral view. Vertebrae are scaled to the same centrum length. Dashed lines indicate missing bone. Abbreviations: pa, parapophysis; poz, postzygapophysis.

is not preserved. The zygapophyses are broken, but the pedicel leading to the postzygapophyses is preserved, which is set off from the diapophyses posterolaterally by a fossa (Fig. 4). All three vertebrae bear fully fused neurocentral junctions with no trace of a suture.

3. Discussion

3.1. Taxonomic affinity of the Adobe Canyon vertebrae

These three vertebrae (ASDM 482, 485, 552) pertain to a single individual because they were found in close association and are similar in size and state of fusion. The posterior cervical vertebrae (ASDM 482, 552) resemble those of hadrosaurids such as *Gilmoreosaurus mongoliensis* and *Hypacrosaurus altispinus* because they are opisthocoelous, hexagonal in cross-section, and have axially elongate parapophyses positioned near the condyle (Fig. 3). Likewise, the dorsal vertebra is very similar to that of Late Cretaceous hadrosaurids, such as the Campanian *Gryposaurus notabilis* (AMNH 5350; Fig. 4), which has a weakly keeled centrum and posterodorsally projecting diapophyses separated posteriorly from the postzygapophyses by a well-defined fossa on each side. The axial skeleton is not currently a rich source of information for phylogenetic studies of hadrosaurs (e.g., Horner et al., 2004), so a precise phylogenetic position for these Adobe Canyon vertebrae is not possible at this time.

The posterior cervical vertebrae (ASDM 482, 552) are nearly identical to a vertebra from the Adobe Canyon described by McCord (1997:620) as the caudal vertebra of a “titanosaurid” sauropod (UALP 4005; Fig. 3C). This putative titanosaur caudal vertebra currently constitutes the specimen that ends the sauropod hiatus in the middle-late Campanian. These posterior cervical vertebrae (UALP 4005; ASDM 482, 552) share a nearly identical hexagonal centrum shape, dorsolaterally projecting diapophyses/neural arch pedicles, and a wide neural canal. The parapophyses of UALP 4005 are smaller than those of either of the ASDM specimens, due to breakage and/or intracolumnar variation. Like the ASDM specimens described above, UALP 4005 also comes from the shale member of the Fort Crittenden Formation in the Adobe Canyon (Fig. 1.; see Heckert et al., 2003; Lucas and Heckert, 2005 for discussion of the provenance of UALP 4005). Their identical morphology and provenance suggest that they belong

to the same species, but this cannot be known with certainty until apomorphies can be identified.

McCord (1997: 620) regarded UALP 4005 as being “virtually indistinguishable from *Alamosaurus sanjuanensis*” but our study of vertebral remains from Adobe Canyon reveals several notable differences with *Alamosaurus* and other titanosaurs. UALP 4005 has a hexagonal cross-section of its centrum due to ventromedially-sloping lateral walls, but the anterior caudal centra of *Alamosaurus* are subquadangular and taller than wide in anterior and posterior views. Although the cross-sections of more distal caudal centra of *Alamosaurus* are subcircular in cross-section or wider than tall (Gilmore, 1946: pl. 8), none are hexagonal in anteroposterior views. Additionally, the neural canal is substantially larger relative to the centrum in the UALP 4005 than in *Alamosaurus*. The transverse processes in *Alamosaurus* span the neurocentral junction, whereas the laterally-projecting processes of UALP 4005 (interpreted as parapophyses here) are located at the mid-height of the centrum, below the neurocentral junction. The Adobe Canyon vertebrae are not referable to *Alamosaurus*.

Other titanosaurs have a vertebral centrum cross-section that more closely resembles the Adobe Canyon vertebrae, but other features distinguish them. The anterior and middle caudal vertebrae of some South American titanosaurs (e.g., *Neuquensaurus australis*, Fig. 3A) resemble the Adobe Canyon vertebrae in their elongation, development of their condyles, medioventrally-sloping lateral walls (imparting a subhexagonal centrum shape in anterior/posterior views), and their subtle paramedian processes on the rim of the condyle, which could be interpreted as chevron facets. However, the Adobe Canyon vertebrae do not resemble the caudal vertebrae of titanosaurs in that their neural arches are set off dorsolaterally by an embayment (Fig. 3) from a stalk-like lateral process (interpreted here as a parapophysis). Likewise, the right neural arch pedicle of ASDM 482 bears a trough of finished bone (Fig. 2) that indicates the presence of a separate diapophysis and neural canal border. The subtle paramedian processes on the ventral rim of the condyle are not chevron facets based on their shape and position. Similar processes are present on the cervical vertebrae of some hadrosaurids, such as *H. altispinus* (AMNH 5272, M. D'Emic pers. obs.). Another salient feature that the Adobe Canyon vertebrae and hadrosaurid cervical vertebrae share is a large neural canal diameter relative to centrum size (Fig. 3). Because of these similarities, UALP 4005, ASDM 482, and ASDM 552 are regarded as cervical vertebrae of a hadrosaurid dinosaur, a taxonomic decision strengthened by the association of the ASDM specimens with a hadrosaurid dorsal vertebra.

Four vertebrae from Chihuahua, Mexico, were regarded as belonging to an indeterminate “titanosaurid” by Montellano-Ballesteros (2003:160). One of these vertebrae, IGM 6080–2, has concave and convex articular ends, which indicates that it is either strongly procoelous or opisthocelous. Another vertebra, IGM 6080–5, resembles some of the sacral vertebrae of *G. notabilis* (AMNH 5350; Lull and Wright, 1942: pl. 5C). These vertebrae cannot be definitively identified as titanosaur or hadrosaurid vertebrae, an assessment that will remain ambiguous until more diagnostic remains are discovered. Should they be positively identified as a titanosaur, the age of the sediments that they come from, which are presently regarded as either Campanian or Maastrichtian, should be investigated further.

3.2. The end of the sauropod hiatus

Hypotheses explaining the North American sauropod hiatus require precise age dates and identifications for the sauropod taxa bounding that interval, as well as information about their paleoenvironment and about Late Cretaceous paleogeography. The two main hypotheses explaining the absence of sauropods during much of the Late Cretaceous of North America, the “immigrant” and “inland herbivore” hypotheses (Lucas and Hunt, 1989), depend on whether or not *Alamosaurus*' closest relatives are found on North America or another landmass, and if the sauropod hiatus represents a true absence, or some bias.

As shown above, no definitive titanosaur fossils exist before the Maastrichtian in North America. Lucas and Sullivan (2000) reported sauropod specimens from the Campanian De–Na–Zin Member of the Kirtland Formation, but these and all definitive sauropod specimens from the San Juan Basin are now regarded as pertaining to the Maastrichtian Naashoibito Member of the Ojo Alamo Formation (Williamson and Weil, 2008; R. Sullivan, pers. comm. 2010). Although there are reports of possible titanosaurs from the Early Cretaceous of North America (e.g., Britt et al., 1998; Tidwell and Carpenter, 2007), none bear features that indicate close affinities with *Alamosaurus*, which weakens support for the existence of an unsampled lineage of inland sauropods in the Late Cretaceous of North America. Instead, all cladistic analyses that include *Alamosaurus* resolve it as a derived saltasaurid titanosaur, and although its lower-level relationships within that group are uncertain, all of its proposed sister-taxa have been from either Asia or South America (e.g., Salgado et al., 1997; Wilson, 2002; González Riga, 2003; Upchurch et al., 2004; Calvo et al., 2008). These results suggest that *Alamosaurus* likely reappeared in the Maastrichtian of North America via dispersal from either Asia or South America (Lucas and Hunt, 1989; Wilson and Sereno, 1998).

Determining the dispersal route for *Alamosaurus* requires information about potential land bridges linking it to its putative Asian or South American sister taxa. The appearance of neoceratopsians (Chinnery et al., 1998), oviraptorosaurs (Ostrom, 1970), and therizinosaurids (Clark et al., 2004) on Asia and North America in the late Aptian–Cenomanian (ca. 100 Ma; Cifelli et al., 1997; Kirkland and Madsen, 2007) provides evidence of a land connection between those landmasses. This land connection appears to have been open to dinosaurs through the Late Cretaceous, as indicated by closely related Asian and North American pachycephalosaurids, hadrosaurids (Sereno, 1999; Godefroit et al., 2003), tyrannosaurids (Sereno et al., 2009), alvarezsaurids (Longrich and Currie, 2008), troodontids (Turner et al., 2007), and dromaeosaurs (Longrich and Currie, 2009). In contrast, it does not appear that land connections between North America and South America were in place until the latest Campanian–Early Maastrichtian, as evidenced by the presence of the derived hadrosaurid *Secernosaurus koernerii* in South America, whose successive sister-taxa are from pre-Maastrichtian sediments of North America (Prieto-Marquez and Salinas, 2010).

Dinosaur fossil evidence suggests that an Asiatic land bridge was present during the last ca. 35 million years of the Cretaceous, but the paleo-Panamanian land bridge does not appear to have been utilized by dinosaurs until about the last 5 million years of the Period (Cifelli et al., 1997; Prieto-Marquez and Salinas, 2010; see above). It appears that titanosaur sauropods could have taken advantage of either land bridge to North America. Although it has been suggested that hadrosaurids and titanosaurs had distinct environmental preferences (coastal/marginal marine for hadrosaurids, intramontane basin/alluvial plain for titanosaurs; Lehman, 1987, 2001; Sampson and Loewen, 2005; Butler and Barrett, 2008a,b; Mannion and Upchurch, 2010), these preferences may not have prevented some titanosaurs and hadrosaurids from taking advantage of the same dispersal routes. In some cases titanosaurs and hadrosaurids are recovered from the same formations in North America and in South America (specifically, in the cases of *Alamosaurus* and *Secernosaurus*), suggesting that some members of these groups shared habitats (Bonaparte et al., 1984; Williamson, 2000; Sullivan and Lucas, 2006). Determining the origin of *Alamosaurus* in the Maastrichtian of North America will require developing a robust hypothesis for its lower-level phylogenetic relationships.

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