



A re-evaluation of the ‘mid-Cretaceous sauropod hiatus’ and the impact of uneven sampling of the fossil record on patterns of regional dinosaur extinction

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ARTICLE INFO

Article history:

Received 6 July 2010

Received in revised form 10 November 2010

Accepted 6 December 2010

Available online 10 December 2010

Keywords:

Biogeography

Dinosauria

Dispersal

Extinction

Paleoecology

Titanosauria

ABSTRACT

The mid-Cretaceous of North America and Europe has long been noted for the absence of sauropod dinosaurs, leading several authors to suggest that this depauperate interval is a consequence of an end-Albian sauropod extinction. This time period has become known as the ‘mid-Cretaceous sauropod hiatus’, with the subsequent presence of titanosaurian sauropods in the latest Cretaceous of North America and Europe interpreted as the result of dispersal of taxa from South America and Africa, respectively. However, several lines of evidence indicate that this hiatus is probably a sampling artefact. New fossil and trackway discoveries have considerably shortened the hiatus, reducing it to the Turonian–early Campanian in North America, and to just two short intervals in the late Cenomanian–early Turonian and late Coniacian–Santonian of Europe. Palaeoenvironmental analyses of sauropods demonstrate an inland terrestrial preference for titanosaurs, the dominant Late Cretaceous sauropods; however, during the hiatus there was a decline in inland deposits and increase in coastal sediments in Europe and North America, which would have greatly reduced the probability of preserving titanosaurs. Neither the decline in inland deposits, nor the ‘sauropod hiatus’, occurred elsewhere in the world. Statistical comparisons also demonstrate a significant positive correlation between fluctuations in inland deposits and sauropod occurrences during the mid–Late Cretaceous in Europe and North and South America. Lastly, cladistic analyses do not place latest Cretaceous North American and European titanosaurs within South American and African clades, contradicting the predictions of the ‘austral immigrant’ hypothesis. The latter hypothesis also receives little support from biogeographical analysis of dispersal among titanosaurs. Thus, the ‘sauropod hiatus’ of North America and Europe is most plausibly interpreted as the product of a sampling bias pertaining to the rarity of inland sediments and dominance of coastal deposits preserved in these two regions during the mid-Cretaceous. The presence of titanosaurs in these areas during the latest Cretaceous can be explained by dispersal from Southern Hemisphere continents, but this is no more probable than descent from Early Cretaceous incumbent faunas or dispersal from Asia.

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1. Introduction

Sauropods were a globally distributed group of mega-herbivorous dinosaurs, comprising a significant and diverse part of Mesozoic terrestrial ecosystems (McIntosh, 1990; Upchurch, 1995; Upchurch et al., 2004; Wilson and Sereno, 1998). This clade is thought to have reached its zenith in diversity during the Late Jurassic, with peaks also present in the Middle Jurassic, late Early Cretaceous and latest Cretaceous, although the latter two are partly artefacts of sampling biases (Barrett et al., 2009; Mannion et al., in press; Upchurch and Barrett, 2005).

Several workers have observed that sauropod dinosaurs are absent from North American and European deposits from approximately the Cenomanian to the Campanian inclusive (Le Loeuff, 1993; Le Loeuff

and Buffetaut, 1995; Lucas and Hunt, 1989), whereas they are relatively common in South America, Asia and Africa during this time interval (see reviews in: Upchurch et al., 2004; Weishampel et al., 2004; Salgado and Bonaparte, 2007; Mannion, 2009; Wilson and Upchurch, 2009). This absence has been termed the ‘sauropod hiatus’ (Lucas and Hunt, 1989). The latter authors proposed two alternative hypotheses to explain this hiatus. The first of these, the ‘inland herbivore’ scenario, attempts to explain the North American sauropod hiatus as the product of a sampling bias. Thus, according to this hypothesis, North American Cenomanian–Campanian sauropods have not been found because they were restricted to inland terrestrial environments in a region where the sedimentary record is almost entirely composed of coastal deposits. Lehman (2001) proposed the ‘descent from the highlands’ hypothesis to explain this, in which he suggested that rising sea levels in the Late Cretaceous of North America may have resulted in isolation of upland faunas (which included titanosaurs), whereas the dominant ornithischian dinosaurs (ceratopsians and hadrosaurids) were better adapted to coastal

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environments (see [Butler and Barrett \(2008\)](#) for further work on the environmental associations of Cretaceous ornithischians). [Lehman \(2001, p. 322\)](#) then posited that the return of sauropods in the latest Cretaceous might ‘...simply record a shifting of existing species to lower elevations as altitudinal life zones expanded with the regression of the interior epeiric sea’. Thus, upland faunas might have ‘...largely escaped the reach of the fossil record, persisting ultimately to descend into nearby inland areas’ and perhaps later encroaching into ‘lower altitudes as the climate in the western interior became increasingly dry and continental’ ([Lehman, 2001, p. 322](#)). However, [Lucas and Hunt \(1989\)](#) rejected the ‘inland herbivore’ scenario based on the absence of sauropods in the Two Medicine Formation of Montana, USA, and the Judith River Formation of Alberta, Canada; both representing inland terrestrial deposits of Campanian age and both rich in dinosaurs other than sauropods ([Carrano, 2009; Weishampel et al., 2004](#)).

[Lucas and Hunt’s \(1989\)](#) second hypothesis, the ‘austral immigrant’ scenario, proposed that sauropods became extinct in North America at the end of the Albian and then re-appeared during the Maastrichtian as a result of immigrations from southern continents. They suggested that the presence of titanosaurid sauropods throughout the Cretaceous in South America, and the putative land-bridge between South and North America in the Campanian–Maastrichtian ([Gayet et al., 1992; Iturralde-Vinent, 2006; Iturralde-Vinent and MacPhee, 1999](#)), provided support for this reinvasion scenario (see also [Sloan, 1970; Kues et al., 1980; Bonaparte, 1984; Lehman, 1987](#)). Furthermore, [Lucas and Hunt \(1989\)](#) argued that *Alamosaurus* (the only currently known Late Cretaceous sauropod taxon from North America) was a close relative of South American titanosaurs, providing further evidence for a Gondwanan re-invasion in the Maastrichtian. [Lucas and Hunt \(1989\)](#) posited that the North American sauropod extinction may have been related to a late Albian marine transgression ([Kauffman, 1984a,b; Schröder-Adams et al., 1996](#)), whereas [Salgado and Coria \(2005\)](#) hypothesised that it might pertain to the end-Cenomanian extinction event that predominantly affected marine faunas ([Bambach, 2006; Eaton et al., 1997; Harries and Little, 1999; Kauffman, 1984a](#)). Finally, [Buffetaut \(1989\)](#) also supported the possibility of a mid-Cretaceous North American sauropod extinction, but proposed a mechanism that involved competitive replacement by ornithischian dinosaurs.

As mentioned above, other authors ([Le Loeuff, 1993; Le Loeuff and Buffetaut, 1995](#)) have commented on a sauropod hiatus in Europe between the late Cenomanian and late Campanian and attempted to explain it in similar terms as [Lucas and Hunt’s \(1989\)](#) ‘austral immigrant’ scenario. [Le Loeuff and Buffetaut \(1995, p. 183\)](#) wrote: ‘The early Campanian faunas are remarkable because of the absence of titanosaurid dinosaurs, which are the dominant herbivorous dinosaurs in the late Campanian and early Maastrichtian. This can suggest a post-Cenomanian extinction of this group in Europe followed by a late Campanian immigration’, and [Le Loeuff \(1993, p. 112\)](#) commented: ‘They would have reached Europe again, probably from Africa, during the late Campanian’. [Buffetaut \(1989, p. 70\)](#) also considered an austral immigration likely, writing: ‘...the occurrence and abundance of titanosaurid sauropods in the Maastrichtian land faunas of Europe can definitely be interpreted as indicating Gondwanan affinities’. However, [Le Loeuff \(1993, p. 112\)](#) noted that the richest early Campanian European non-marine localities were deposited in estuarine environments and cautioned that ‘...a paleoecological bias is not unlikely, titanosaurids being probably more continental animals’.

Here we review and re-interpret the evidence for the mid-Cretaceous ‘sauropod hiatus’ in North America and Europe, testing the two competing hypotheses outlined by [Lucas and Hunt \(1989\)](#). We utilise recent fossil and trackway discoveries, phylogenetic and palaeoecological studies, statistical tests for the presence of sampling biases in the fossil record, and a new palaeobiogeographical analysis to evaluate the ‘austral immigrant’ scenario.

2. Materials and methods

2.1. Data

We extracted substage level data on numbers of Aptian–Maastrichtian sauropod individuals (558 body fossils and 377 trackways) and localities (388 body fossil sites and 153 tracksites) from a recent sauropodomorph database ([Mannion and Upchurch, 2010a; Mannion et al., in press](#)) (see also [Fig. 1](#)). Numbers of individuals and localities were determined following the protocol outlined by [Mannion and Upchurch \(2010a\)](#). Numbers of dinosaur-bearing collections (DBC) were collated from *The Paleobiology Database* ([www.paleodb.org; Carrano, 2009](#)). Dinosaur-bearing, rather than sauropod-bearing, collections were used because the former incorporates all units capable of preserving dinosaurs: if a collection is devoid of sauropods, but preserves other dinosaurs, this suggests that sauropods may have been genuinely absent in this region/environment ([Barrett et al., 2009; Mannion et al., in press; Upchurch and Barrett, 2005](#)). All data used in this study are provided in the Supplementary materials.

2.2. Sampling and palaeoenvironmental analyses

In order to examine the effect of the uneven sampling of the fossil record, we tested for statistically significant correlations between sauropod abundance (i.e. numbers of individuals and localities) and numbers of DBCs. We examined each continent separately (i.e. North America, Europe, South America, Asia and Africa), excluding Australasia and Antarctica because of poor coverage in these regions during the time interval under investigation. Sauropod abundance for each continent was calculated by summing the number of individuals, or localities, within each substage. DBCs were divided into inland and coastal/marine categories for each time bin (see [Mannion and Upchurch \(2010a\)](#) for further details of these environmental categories; see also [Butler and Barrett, 2008; Butler et al., in press](#)). Our analyses utilise both the numbers of inland and coastal DBCs themselves, as well as the ratio of inland to coastal DBCs in order to determine how the relative quantity of each of these environmental categories fluctuated during the Aptian–Maastrichtian.

In order to combat possible problems of spurious correlations caused by trend and autocorrelation, each data series was log transformed and first differenced (i.e. the differences between successive time bins) prior to testing for correlations ([McKinney, 1990; Raup and Crick, 1982](#)). Two non-parametric statistical tests (Spearman’s rank and Kendall’s tau) were then used to test for correlation between detrended time series ([Hammer and Harper, 2006](#)), e.g. North American sauropod individuals vs. North American inland DBCs. All statistical analyses were implemented in PAST ([Hammer et al., 2001](#)).

2.3. Phylogenetic analysis and biogeographical methods

Numerous previous studies have produced phylogenies for a selection of titanosaurian genera ([Calvo et al., 2007; Curry Rogers, 2005; Curry Rogers and Forster, 2001; González Riga et al., 2009; Salgado et al., 1997; Sanz et al., 1999; Upchurch, 1995, 1998, 1999; Upchurch et al., 2004; Wilson, 2002; Wilson and Sereno, 1998](#)). However, in most cases these studies included a relatively small number of titanosaurs as part of analyses of either global sauropod relationships (e.g. [Upchurch et al., 2004; Wilson, 2002](#)), or analyses designed to identify the relationships of a newly discovered titanosaur genus (e.g. [Calvo et al., 2007; González Riga et al., 2009](#)). The data matrices presented by such studies are not suitable for testing the ‘austral immigrant’ hypothesis because they under-sample Late Cretaceous European forms. Therefore, in this study we utilise the data matrix of [Curry Rogers \(2005\)](#). This includes the North American

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