

First spinosaurid dinosaur from Australia and the cosmopolitanism of Cretaceous dinosaur faunas

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A cervical vertebra from the Early Cretaceous of Victoria represents the first Australian spinosaurid theropod dinosaur. This discovery significantly extends the geographical range of spinosaurids, suggesting that the clade obtained a near-global distribution before the onset of Pangaeon fragmentation. The combined presence of spinosaurid, neovenatorid, tyrannosauroid and dromaeosaurid theropods in the Australian Cretaceous undermines previous suggestions that the dinosaur fauna of this region was either largely endemic or predominantly ‘Gondwanan’ in composition. Many lineages are well-represented in both Laurasia and Gondwana, and these observations suggest that Early–‘middle’ Cretaceous theropod clades possessed more cosmopolitan distributions than assumed previously, and that caution is necessary when attempting to establish palaeobiogeographic patterns on the basis of a patchily distributed fossil record.

Keywords: Theropoda; Spinosauridae; palaeobiogeography; Cretaceous

1. INTRODUCTION

Palaeobiogeographic scenarios have had a major influence on debates regarding the evolution, diversity and palaeoecology of non-avian dinosaurs [1,2]. The most prevalent relate to apparent differences between the Cretaceous dinosaur faunas of Laurasia and Gondwana, with ‘characteristic’ taxon sets identified in the Northern and Southern Hemispheres [2]. Until recently, these scenarios posited that Laurasian biomes were characterized by diverse ornithischian clades (e.g. hadrosaurids, ceratopsians and ankylosaurs) and a theropod fauna composed largely of coelurosaurians (e.g. tyrannosauroids, ornithomimosaurians and dromaeosaurids). In contrast, ornithischians and coelurosaurians were considered rare in Gondwana, with a theropod fauna dominated by abelisauroids and carcharodontosaurians.

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Within this framework, more detailed scenarios interpreted Cretaceous dinosaur distributions as evidence for various Gondwanan fragmentation hypotheses [3]. Such scenarios are difficult to test owing to uncertainties in palaeogeographical reconstructions, differing opinions over identification of taxa from key localities, and poor sampling of Gondwanan Cretaceous dinosaur faunas [1,2]. Consequently, little consensus exists on these issues.

New discoveries from the late Early Cretaceous of Australia provide much needed data on dinosaur distribution across Gondwana. These finds permit more detailed comparisons between Australian dinosaur faunas and those from elsewhere than had been possible previously [4–7]. Here, we describe the first spinosaurid theropod from the Early Cretaceous of Australia, which has major implications for Early–‘middle’ Cretaceous theropod palaeobiogeography. A previous report of an Australian ‘spinosauroid’ (i.e. megalosauroid) based on an isolated ulna from the Eumeralla Formation of Dinosaur Cove, Victoria [4] is erroneous: reappraisal indicates that this specimen represents a neovenatorid allosauroid [5,6,8].

2. MATERIAL AND METHODS

Museum Victoria, Melbourne (NMV) specimen P221081 is an isolated cervical vertebra, lacking most of the neural arch (figure 1*a–e*). It is from the Eumeralla Formation of the Otway Group (late Aptian–early Albian, Early Cretaceous: [9]) at the ‘Eric the Red west’ site, east of Crayfish Bay, Victoria, Australia. A full description of NMV P221081 are presented in the electronic supplementary material: features of systematic and taxonomic significance are discussed below. The small size of the specimen (maximum centrum length = 42 mm) and the lack of fusion between the centrum and neural arch suggest that the vertebra pertains to a juvenile.

3. RESULTS

The character state combination present in NMV P221081 supports its referral to Spinosauridae on the basis of character distributions gleaned from recent large-scale theropod phylogenies [8]. Presence of a single, anteriorly situated pneumatic foramen (‘pleurocoel’) demonstrates referral to the major clade Tetanurae, which consists of megalosauroids (formerly ‘spinosauroids’), allosauroids and coelurosaurians. Within Tetanurae, the strongly opisthocoeleous centrum is seen in derived members of Allosauroidae and Megalosauroidae. Two additional features, subdivision of the pneumatic fossa by a simple, short accessory lamina (figure 1*e,h*), and an elongate centrum (length:height ratio > 2.0), both support referral to Spinosauridae, a widely distributed clade of Cretaceous megalosauroids. The pneumatic fossa in some carcharodontosaurians is also subdivided by a lamina, but in this clade, the lamina is a more substantial buttress of bone that divides the fossa into two widely separated openings, rather than the slender sheet of bone present in some spinosaurids. NMV P221081 can be further excluded from Carcharodontosauria as it lacks camellate internal bone structure (a condition in which the bone contains numerous small, irregular pneumatic spaces). In most respects, NMV P221081 is effectively identical to the cervical vertebrae of the European spinosaurid *Baryonyx walkeri* (figure 1*f–i*; Natural History Museum, London R9951; [10]), sharing all of the above mentioned character states and the same overall morphology as the latter taxon. Given

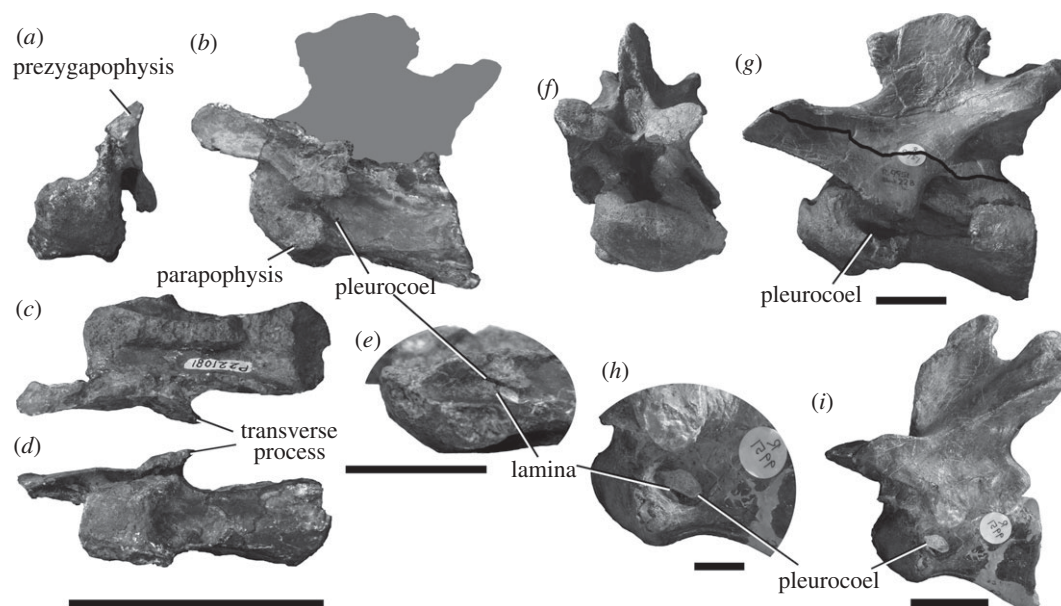


Figure 1. Spinosaurid cervical vertebrae. (a–e) NMV P221081, (f–i) *Baryonyx walkeri* NHMUK R9951: (f,g) eighth and (h,i) third cervical vertebrae. Shown in (a,f) anterior, (b,g) left lateral, (c) dorsal, (d) ventral, and right lateral (i, reversed) views with (e,h) magnifications of the pleurocoel. Area of grey tone in (b) indicates proposed reconstruction, highlighted area in (g) indicates the portion not preserved in NMV P221081. Scale bars, (a–d, f–g, i) 50 mm and (e, h) 20 mm.

the fragmentary nature of NMV P221081, its lack of autapomorphic features and its marked similarity to material of several spinosaurid taxa, we refrain from naming the specimen and do not refer it to any named spinosaurid taxon, regarding it as Spinosauridae gen. et sp. indeterminate. Full discussion of the phylogenetic significance of each of these features, and comparisons with other theropod taxa, is provided in the electronic supplementary material.

4. DISCUSSION

Three scenarios have been posited for the Cretaceous fragmentation of Gondwana [3]: initial separation of Africa from the rest of Gondwana ('Africa first' model); a split between a conjoined South American/African continent (i.e. western Gondwana) and the remaining Gondwanan fragments ('Samafrica' model); and almost simultaneous separation of all Gondwanan continents ('Pan-Gondwana' model). Smith *et al.* [4] noted the shared presence of megaraptoran theropods in South America and Australia, which they interpreted as support for continuing Early Cretaceous faunal interchange between eastern and western Gondwana. These authors, therefore, rejected the 'Samafrica' model and suggested that South America, Antarctica and Australia retained connections to each other ('Africa first' model) [4]. Subsequently, Agnolin *et al.* [6] used Sørensen's similarity index (SSI, values between 0 and 1, higher values indicating higher faunal similarity: see the electronic supplementary material) to assess the similarity between dinosaur faunas on different palaeocontinents. These broader-scale comparisons incorporated numerous reidentifications of Australian dinosaur specimens, and led these authors to modify their previous views. They concluded that the 'Samafrica'

model could not be rejected, but that the Australian dinosaur fauna was most similar to that from South America, with major differences between the faunas of Laurasia and Gondwana. Agnolin *et al.* [6] obtained SSIs of 0.55–0.72 when comparing the Australian fauna to those of other Gondwanan continents, contrasting with 0.43–0.58 when compared with Laurasian continents. Among the Laurasian continents, European faunas were deemed most similar to those from Gondwana.

However, the SSI values presented by Agnolin *et al.* [6] are not useful in identifying patterns of faunal connectivity (see the electronic supplementary material for additional details). Firstly, this test is inappropriate for distinguishing palaeobiogeographic hypotheses, as it does not take clade history into account, but looks at distributions within a single timeslice. As a result, it is not clear whether similarities detected by SSIs reflect genuine palaeobiogeographic signals or 'homoplasy' (caused by regional extinction, earlier vicariance or geodispersal). Secondly, this test is strongly dependent on the number of clades compared, so that sampling issues (e.g. collection effort or amount of available fossiliferous rock in different regions) can have a strong influence on the result: poorly sampled areas might (wrongly) appear either highly similar, or totally dissimilar, to a well-sampled area, because sampling failure is interpreted as genuine clade absence. Thirdly, there is no taxonomic equivalency in the clades selected by Agnolin *et al.* [6]: some represent paucispecific-derived clades, while others are much more inclusive. These arbitrary taxonomic divisions can bias the results, as they can mask the true levels of underlying species-richness. Finally, there are several instances in which the presence/absence scores used in the analysis of Agnolin *et al.* [6] contradict existing taxonomic accounts (e.g. there are currently no known stegosaurs from the North or South American

Cretaceous ([11], *contra* [6])). Reanalysis of a corrected dataset based on Agnolin *et al.* [6], and including the material described herein, shows no unambiguous support for the Gondwanan affinities of Australian dinosaur faunas (see the electronic supplementary material). The highest SSIs obtained by comparison with the Australian fauna are for South America and Europe (both 0.70), the second highest values, for comparisons between Australia and either Antarctica or Asia (both 0.67), are almost indistinguishable from this figure. These values are all much higher than those calculated for comparisons between Australia and the remaining Gondwanan continents (Africa, India and Madagascar, which range from 0.2 to 0.52; see the electronic supplementary material). If this analysis is restricted further, to include only Early–‘middle’ Cretaceous faunas, the highest SSI values obtained are between Australia and Europe (0.76) or Asia (0.73), whereas the SSI for South America is 0.67 (see the electronic supplementary material). A literal reading of these results implies that the taxonomic composition of Early–‘middle’ Cretaceous dinosaur faunas was broadly similar over large areas and none of these results provides strong support for the traditional split between Laurasian and Gondwanan dinosaur faunas. These results also offer weak support for the ‘Africa-first’ hypothesis of Gondwanan fragmentation, as SSI values comparing Australia and Africa are consistently lower than those for South America (see the electronic supplementary material).

We propose that the presence of an Australian Cretaceous spinosaurid, in combination with other recent Gondwanan discoveries of clades previously thought to be restricted to Laurasia (e.g. tyrannosauroid and dromaeosaurid theropods, ankylosaurid ankylosaurs, iguanodontian ornithopods: [6,7,12]), provides evidence for the cosmopolitan distribution of many dinosaur clades during the Early–‘middle’ Cretaceous. These discoveries are mirrored by other work that has revealed the presence of many formerly ‘Gondwanan’ clades in Laurasia, such as rebbachisaurid sauropods, and abelisauroid and carcharodontosaurian theropods [8,13,14]. Additionally, recent phylogenetic analyses have identified sister-group relationships between Cretaceous genera that cross the Gondwanan/Laurasian ‘divide’: for example, the Australian neovenatorid theropod *Australovenator* is the sister-taxon of the Japanese *Fukuiraptor* [8], and the Australian titanosaurian sauropod *Diamantinasaurus* is most closely related to *Opisthocoelicaudia* from Mongolia [5]. Consequently, NMV P221081 is part of a growing body of evidence that seriously undermines the prevalent view of pronounced north–south differences between Early–‘middle’ Cretaceous dinosaur faunas. Nevertheless, we recognize that some dinosaur clades are more abundant or diverse in particular regions at this time (e.g. titanosaurian sauropods are much more abundant in South America than Europe: [14]). However, clade abundance will be strongly influenced by local and regional variations in palaeoenvironmental conditions [15], not just biogeographic history. Abundance measures are not, therefore, appropriate criteria for establishing general distribution patterns (which are reliant on additional factors, especially palaeogeography and regional extinction), as they have sometimes been used in the past

(see [1,3]). Moreover, abundance and diversity patterns are both strongly influenced by a plethora of sampling biases, geological, biological and anthropic [14,16,17], which have not generally been accounted for in analyses of dinosaur palaeobiogeography. Until such analyses are carried out in concert with rigorous, quantitative cladistic biogeographic analyses [1], few definite conclusions can be drawn about the finer-scale patterns that might exist within a more cosmopolitan, possibly pan-global, Early–‘middle’ Cretaceous dinosaur fauna.

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