A *Megaraptor*-like theropod (Dinosauria: Tetanurae) in Australia: support for faunal exchange across eastern and western Gondwana in the Mid-Cretaceous

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The fossil record of Australian dinosaurs in general, and theropods in particular, is extremely sparse. Here we describe an ulna from the Early Cretaceous Eumeralla Formation of Australia that shares unique autapomorphies with the South American theropod *Megaraptor*. We also present evidence for the spinosauroid affinities of *Megaraptor*. This ulna represents the first Australian non-avian theropod with unquestionable affinities to taxa from other Gondwanan landmasses, suggesting faunal interchange between eastern and western Gondwana during the Mid-Cretaceous. This evidence counters claims of Laurasian affinities for Early Cretaceous Australian dinosaur faunas, and for the existence of a geographical or climatic barrier isolating Australia from the other Gondwanan continents during this time. The temporal and geographical distribution of *Megaraptor* and the Eumeralla ulna is also inconsistent with traditional palaeogeographic models for the fragmentation of Gondwana, but compatible with several alternative models positing connections between South America and Antarctica in the Mid-Cretaceous.

Keywords: Dinosauria; *Megaraptor*; Cretaceous; Australia; palaeobiogeography; Gondwana

1. INTRODUCTION

The fossil record of Australian dinosaurs in general, and theropods in particular, is extremely sparse ([Molnar 1991](#)). Described Cretaceous theropod remains from the Early Cretaceous of southern Victoria include material from the Upper Strzelecki Group (Middle Valanginian–Aptian) that has been identified as *Allosaurus* (Molnar *et al.* 1981, 1985). This specimen represents the only continental tetrapod from the Cretaceous of Australia that has been referred to a genus known from another continent ([Molnar 1992](#)). Several authors have challenged Molnar *et al.*'s (1981, 1985) interpretation of this specimen as an allosaurid (e.g. Welles 1983; Chure 1998, 2000, unpublished dissertation) and, recently, it has been reinterpreted as an abelisauroid (Agnolin *et al.* 2005; Salisbury *et al.* 2007; R. Molnar 2008, personal communication), although further comparisons are required to confirm this. Slightly younger theropod specimens from the Eumeralla Formation at Dinosaur Cove (Late Aptian–Early Albian) have been referred to

coelurosaurian clades that otherwise have exclusively Laurasian distributions, such as ornithomimosaurs (*Timimus hermani*; Rich & Vickers-Rich 1994) and oviraptorosaurs (Currie *et al.* 1996). These identifications, coupled with the presence of ceratopsians (Rich & Vickers-Rich 2003), and the perceived absence of diagnostic remains of typical Gondwanan theropod clades such as abelisaurids, noasaurids, carcharodontosaurids and spinosaurids, has prompted researchers to conclude that the Early Cretaceous dinosaur fauna of Australia shares stronger affinities with Laurasian faunas than with other Gondwanan faunas (e.g. Rich & Vickers-Rich 1994, 2003; Currie *et al.* 1996; Vickers-Rich & Rich 1997; though see Molnar 1992; Upchurch *et al.* 2002). Until the recent discovery of the Yixian Formation fauna, several of the Australian remains were interpreted as the earliest records for their respective groups, and researchers have suggested that Australia and/or Gondwana may have been the centre of origin for some of these dinosaur clades (Rich & Vickers-Rich 1994; Currie *et al.* 1996; Vickers-Rich & Rich 1997).

Among the remains collected from the Eumeralla Formation at Dinosaur Cove, Rich & Vickers-Rich (2003; fig. 8) figured but did not describe an isolated left theropod ulna (NMV P186076; figure 1). This ulna shares unique autapomorphies with the enigmatic

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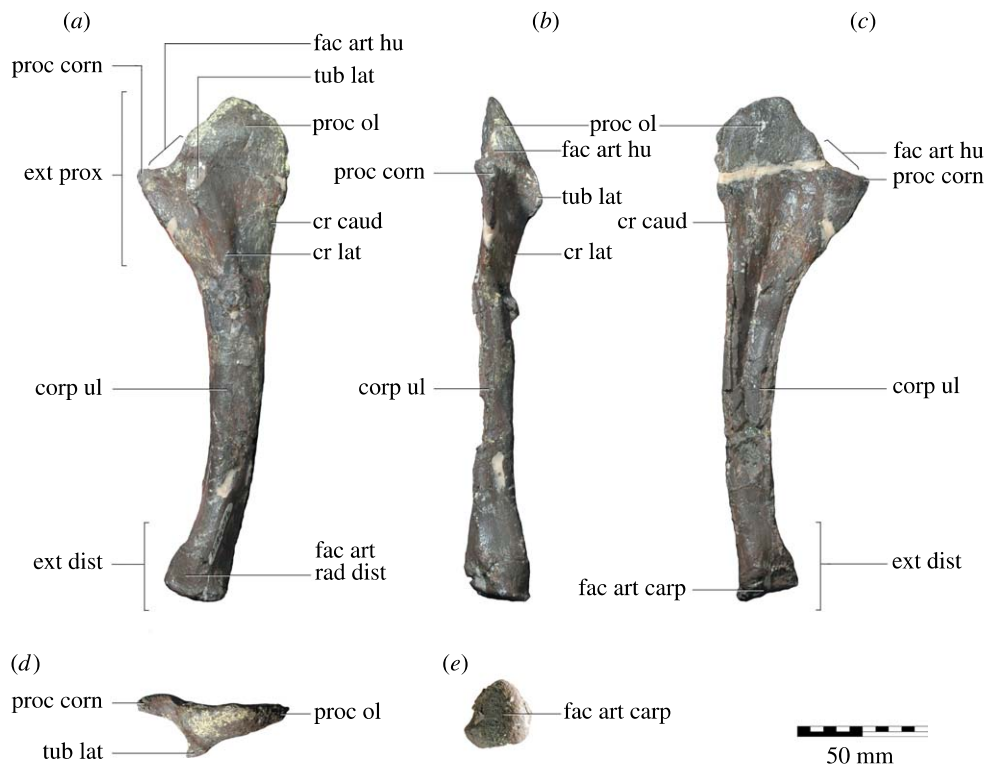
Figure 1. Cf. *Megaraptor* (NMV P186076), left ulna: (*a*) lateral aspect, (*b*) cranial aspect, (*c*) medial aspect, (*d*) proximal aspect (cranial is to the left and medial is to the top of the page), (*e*) distal aspect (medial is to the left and cranial is to the top of the page). Abbreviations: corp ul, ulnar shaft; cr caud, caudal crest; cr lat, lateral crest; ext dist, distal extremity; ext prox, proximal extremity; fac art carp, carpal articular surface; fac art hu, humeral articular surface; fac art rad dist, distal radial articular surface; proc corn, coronoid process; proc ol, olecranon process; tub lat, lateral tuberosity.

Argentine theropod *Megaraptor* (Novas 1998; Calvo *et al.* 2004; Salisbury *et al.* 2007). In addition to somphospondyl titanosauriforms (Salgado 1993; Molnar 2000; Molnar & Salisbury 2005; Salisbury *et al.* 2006), this specimen represents some of the best evidence thus far for what can be considered Gondwanan elements in the Early Cretaceous dinosaur fauna of Australia. Herein, we describe this specimen and provide evidence for its affinities. We also present evidence for the phylogenetic relationships of *Megaraptor*, and discuss the implications for Gondwanan theropod palaeobiogeography and diversity through time in light of the Australian material.

2. DESCRIPTION AND COMPARATIVE ANATOMY

(**a**) *Systematic palaeontology*
Theropoda (Marsh 1881)
Tetanurae (Gauthier 1986)
cf. *Megaraptor* (Novas 1998)

(**b**) *Material*
NMV P186076, a nearly complete left ulna (figure 1; see electronic supplementary material 1 for institutional abbreviations).

(**c**) *Locality and horizon*
NMV P186076 was found at Dinosaur Cove, near Cape Otway, Victoria, Australia (38°46′53±1′ S, 143°24′14±1′ E, World Geodetic Standard 1984; figure S2 in the electronic supplementary material). It was collected *in situ* in 1989 from a palaeostream channel during tunnelling operations in the First Cross Tunnel at

the 'Slippery Rock' site, Dinosaur Cove, as part of a series of excavations between 1984 and 1994 overseen by Rich & Vickers-Rich (2000; fig. 44).

Material from Dinosaur Cove is known to pertain to the Eumeralla Formation (Middle Valanginian–Albian) of the Otway Group, and is dated palynologically as Early Cretaceous, and specifically as Late Aptian–Early Albian (Wagstaff & McEwen-Mason 1989). This formation has produced a diverse vertebrate fauna. In addition to the aforementioned theropod material, this fauna includes ornithopod dinosaurs, pterosaurs, crocodyliforms, bony fishes, ceratodid lungfishes and a monotreme (Rich & Vickers-Rich 2000; Pridmore *et al.* 2006).

(**d**) *Description and comparisons*
NMV P186076 has a total length of 192.6 mm. It is well preserved, but the shaft and proximal extremity show some breaks and are missing small areas. The medial surface of the shaft and distal-most part of the proximal extremity are crushed, and the proximal portion of the lateral crest is broken. The articular surface of the olecranon process is slightly abraded.

Overall, the ulna is massive proximally but tapers to a slender shaft distally. The caudal surface of the bone has a modestly convex outline, whereas the cranial surface is concave. The olecranon process is proportionately very large and rises dorsally above the humeral articular surface (=‘sigmoid notch’ of some authors) as a tall blade. Unlike the condition in most theropods, such as *Dilophosaurus* (UCMP 37302) and *Piatnitzkysaurus* (PVL 4073), which have a low olecranon process that is roughly spherical,

the olecranon of NMV P186076 is dorsally expanded but strongly compressed mediolaterally. Despite this, the olecranon process of NMV P186076 still retains a proximally convex outline in lateral aspect, as is typical for most theropods. Several spinosaurids, including *Baryonyx walkeri* (BMNH R9951) and *Suchomimus tenerensis* (MNN GAD 500; =*Baryonyx tenerensis* of some authors; e.g. Sues *et al.* 2002), have a hypertrophied olecranon process that is flattened mediolaterally. However, in these taxa, the long axis of the olecranon process is directed proximocaudally in relation to the long axis of the shaft, rather than proximally as in NMV P186076 and other theropods. The olecranon process of *Suchomimus* and *Baryonyx* also extends more medially at an oblique angle relative to the coronoid process (=‘anterior process’ of some authors) when viewed proximally, whereas in most other theropods, including NMV P186076, the long axis of the olecranon is in the same plane as the long axis of the coronoid process (figure S3 in the electronic supplementary material). The olecranon process of NMV P186076 continues as a blade-like crest onto the caudal surface of the proximal extremity, fading out along the proximal-most third of the ulnar shaft. A blade-like caudal olecranon crest also occurs in the holotype of *Megaraptor namunhuaiquii* (MCF-PVPH 79), and in a referred specimen (MUCPv 341). This morphology is not observed in any other theropod taxa (figures S3 and S4 in the electronic supplementary material).

An interesting feature of NMV P186076 is the presence of a well-developed proximodistally aligned crest on the lateral surface of the proximal half of the ulna (figure 1*a*). The lateral-most projection of this crest is missing, but based on its shape on either side of the break, it most likely formed a rounded tuberosity (the ‘lateral’ or ‘radial’ tuberosity). The lateral tuberosity would have been level with the apex of the coronoid process in lateral aspect, and was probably continuous with the humeral articular surface proximally. Distal to the broken tuberosity, the lateral crest extends onto the proximal half of the ulnar shaft, gently arching caudally. This unusual morphology is present in no other theropod taxon, with the exception of the holotype and referred specimens of *M. namunhuaiquii*. Several spinosauroids, including *Poekilopleuron* (YPM 4839), *Torvosaurus* (UCRC PVC25), *Baryonyx* and *Suchomimus*, have lateral tuberosities that are well developed relative to most theropods (figures S3 and S4 in the electronic supplementary material). However, in these taxa, it is only the lateral tuberosity that is enlarged, and there is no evidence of a proximodistally aligned crest extending distally from it as there is in NMV P186076 and *M. namunhuaiquii*.

The coronoid process of NMV P186076 projects cranially from the proximal extremity to form a sharp triangular outline in lateral and medial aspects. The medial surface of the coronoid process is flat, and continuous with the medial surface of the olecranon process, as in the holotype (MCF-PVPH 79) and referred specimen (MUCPv 341) of *M. namunhuaiquii*. In spinosauroids such as *Torvosaurus*, *Baryonyx* and *Suchomimus*, this surface is slightly medially concave.

The expanded blade-like distal portions of the olecranon process and the lateral crest of NMV P186076 form the borders of a broad caudolaterally facing shallow fossa. This area may represent an insertion for the m. triceps brachii complex as in modern crocodyliforms

(Meers 2003). The size and position of this insertion indicate powerful forearm extension, and by inference, a proportionally large manus. Among theropods, a similarly well-developed fossa is only present in the holotype and referred specimens of *M. namunhuaiquii*, a taxon distinguished by its proportionally large manus with enlarged unguals. In the spinosaurids *Baryonyx* and *Suchomimus*, which also have a large manus and unguals, the junction of the olecranon crest and lateral tuberosity also creates a large fossa, though this fossa is considerably broader and shallower than in NMV P186076 and *M. namunhuaiquii*, and faces more caudally.

The ulnar shaft of NMV P186076 attenuates rapidly distal to the caudal crest associated with the olecranon process. The distal extremity is only weakly expanded relative to the shaft, in contrast to spinosaurids, in which the distal extremity of the ulna is broadly expanded mediolaterally (figure S5 in the electronic supplementary material). The craniolateral face of the distal extremity is flattened slightly, being demarcated from the more convex proximal parts of the shaft by a low lateral ridge. This surface presumably articulated with the distal extremity of the radius. Novas (1998) figured a shallow flattened depression located in an identical part of the ulna of the holotype of *M. namunhuaiquii*. The referred specimen of *M. namunhuaiquii* (MUCPv 341) is also flattened in this region, though not as depressed as in the holotype specimen. Novas (1998) considered the triangular outline of the distal articulation of *M. namunhuaiquii* as diagnostic of this taxon. In both the holotype and referred specimens of *M. namunhuaiquii*, the distal articular surface of the ulna is slightly expanded medially into a rounded point, though this expansion is more prominent in the holotype specimen. A slight medial expansion is evident in NMV P186076, but it is less distinct than that of *M. namunhuaiquii* (figure S5 in the electronic supplementary material).

Despite the marked similarities between the morphology of NMV P186076 and the ulnae currently attributed to *M. namunhuaiquii*, several minor differences exist, though it is not clear whether these differences can be attributed to ontogenetic or individual variation, or whether they constitute distinct features of the Australian specimen and the taxon to which it pertains. NMV P186076 is considerably smaller, having a maximum length that is just over half that of both described ulnae of *M. namunhuaiquii*. It also lacks the distinctly triangular distal outline of the distal articular surface observed in MCF-PVPH 79, MUCPv 412 and MUCPv 341, a feature considered diagnostic of *M. namunhuaiquii* by both Novas (1998) and Calvo *et al.* (2004; figure S5 in the electronic supplementary material). The shaft of NMV P186076 is also more curved than that of the holotype ulna of *M. namunhuaiquii*, which is nearly straight (figure S4 in the electronic supplementary material). A slight degree of curvature is observed in a referred specimen (MUCPv 341) of *M. namunhuaiquii* from Lago Barreales (figure S4 in the electronic supplementary material). The olecranon process of NMV P186076 is slightly more proximocaudally convex than in either the holotype or the referred specimen of *M. namunhuaiquii*, and its cranial edge that continues onto the humeral articular surface is steeper and exhibits a slight sigmoid curvature compared with the olecranon processes of the *M. namunhuaiquii* specimens.

(e) *Taxonomic conclusions*

In common with *M. namunhuaiquii*, NMV P186076 possesses: (i) a proximocaudally expanded blade-like olecranon process that extends distally as a caudal olecranon crest and (ii) a pronounced lateral tuberosity that is continuous distally with a distinct lateral crest. These features are well preserved in two specimens of *M. namunhuaiquii* (MCF-PVPH 79 and MUCPv 341), and in NMV P186076, and in none is this area affected by damage or deformation. No other theropod displays these traits in their ulna. Although several spinosaurids (e.g. *Baryonyx* and *Suchomimus*) possess an enlarged and mediolaterally compressed olecranon process, it differs both in shape and its angle relative to the lateral tuberosity. Novas (1998) cited the triangular outline of the distal extremity of the ulna as an autapomorphy of *M. namunhuaiquii*. Although Calvo *et al.* (2004) noted some minor variation in the degree of medial expansion of the distal ulna between the holotype and a referred specimen (MUCPv 341) of *M. namunhuaiquii*, they also considered this morphology unique to the species. However, at least some specimens of *Allosaurus* (e.g. YPM 4944), and *Poekilopleuron*, possess similar medial expansions of the distal ulna, though most other tetanurans (e.g. *Piatnitzkysaurus*; *Torvosaurus*), and more basal theropods (e.g. *Liliensternus* MB R. 2175) do not (figure S5 in the electronic supplementary material). Unlike the Argentine specimens of *M. namunhuaiquii*, the distal articular surface of NMV P186076 has a circular rather than distinctly triangular outline, which may be a derived trait of *M. namunhuaiquii*. This difference, and possibly its smaller size, indicates that NMV P186076 is most likely distinct from *M. namunhuaiquii*, as defined by Novas (1998) and Calvo *et al.* (2004). While further discoveries may demonstrate that NMV P186076 pertains to an Australian species of *Megaraptor*, it is equally probable that it represents a taxon that is closely related to, but distinct from *Megaraptor*. In the absence of any material to the contrary, we therefore consider it judicious to refer NMV P186076 to Tetanurae cf. *Megaraptor*. The minor differences between *M. namunhuaiquii* and NMV P186076 do not warrant erecting a new taxon for the Australian material without more data (see electronic supplementary material 6 for emended systematic palaeontology for *Megaraptor*).

3. PHYLOGENETIC ANALYSIS

To assess the relationships of *Megaraptor* and NMV P186076, we performed a phylogenetic analysis using a dataset modified from that of Smith *et al.* (2007). In addition to *Megaraptor* and NMV P186076, the carcharodontosaurid *Mapusaurus* was added to the dataset. Several new characters were constructed, and codings for some taxa were revised. In total, 58 taxa were scored for 353 characters (see electronic supplementary material 6 for a complete character list and codings for all included taxa). Phylogenetic analyses were performed using PAUP* v. 4.0b10 (Swofford 2002). Bootstrap support (Felsenstein 1985) and Bremer decay indices (Bremer 1988) were calculated to assess support for nodes in the resulting most parsimonious trees (MPTs) (see electronic supplementary material 7 for additional details of the phylogenetic analyses).

4. DISCUSSION

(a) *Phylogenetic and palaeobiological implications*

NMV P186076 represents the first Cretaceous dinosaur specimen from Australia that can confidently be allied with a genus known from another continent. Several minor differences between NMV P186076 and the South American *Megaraptor* material do exist, the most notable of which is the smaller size of the Australian specimen. Although ecological factors related to palaeoclimate and/or high palaeolatitude (Rich *et al.* 1988, 1992) have been suggested as possible explanations for the predominance of small-bodied dinosaurs in the Victorian assemblage, there is currently not enough evidence to assess whether the smaller size of NMV P186076 is due to: (i) phylogenetic divergence (potentially related to the above factors), (ii) ontogeny, or (iii) individual variation. Additionally, the bias towards smaller individuals in the Victorian assemblages probably relates to taphonomic processes (Rich *et al.* 1988; T. H. Rich 2007, personal communication).

Owing primarily to a dearth of diagnostic material, the phylogenetic position of *Megaraptor* has remained elusive since its discovery (Novas 1998; Calvo *et al.* 2004). Novas (1998) tentatively referred *Megaraptor* to the derived theropod clade Coelurosauria, primarily based on the gracile proportions of the third metatarsal of the holotype specimen. Recovery and description of additional *Megaraptor* remains by Calvo *et al.* (2004) allowed for some clarification of the taxon's affinities. Calvo *et al.* (2004) discussed a variety of features in the axial skeleton of *Megaraptor*, which are also present in carcharodontosaurids, but also noted that the appendicular material of *Megaraptor* shares several traits with spinosauroids (e.g. *Baryonyx* and *Torvosaurus*). Although they presented no phylogenetic analysis, Calvo *et al.* (2004) suggested that the suite of characters present in *Megaraptor* allow it to be considered a non-neotetanuran (=Allosauroidea and Coelurosauria, *sensu* Sereno 1999) tetanuran theropod, and further proposed that it represents a unique theropod lineage, distinct from the main theropod clades present at this time (e.g. Abelisauroidea, Spinosauridae, Carcharodontosauridae and Allosauridae). Smith *et al.* (2007) presented the first cladistic analysis of the phylogenetic relationships of *Megaraptor*, recovering it as a carcharodontosaurid more closely related to *Giganotosaurus* and *Carcharodontosaurus* than to either *Tyrannotitan* or *Sinraptor*. However, support for this result is relatively weak and based mainly on several vertebral synapomorphies (all of which exhibit some level of homoplasy) including the presence of two cervical pleurocoels, the staggered position of the paired cervical pleurocoels separated by a solid oblique strut of bone, a prezygapophyseal–epipophyseal crest on the cervical neural arch and the presence of pleurocoels in the caudal vertebrae (Smith *et al.* 2007; figure S9 in the electronic supplementary material). Hyposphene/hypantrum-like accessory articulations in the cervical vertebrae are also present in *Megaraptor* and carcharodontosaurids, though the distribution of this character among theropods is poorly documented (Smith *et al.* 2007; figure S9 in the electronic supplementary material).

Phylogenetic analysis of the complete dataset resulted in the recovery of 172 MPTs, each of 853 steps, with a consistency index of 0.484, and a retention index of 0.772. *Megaraptor* and NMV P186076 are recovered as derived
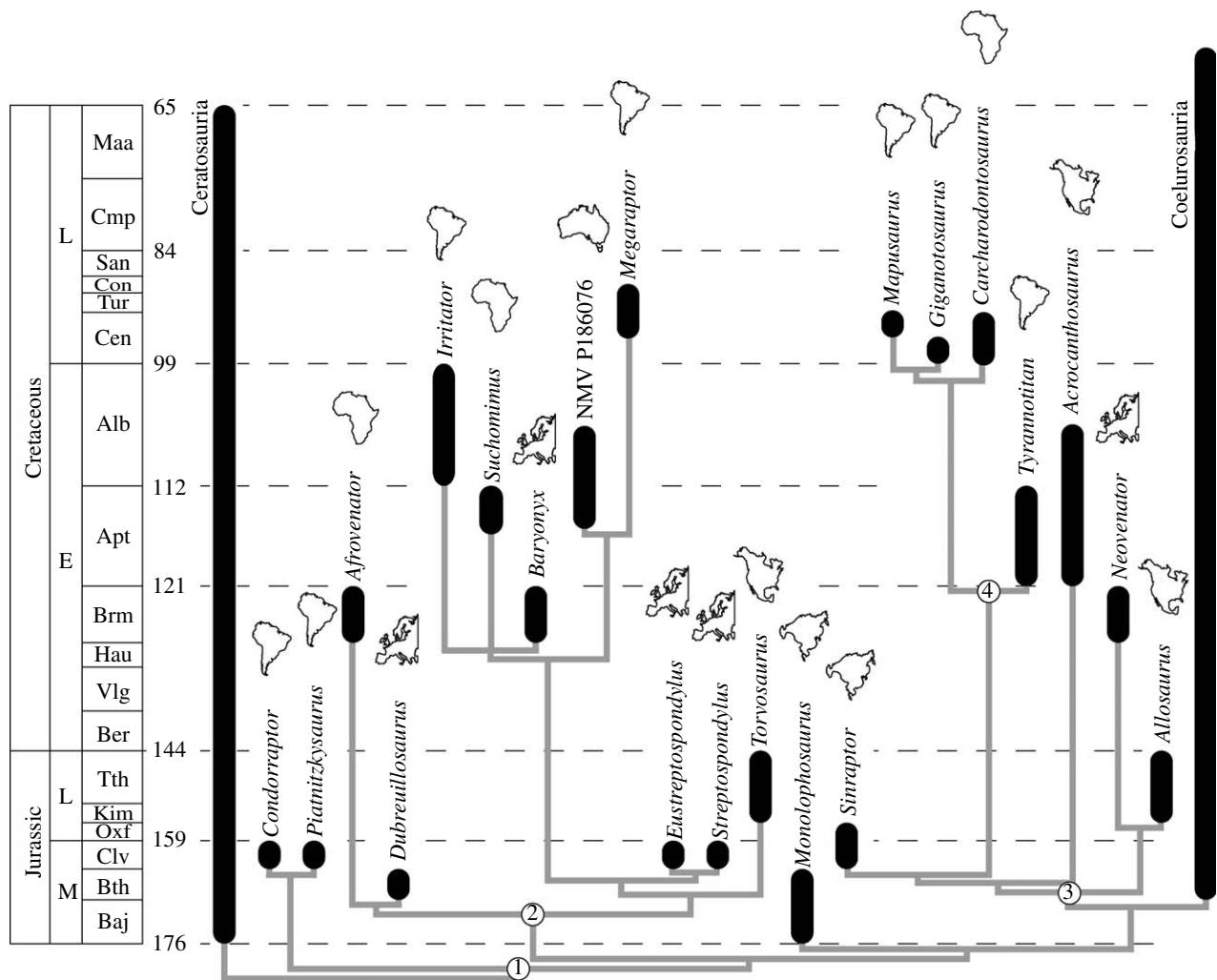
Figure 2. Phylogenetic, temporal and geographical relationships among non-coelurosaurian tetanurans. Tree is based on one preferred representative of 172 MPTs (see S7 in the electronic supplementary material). The majority of taxa are known from single specimens and/or horizons, so range bars reflect uncertainty in age rather than actual stratigraphic range. Several clades are indicated: node 1, Tetanurae; node 2, Spinosauroidea; node 3, Allosauroidea; node 4, Carcharodontosauridae. Shapes above taxa correspond to continental area/s in which the taxon occurs.

members of Spinosauroidea (figure 2; electronic supplementary material 8). Three additional steps are required to recover *Megaraptor* and NMV P186076 as members of Carcharodontosauridae, similar to the topology recovered in the original analysis of Smith *et al.* (2007). Bootstrap and Bremer support values for Spinosauroidea and its less-inclusive clades are low (figure S8 in the electronic supplementary material), and suggest that the phylogenetic relationships of *Megaraptor* should still be regarded as tentative (Calvo *et al.* 2004; Smith *et al.* 2007). However, several characters support the placement of *Megaraptor* as a spinosauroid, including: a hypertrophied manual ungual I-2 (present in *Baryonyx*, *Suchomimus*, *Megaraptor* and *Torvosaurus*; convergently present in *Sinosauropteryx*); a hypertrophied ulnar lateral tuberosity (present in *Baryonyx*, *Suchomimus*, *Megaraptor*, NMV P186076 and *Torvosaurus*); a manual phalanx I-1 with a pronounced ventral groove (present in *Baryonyx* and *Megaraptor*); and a compressed blade-like olecranon process (present in *Baryonyx*, *Suchomimus*, *Megaraptor*, NMV P186076 and absent in *Torvosaurus*). An additional feature that *Megaraptor* shares with the spinosaurids *Baryonyx* and *Suchomimus* is the presence of an expanded triangular cranial process on the proximal radius (figure S9 in the

electronic supplementary material). Though the distribution of this character among theropods is poorly documented at present, a hypertrophied cranial process of the radius is absent in the allosaurid *Allosaurus* (YPM 4944), and the carcharodontosaurid *Mapusaurus* (Coria & Currie 2006).

The stratigraphic range extension provided by NMV P186076 is in accord with the length of the ghost lineage separating *Megaraptor* from the Spinosauridae, which originated by the Barremian. Furthermore, given the Late Turonian–Early Coniacian age of the Portezuelo Formation (Leanza *et al.* 2004), *Megaraptor* represents the youngest known member of Spinosauroidea, and increases the overlap between typical 'Middle' and 'Late' Cretaceous Gondwanan theropod faunas (Novas *et al.* 2005; Smith *et al.* 2007). Additional fossil material of *Megaraptor* and/or its close relatives will be crucial to testing the robustness of its placement within Spinosauroidea, and further refining the phylogenetic affinities of this enigmatic taxon.

(b) *Palaeobiogeographic implications*
NMV P186076 represents the first Australian theropod with well-supported affinities to a taxon from another Gondwanan landmass, and suggests faunal interchange
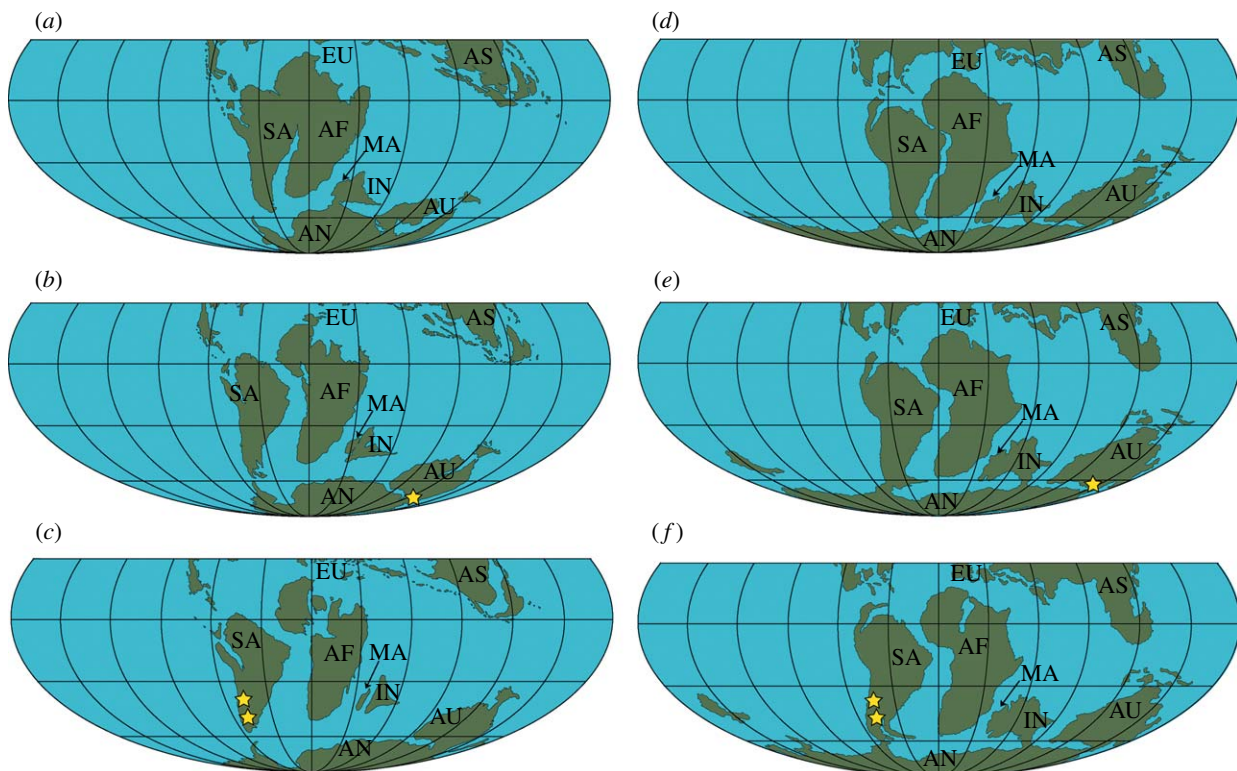
Figure 3. (*a–c*) Palaeogeographic reconstructions depicting the 'traditional' model of Gondwanan fragmentation (Smith *et al.* 1994; Scotese 2001), and the 'Africa-first' model (*d–f*; Hay *et al.* 1999). Reconstructions are shown for *ca* (*a,d*) 120 Myr ago, (*b,e*) 105 Myr ago and (*c,f*) 90 Myr ago. Yellow stars indicate NMV P186076 and *Megaraptor* localities.

between the eastern and western extremes of this super-continent at least by the Turonian, and possibly during the later part of the Early Cretaceous (Calvo *et al.* 2004). Importantly, this biogeographic signal derives from the close relationship between NMV P186076 and *Megaraptor*, and is not dependant on the inferred spinosauroid affinities of *Megaraptor*, though it should also be noted that Cretaceous spinosauroids are predominantly a Gondwanan clade (Sereno *et al.* 1998; Sues *et al.* 2002). Thus, in addition to unique faunal elements such as the basal iguanodontian *Muttaburrasaurus* (Bartholomai & Molnar 1981), and relicts of ancient lineages such as temnospondyl amphibians (Warren *et al.* 1997), ausktribosphenid and monotrematan mammals (Pridmore *et al.* 2006; australo-sphenidans *sensu* Kielan-Jaworowska *et al.* 2004), dicynodont synapsids (Thulborn & Turner 2003) and the freshwater mussel *Mesohydriaela ipsviciensis* (Dettmann *et al.* 1992), there is now clear evidence for palaeobiogeo-graphic connections to the rest of Gondwana as predicted from palaeogeographic reconstructions (Smith *et al.* 1994; Hay *et al.* 1999; Scotese 2001; Sereno *et al.* 2004), and hitherto only weakly supported by palaeobiogeographic analyses (Molnar 1992; Upchurch *et al.* 2002) or tentative referrals (Molnar 1992, p. 261; Rauhut 2005, p. 105). Somphospondyl titanosauriform sauropods have recently been recognized as a common element of northern Australia's Mid-Cretaceous dinosaur fauna (Salgado 1993; Molnar 2000; Molnar & Salisbury 2005; Salisbury *et al.* 2006), which is reminiscent of the South American Cretaceous. Reports of Australian dinosaurs with potential palaeobiogeographic connections to Asia, such as ornitho-mimosaurs, oviraptorosaurs and neoceratopsians (Rich & Vickers-Rich 1994, 2003; Currie *et al.* 1996) have recently

been questioned (Salisbury *et al.* 2007), with alternative interpretations supporting links to terrestrial vertebrate faunas from adjoining Gondwanan landmasses (Salisbury *et al.* 2007). The presence of *Megaraptor*, or a close relative, in the Early Cretaceous of Australia also weakens claims for the existence of a geographical or climatic barrier isolating Australia from the rest of Gondwana during this time (Rich *et al.* 1988; Molnar 1992; Thulborn & Turner 2003).

Although a quantitative analysis of the palaeobiogeo-graphic relationships of the Early Cretaceous fauna of Australia is beyond the scope of the present paper, it can be instructive to assess the relative consistency of the new data presented here with existing palaeogeographic models. Three general models have been proposed regarding the fragmentation of Gondwana during the Cretaceous (Upchurch 2006, 2008). These include: (i) a 'traditional' model, in which Gondwana is initially divided into separate western (Africa and South America) and eastern (Antarctica, India, Madagascar and Australia) parts in the Early Cretaceous, *ca* 138 Myr ago (figure 3*a–c*; Smith *et al.* 1994; Scotese 2001), (ii) the 'Africa-first' model, in which Africa is isolated from other Gondwanan landmasses before the beginning of the Late Cretaceous, and South America, Antarctica, and Australia remain connected until the Early Tertiary (figure 3*d–f*; Hay *et al.* 1999; Krause *et al.* 2007), and (iii) the 'Pan-Gondwana' model, in which three land bridges connected the southern continents through the Early Cretaceous and were severed during a relatively brief interval at the beginning of the Late Cretaceous (Sereno *et al.* 2004). The presence of NMV P186076 in the Late Aptian–Early Albian of Australia and *Megaraptor* as early as the Middle Cenomanian of Argentina is largely consistent

with models (ii) and (iii), which suggest more cosmopolitan distributions of Mid-Cretaceous terrestrial taxa. Alternative palaeogeographic scenarios, such as an initial rifting of western and eastern Gondwana followed by subsequent reconnection of South America and Antarctica, could also account for the observed pattern of *Megaraptor* and NMV P186076 distribution, and that of other Cretaceous vertebrates (Turner 2004; Upchurch 2006, 2008). However, reconciling the temporal and geographical distributions of *Megaraptor* and NMV P186076 with the traditional palaeogeographic model would require either (i) cross-seaway dispersal of *Megaraptor* or a close relative during the Mid-Cretaceous or (ii) that the most recent common ancestor of the Australian and Argentine materials existed prior to the Valanginian (*ca* 138 Myr ago), and the two lineages were isolated during the initial split between western and eastern Gondwana. Depending on the exact age of *Baryonyx* and phylogenetic resolution within Spinosauroidea, ghost lineages implied by phylogeny may extend the lineage leading to *Megaraptor* and NMV P186076 to the base of the Barremian (figure 2), but do not necessarily extend the age of the most recent common ancestor of NMV P186076 and *Megaraptor*. Thus, we consider the observed temporal and geographical distribution of NMV P186076 and *Megaraptor* to be less consistent with the traditional model of Gondwanan fragmentation, and more consistent with a model that proposes connections between Australia, Antarctica and South America during the Mid-Cretaceous (Hay *et al.* 1999; Sereno *et al.* 2004; Krause *et al.* 2007).

Geological evidence suggests that land connections between southern South America and the West Antarctic Archipelago persisted until at least the Late Eocene, at the earliest proposed opening of the Drake Passage (Livermore *et al.* 2005). It was not until the Late Cretaceous (*ca* 84 Myr ago; Veevers *et al.* 1991) that Australia and Antarctica began to separate, with the continental microplate of the South Tasman Rise between southeastern Australia and Antarctica submerging as early as the Late Cretaceous (*ca* 64 Myr ago; Woodburne & Case 1996). Thus, both land connections between South America and Antarctica, and Antarctica and Australia were not likely to have been severed until long after the occurrence of NMV P186076 in Australia and *Megaraptor* in Argentina. Fossil evidence from terrestrial vertebrates (including dinosaurs) also supports the maintenance of these land connections into the Late Cretaceous and Early Tertiary (Woodburne & Case 1996; Rougier *et al.* 1998; Case *et al.* 2000; Krause *et al.* 2007). Furthermore, distribution patterns of numerous extant plants and animals are consistent with the inference of significant amounts of dispersal between Australia and South America during the Late Cretaceous–Early Tertiary (Sanmartín & Ronquist 2004).

Finally, if *Megaraptor* is indeed a member of Spinosauroidea, NMV P186076 represents the first occurrence of this group in Australia, and would further predict the presence of spinosauroids in Antarctica during the Mid-Cretaceous. Analysis of Cretaceous terrestrial vertebrate palaeobiogeography has been hampered by lack of phylogenetic control, and poor records in several geographical areas, including Australia (Molnar 1992; Upchurch *et al.* 2002; Turner 2004; Krause *et al.* 2007).

NMV P186076 adds a crucial, phylogenetically constrained data point from such an area, which may be valuable to future palaeobiogeographic analyses.

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