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Gondwana Research

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# A large-clawed theropod (Dinosauria: Tetanurae) from the Lower Cretaceous of Australia and the Gondwanan origin of megaraptorid theropods

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## ARTICLE INFO

### Article history:

Received 29 October 2014

Received in revised form 5 August 2015

Accepted 5 August 2015

Available online xxxx

Handling Editor: I.D. Somerville

### Keywords:

Megaraptoridae

Dinosauria

Griman Creek Formation

Palaeobiogeography

Gondwana

## ABSTRACT

Megaraptoridae comprises a clade of enigmatic Gondwanan theropods with characteristic hypertrophied claws on the first and second manual digits. The majority of megaraptorids are known from South America, although a single genus (*Australovenator*) plus additional indeterminate material is also known from Australia. This clade has a controversial placement among theropods, and recently has been interpreted alternatively as a carcharodontosaurian or a tyrannosauroid lineage. We describe new fragmentary but associated postcranial remains from the opal fields of Lightning Ridge (middle-Albian, Griman Creek Formation) in north-central New South Wales. The new unnamed taxon exhibits a number of unusual features that suggest the presence of a hitherto unrecognised Australian megaraptorid. From an Australian perspective, the Lightning Ridge taxon predates *Australovenator* by ca. 10 Ma and is minimally coeval with megaraptoran material reported from the Eumeralla Formation of Victoria (but potentially 6.1–9.5 Ma younger). It is also notable as the largest predatory dinosaur yet identified from Australia and is only the second theropod known from more than a single element. A Bayesian phylogenetic approach integrating morphological, stratigraphic and palaeogeographic information tested both the carcharodontosaurian and tyrannosauroid placements for Megaraptorinae. Regardless of the preferred placement among Tetanurae, rigorous palaeobiogeographic analyses support an Asian origin of Megaraptorinae in the latest Jurassic (about 150–135 Ma), an Early Cretaceous (about 130–121 Ma) divergence of the Gondwanan lineage leading to Megaraptoridae, and an Australian root for megaraptorid radiation. These results indicate that Australia's Cretaceous dinosaur fauna did not comprise simply of immigrant taxa but was a source for complex two-way interchange between Australia–Antarctica–South America leading to the evolution of at least one group of apex predatory dinosaurs in Gondwana.

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## 1. Introduction

Historically, Australia has been viewed as an evolutionary cul-de-sac with regard to its enigmatic dinosaur fauna (Molnar, 1992a, 1997). Two hypotheses currently dominate, which suggest that Australia's dinosaurs were either an aberrant and relict fauna with North American and Asian affinities (e.g. Rich and Rich, 1989; Rich and Vickers-Rich, 1994; Rich, 1996; Rich and Vickers-Rich, 2003; Rich et al., 2014), or alternatively show close affiliations with faunas from western Gondwana, namely South America and Africa (e.g. Smith et al., 2008; Agnolin et al.,

2010; Novas et al., 2013; Poropat et al., 2015). These polarised interpretations stem from a lack of consensus regarding taxonomic identifications, which in turn are a result of the highly fragmentary preservation of many Australian dinosaur specimens (see Agnolin et al., 2010; Poropat et al., 2015). Nevertheless, a Gondwanan affiliation for Australia's dinosaur fauna appears most tenable and is bolstered by similar interpretations of contemporaneous vertebrate groups including crocodyliforms, turtles, and mammals (Luo et al., 2002; Salisbury et al., 2006; Poropat et al., 2015; Sterli et al., 2015). Regardless, there is no convincing evidence to suggest that any major dinosaur lineage originated in Australia. In a marked departure from most other Australian Cretaceous vertebrates, the crocodyliform *Isisfordia duncani* from the latest Lower Cretaceous of Queensland (Salisbury et al., 2006; Tucker et al., 2013) suggests that at least one major clade—the modern crocodyliforms, Eusuchia—originated in Australia.

Of relevance to the current interpretation of Gondwanan dinosaur dispersal is the fossil record of Australian theropods, which almost exclusively comprises isolated elements. Such an inherently limited

**Abbreviations:** LRF, Australian Opal Centre, Lightning Ridge, New South Wales, Australia, Lightning Ridge Fossil; MIWG, Dinosaur Isle, Isle of Wight Museum Service (formerly Museum of Isle of Wight Geology), Sandown, UK; NHMUK, Natural History Museum, London, United Kingdom; NMV, National Museum of Victoria, Melbourne, Victoria, Australia, Palaeontological collections.

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<http://dx.doi.org/10.1016/j.gr.2015.08.004>

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Please cite this article as: Bell, P.R., et al., A large-clawed theropod (Dinosauria: Tetanurae) from the Lower Cretaceous of Australia and the Gondwanan origin of megaraptorid th..., Gondwana Research (2015), <http://dx.doi.org/10.1016/j.gr.2015.08.004>

record has frustrated attempts to properly compare taxa and limited their use in palaeobiogeographic analyses (see Agnolin et al., 2010; Poropat et al., 2015 for recent revisions of Australian dinosaurs). The only named theropod represented by more than a single element is the megaraptorid *Australovenator wintonensis* from the lowermost Upper Cretaceous of central-western Queensland (Hocknull et al., 2009; White et al., 2012; Tucker et al., 2013; White et al., 2013a). In addition to *Australovenator*, Megaraptoridae (*sensu* Novas et al., 2013) consists of three Argentinean genera *Aerosteon*, *Megaraptor*, and *Orkoraptor*, which are generally characterised by their elongate, gracile metatarsus and hypertrophied claws on the first manual digit. The closely related Asian form, *Fukuiraptor* was recovered as the sister taxon to Megaraptoridae (Novas et al., 2013) making Megaraptoridae purely Gondwanan in distribution (Porfiri et al., 2014).

Despite their distinctive morphology, megaraptoran affinities are unclear having been posited as closely related to Carcharodontosauridae within Allosauroidae (Benson et al., 2010a; Carrano et al., 2012; Zanno and Makovicky, 2013) or as deeply nested within Coelurosauria possibly within Tyrannosauroidae (Novas et al., 2013; Porfiri et al., 2014). Here, we report on associated fragmentary remains of a new megaraptorid from the Lower Cretaceous Griman Creek Formation exposed at Lightning Ridge (New South Wales, Australia). The partial remains do not allow an unequivocal classification of the taxon and therefore we refrain from assigning a formal name to it. However, it represents only the second theropod specimen from Australia that comprises more than a single element and, more importantly, provides the basis for revised discussions on the dispersal history of Megaraptora and Australia's role in faunal interchange within Gondwana.

## 2. Locality and geology

LRF 100–106 was excavated from an underground mine at the 'Carter's Rush' opal field, 35 km southwest of the town of Lightning Ridge, north-central New South Wales (Fig. 1). Although the precise stratigraphic provenance of LRF 100–106 is unknown due to the mining process during which the specimen was discovered and excavated (see Comments in the Systematic palaeontology section below), opals and opalised fossils are routinely sourced from the top of the Finch Claystone near its contact with the overlying Wallangulla Sandstone (both pertaining to the Griman Creek Formation, Rolling Downs Group, Surat Basin; Green et al., 1997). Sediments of the Griman Creek Formation consist of primarily non-marine, thinly bedded and interlaminated fine- to medium-grained sandstone and mudstone. Both freshwater and

brackish molluscs occur in the lower part of the formation whereas coals seams and freshwater bivalves are found in the upper deposits, therefore, beds are interpreted as representing a variety of coastal fluvial to estuarine and lagoonal deposits that accumulated on the southern margin of the Eromanga Sea (Dettman et al., 1992; Haig and Lynch, 1993; Green et al., 1997). In particular, deposition is considered to have been initially regressive beach or nearshore marine, followed by paralic to deltaic and finally fluvial floodplain conditions in the upper sequences of the formation (Green et al., 1997). The Griman Creek Formation preserves a poorly known but diverse vertebrate fauna that includes titanosauriform sauropods (Molnar and Salisbury, 2005; Molnar, 2011), megaraptoran theropods (von Huene, 1932; Molnar, 1980a; Agnolin et al., 2010; White et al., 2013b), basal ornithomorphs (von Huene, 1932; Molnar and Galton, 1986), iguanodontian-grade ornithomorphs (Molnar, 1992b), crocodylians (Etheridge, 1917; Molnar, 1980b; Molnar and Willis, 2001), birds (Molnar, 1999), plesiosaurs (Kear, 2006), dipnoans (Kemp, 1993, 1997a,b), chelid and meiolaniform turtles (Smith, 2010; Smith and Kear, 2013), monotremes (Archer et al., 1985; Rich et al., 1989; Flannery et al., 1995), as well as possible indeterminate synapsids (Clemens et al., 2003) and undescribed teleost and chondrichthyan remains (Dettman et al., 1992; PRB, ES pers. obs.).

Direct chronostratigraphic constraints for the Griman Creek Formation are limited to two fission-track analyses on core samples from the eastern margin of the Surat Basin. The first indicates a ~107 myr age, the second suggests that sedimentation ended at ca. 99 myr (Raza et al., 2009) and was followed by a denudation phase responsible for a major unconformity in the area (Korsch and Totterdell, 2009; Totterdell et al., 2009). Similarly, palynofloras of reference unit APK5 are associated with the Griman Creek Formation deposits (*Coptospora paradoxa* spore-pollen zone; Burger, 1980; Dettman et al., 1992; Price, 1997 and references therein), supporting a middle Albian age for this interval. Furthermore, basin-scale correlations between the Surat Basin and the Eromanga Basin deposits to the northwest indicate that the Griman Creek Formation is coeval to the Toolebuc and Allaru formations, both referred to the mid- and upper Albian, respectively (Haig and Lynch, 1993; Gray et al., 2002; Cook, 2012). These units are overlaid by the upper Albian Mackunda Formation and the upper Albian–lower Turonian Winton Formation (see Cook, 2012; Tucker et al., 2013 for a detailed revision of biostratigraphic data). Relevant to this study, detrital zircon ages for the Winton Formation (a pivotal unit preserving a rich and diverse vertebrate fauna which crops out widely across central-western Queensland, north of the study area) record a depositional history during the interval ~103–92 Ma (Tucker et al., 2013).

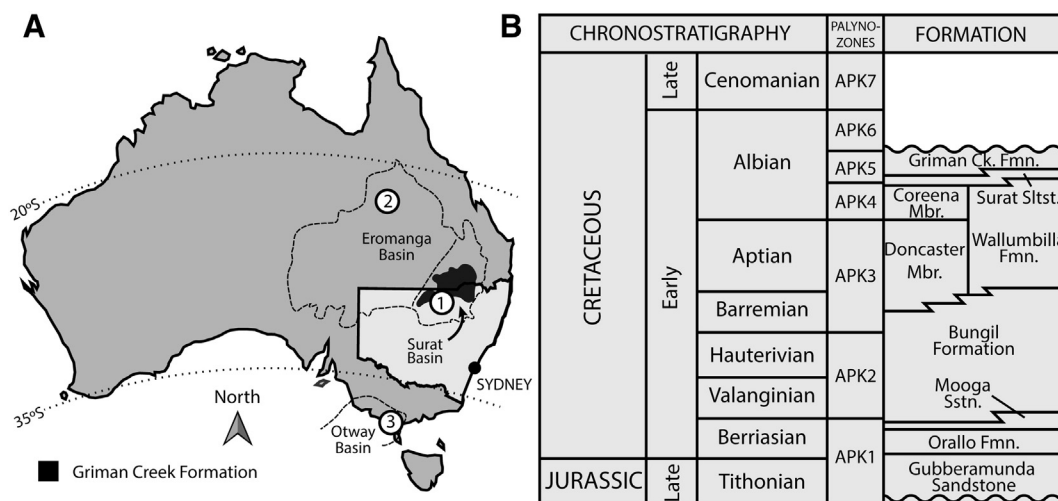


Fig. 1. Locality map (A) showing the major sedimentary basins and locations of megaraptoran discoveries in Australia. 1. Lightning Ridge, NSW (Griman Creek Formation, middle Albian); 2. Winton, Queensland (upper Winton Formation, Cenomanian–Turonian); 3. Otway Basin, Victoria (Eumeralla Formation, late Aptian–early Albian). (B) Chronostratigraphy of the Surat Basin. The Griman Creek Formation has yielded a diverse vertebrate fauna including the remains of the new theropod.

More specifically, rocks containing Australia's only named megaraptorid, *Australovenator*, lie at or close to the Cenomanian–Turonian boundary (94.5–92.5 Ma; Tucker et al., 2013). Thus, *Australovenator* (and associated vertebrate fauna including dinosaurs, crocodyliforms, aquatic squamates, turtles, lungfish and teleost fishes), is roughly 12 million years younger than the deposits (and its constituent fauna) around Lightning Ridge.

### 3. Systematic palaeontology

Dinosauria Owen 1842  
 Saurischia Seeley 1887  
 Theropoda Marsh 1881  
 Tetanurae Gauthier 1986  
 Megaraptora Benson, Carrano, et Brusatte 2010a  
 Megaraptoridae Novas, Agnolin, Ezcurra, Porfiri, et Canale 2013  
 Megaraptoridae gen. et sp. indet.

#### 3.1. Material

The associated but fragmentary postcranial skeleton (LRF 100–106) includes proximal parts of the right ulna and the left or right manual ungual (?)I-2, possible fragments of the distal tibia, the left metatarsal III, the pubic peduncle of the left ilium, numerous rib and gastral rib fragments, and many unidentified fragments. Many of the elements are preserved as natural casts (pseudomorphs) in bluish-grey common opal (potch), which in places shows flashes of reds and blues that are associated with precious opal. Unfortunately, this unusual mode of fossilisation generally results in the total loss of bone microstructure (Rey, 2013), which in this case obviates histological observation that may have provided clues as to the maturity of the individual.

#### 3.2. Locality and horizon

LRF 100–106 was excavated from an underground mine at the 'Carter's Rush' opal field, 35 km southwest of the town of Lightning Ridge, north-central New South Wales. The specimen comes from the top of the Finch Claystone near its contact with the overlying Wallangulla Sandstone (both pertaining to the Griman Creek Formation, Rolling Downs Group, Surat Basin Green et al., 1997), and is middle Albian in age.

#### 3.3. Comments

Opalised fossils at Lightning Ridge (and other opal-bearing regions such as Coober Pedy and Andamooka) are typically discovered following a protracted process of extraction, sieving, washing and sorting of bulk sediments. As a result, fossils discovered during this process are typically small, isolated, and abraded, and any association between specimens is lost. In contrast, LRF 100–106 was discovered *in situ* during excavation of an underground mine at the 'Carter's Rush' opal field. Some of the bones were recognised and manually removed by miners and eventually donated to the Australian Opal Centre in 2005. Regrettably, an unknown number of bones were not recognised and presumably destroyed prior to or during excavation of what was almost certainly a more complete skeleton than is currently represented. Fresh breaks on most of the recovered bones (e.g. ulna, manual ungual) attest to the unfortunate damage done during excavation. Although the original (*in situ*) positions of the bones were not recorded during excavation, the overall paucity of dinosaur fossils and the extreme rarity of large (>10 cm) bones in the Griman Creek Formation all suggest the elements come from a single individual. Moreover, the respective sizes of bones, lack of overlapping elements, and megaraptoran features present on many of the bones are all consistent with their assignment to a single individual. Thus, we reject the possibility that the specimen represents a chimera as has been argued for some other Australian dinosaurs (see

Herne and Salisbury, 2009 and counterargument by Rich et al., 2010). No other fossil remains were found (or at least recognised by the miners) alongside the megaraptoran elements.

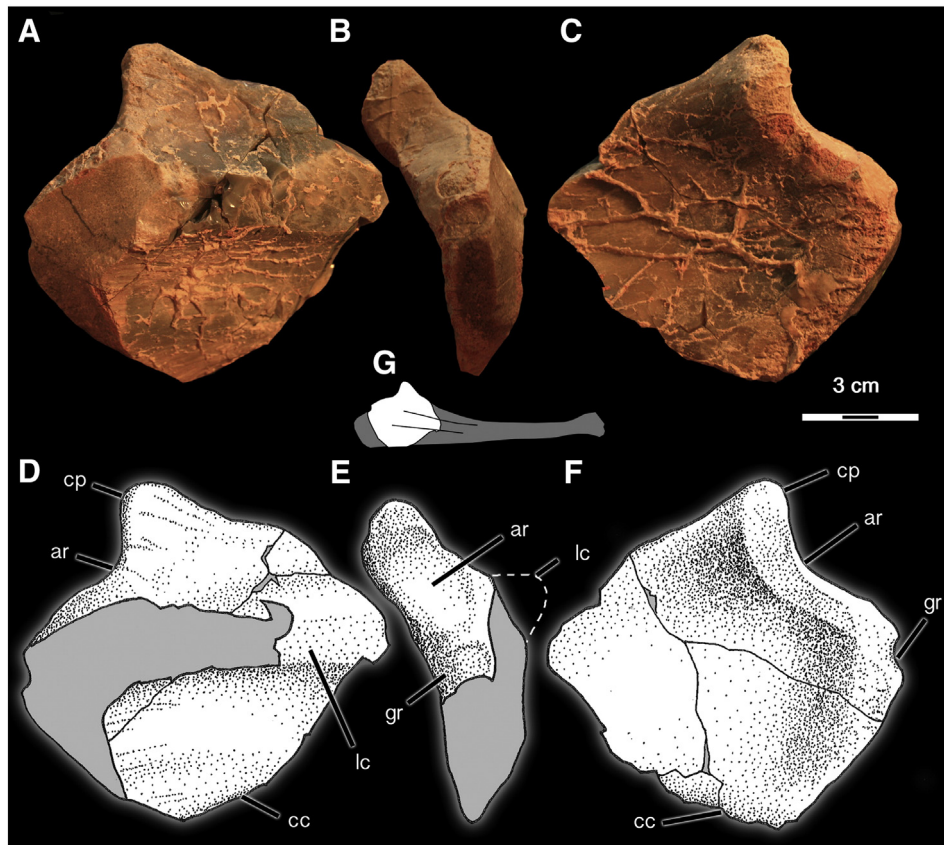
In 1932, a single metacarpal I (NHMUK R3718) also from the Griman Creek Formation at Lightning Ridge was used to erect a new theropod taxon, *Rapator ornitholestoides* (von Huene, 1932). Recent comparisons with *Australovenator* and *Megaraptor* suggest megaraptoran affinities of NHMUK R3718 although there is disagreement regarding the validity of *R. ornitholestoides* (Hocknull et al., 2009; Agnolin et al., 2010; White et al., 2013b). We follow Agnolin et al. (2010) in considering *R. ornitholestoides* as a *nomen dubium* and although NHMUK R3718 and LRF 100–106 may conceivably pertain to the same taxon, there are no overlapping elements to test this hypothesis.

LRF 100–106 is referred to a medium-sized (approx. 6 m long) megaraptorid theropod (see the Discussion section) characterised by the proximal end of metatarsal III strongly asymmetrical (mediolateral aspect) with trapezoidal cranial process extending further distally along the shaft than the caudal process giving an overall ball-peen hammer-shaped profile; and contact for metatarsal II on metatarsal III divided into cranial and caudal halves by a shallow, longitudinal groove. Although no formal taxon is erected, it differs from the only named Australian megaraptorid, *Australovenator*, based on the following combination of features: 1. more robust cranial process on the ulna; 2. more gracile manual ungual I-2 (or II-3) with sharply defined median ridge on proximal articular surface; 3. prominent, broad groove between the articular facet and the flexor tubercle on manual ungual I-2 (convergent in *Megaraptor*); 4. metatarsal III with a well-developed lateral ridge on proximal shaft; and 5. distal articular surface of metatarsal III as wide as it is long.

### 4. Description

#### 4.1. Ulna

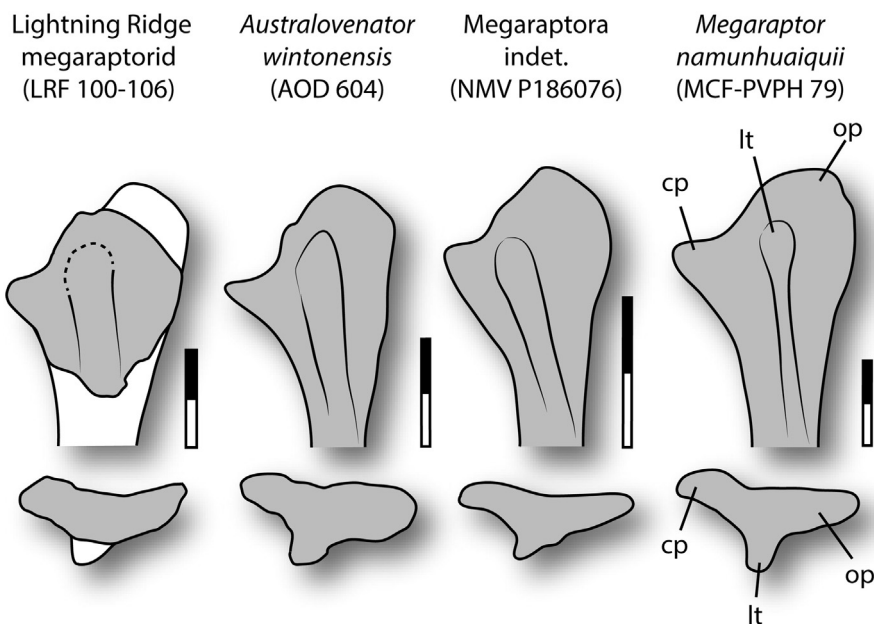
The proximal end of the right ulna consists of the articular surface for the humerus and part of the olecranon process (Fig. 2). In lateral view, the bone is craniocaudally broadest between the cranial process and the caudal crest, tapering distally. The humeral articular surface is arcuate in mediolateral view and flattened across the articular surface to form a smooth contact with the distal humerus. The cranial process is triangular in lateral view and relatively robust, as in *Megaraptor* and the Victorian cf. *Megaraptor*, but unlike the more gracile form of *Australovenator* (Fig. 3). A lateral ridge extends along the midline of the ulna for the full preserved length of the element (Fig. 2D). The ridge is low, symmetrical in section and becomes less prominent distally. Although broken, the crest is reminiscent of the lateral crest present in the megaraptorids *Australovenator*, *Megaraptor*, and cf. *Megaraptor* from Victoria (Novas, 1998; Smith et al., 2008; White et al., 2012). As the proximal part of the crest is broken in LRF 100–106, it is unclear whether it also formed a prominent tuberosity as in *Australovenator* and *Megaraptor* (Fig. 2A, D). Several spinosauroids (*Baryonyx*, *Poikilopleuron*, *Suchomimus*, *Torvosaurus*) also possess a lateral tuberosity; however, they lack the proximodistally-orientated crest present in megaraptorids (Smith et al., 2008). Caudal to the lateral crest, the caudolateral surface forms a shallow but broad fossa, which Smith et al. (2008) posited as the insertion for the m. triceps brachii complex. Such a fossa is present in megaraptorids and some spinosauroids (*Baryonyx*, *Suchomimus*); however, the fossa is more caudally facing in the latter group (Smith et al., 2008). The forelimb osteology is not well known in allosauroids although a caudolateral fossa is absent in *Allosaurus* (Madsen, 1976), *Acrocanthosaurus* (Currie and Carpenter, 2000), and *Concavenator* (Ortega et al., 2010, Fig. 4). Several small neurovascular foramina pierce the surface of this fossa in LRF 100–106. The medial surface is concave and comparatively featureless. Proximally, the sheared base of the olecranon process is mediolaterally compressed; the medial and lateral sides meet to form a sharply



**Fig. 2.** Megaraptoridae gen. et sp. indet. right proximal ulna in (A, D) lateral, (B, E) proximal, and (C, F) medial views. (G) Reconstruction of right ulna showing known parts in white (not to scale). Outline based on *Australovenator*. Grey in A–F = broken bone surface; grey in G = reconstructed areas. ar, ulna–humerus articular surface; cp, cranial process; cc, caudal crest; lc, lateral crest and gr, groove.

defined caudal margin, or crest. A mediolaterally compressed olecranon process and caudal crest are both peculiar to megaraptorids (Smith et al., 2008; Novas et al., 2013). A similar condition is present in *Suchomimus* and *Baryonyx*; however, in these taxa the olecranon process (in proximal view) is distally expanded compared to the triangular

process in megaraptorids. In addition, the olecranon process and cranial process of LRF 100–106 and megaraptorids are in the same craniocaudal plane when viewed proximally, whereas they form a comparatively acute angle in *Baryonyx* and *Suchomimus* (Smith et al., 2008). Separating the olecranon process and the proximal articular surface is a shallow,



**Fig. 3.** Comparison of megaraptorid proximal left ulnae. Right ulna of the Lightning Ridge theropod reversed for clarity. Scale bars = 5 cm. cp, cranial process; lt, lateral tuberosity and op, olecranon process.

transverse sulcus visible in lateral aspect (Fig. 2C, F). This sulcus exposes the internal trabecular bone, therefore it is unclear whether this feature is real or an artefact; the latter may be more likely given its close proximity to other fractures (e.g. on the lateral crest and olecranon process). A small sulcus is present on the right ulna of *Australovenator* (absent on the left), where it too is associated with a break in the specimen (White et al., 2012; S. Salisbury pers. comm. 2014). No sulcus is evident in any specimen referred to *Megaraptor* (Novas, 1998, Fig. 1; Agnolin et al., 2010, Fig. 19) nor in an isolated megaraptoran ulna (NMV P186076) from the Aptian–Albian of Victoria (Smith et al., 2008; Fig. 3).

#### 4.2. Manual unguis

The proximal end of a manual unguis is identified as belonging to digit I or digit II based on its large size, which is comparable to that of *Australovenator* (Table 1). It preserves the proximal articular surface, flexor tubercle and part of the unguis blade (Fig. 4). Parts of the lateral and palmar surfaces are obscured by opal spicules (a product of diagenesis); however, enough can be discerned to tell that the unguis was strongly mediolaterally compressed and tapered to a sharp edge along its inner curvature (palmar margin). The proximal articular surface is dorsoventrally elongate (height to width ratio = 2:1), ovoid, and strongly ginglymoid (Fig. 4A, E), typical of megaraptoran theropods (Novas, 1998; Novas et al., 2013). The lateral and medial margins of the articular surface extend as low ridges onto the dorsal part of the unguis continuing a short distance distally before converging at the midline. These ridges delineate a raised proximodorsal extensor tubercle, the dorsal portion of which is missing in this specimen. Immediately distal to this region, both lateral and medial sides of the unguis are ornamented by numerous, fine, axially-orientated striations. In both *Australovenator* (White et al., 2012) and *Megaraptor* (Novas, 1998; Calvo et al., 2004), the distal halves of the medial and lateral grooves are asymmetrically positioned so that the medial groove is positioned higher than the lateral one. Although both grooves are present in LRF 100–106, not enough of the claw is preserved to identify whether they were similarly asymmetrical. As a result, it is not currently possible to identify whether this element is from the left or right side. The flexor tubercle is low as in *Australovenator* (White et al., 2012) and *Megaraptor* (Novas, 1998), square in palmar view and separated from the proximal articular surface by a deep sulcus. This sulcus extends distally onto the lateral and medial surfaces of the unguis (Fig. 4E, F). The flexor tubercle is subdivided into discrete regions in palmar view (Fig. 4H): proximally, it forms a flattened, transverse rectangular platform. The platform is delineated distally by a low transverse ridge in front of which are two shallow depressions (medial and lateral flexor facets) separated by a median ridge.

**Table 1**

Comparative measurements (in mm) of select elements in three megaraptorids. As identification of manual unguis I-2 is tentative for LRF 100–106, comparative measurements are included for both unguis I-2 and II-3.

Data from Novas (1998), Calvo et al. (2004), and White et al. (2012).

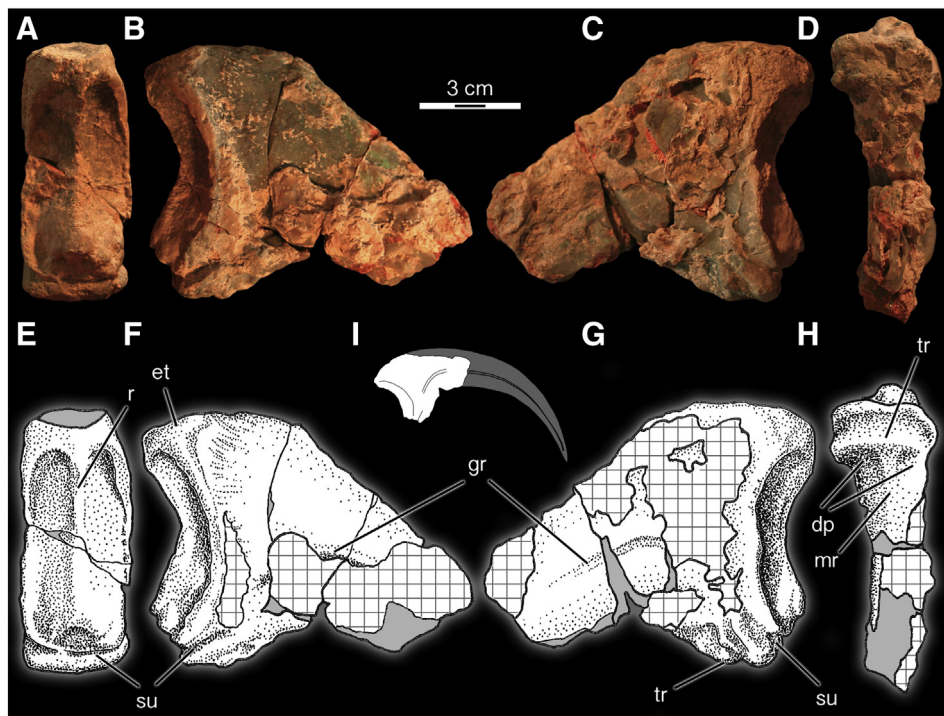
		LRF 100–106	<i>Australovenator</i> <i>wintonensis</i>	<i>Megaraptor</i> <i>namunhuaiquii</i>
Manual unguis I-2	Articular facet height	58	44.97	?
	Proximal width	31	26.08	?
	Proximal height	68	59.84	95
	Articular facet height:proximal width	1.87	1.72	?
Manual unguis II-3	Articular facet height	?	45.89	?
	Proximal width	?	24.88	?
	Proximal height	?	55.13	65
	Articular facet height:proximal width	?	1.84	?
Metatarsal III	Length	350	322	450?
	Proximal width	43	36.94	?
	Proximal length (craniocaudally)	94	79.43	?
	Distal width	51.5	53.54	75
	Distal length (medial maleolus)	51	47.45	?

#### 4.3. Pubic peduncle of ilium

An incomplete, triangular bone is tentatively identified as the ventral end of the pubic peduncle of the ilium. This element is known in two megaraptorans, *Fukuiraptor* (Azuma and Currie, 2000; Benson et al., 2010a) and *Aerosteon* (Serenio et al., 2008; Novas et al., 2013). The bone is broken transversely exposing numerous matrix-filled voids. The smooth, ovoid walls of the intervening bone (=opal), suggests these structures are real and not artefacts of the opalisation process. We interpret these spaces as pneumatic chambers (Fig. 5C). Pneumatisation of the ilium is a derived feature shared by *Megaraptor* and *Neovenator* (Serenio et al., 2008; Benson et al., 2010a). In ventral aspect, the bone forms an asymmetrical triangle; the medial and lateral sides are caudally divergent, although the medial edge extends further caudally than the lateral edge forming a sharply attenuating caudal process in distal view (Fig. 5C). The medial and lateral caudal processes are separated by a broad concavity that forms the acetabular margin. This contrasts with the condition in other megaraptorans for which this element is preserved and most tetanurans in which the pubic peduncle is broadly U-shaped in distal view (e.g. Novas et al., 2013, Fig. 15). It also differs from the heart-shaped outline of megalosauroids (*Eustreptospondylus*, Sadleir et al., 2008; *Megalosaurus*, Benson, 2009). The ventral articular surface is obscured by matrix but weakly convex in lateral view and tapers dorsally such that the articular surface is the longest and broadest part of the preserved element. The medial and lateral surfaces are ornamented by fine dorsoventrally-orientated striations (Fig. 5A, B), which are likely scars representing the attachment site for connective tissues between the pubic peduncle and the pubis (Hutchinson, 2001). The pubic peduncle has a length to width ratio of 1.6, consistent with *Sinraptor* and *Megalosauroides*, but lower than *Aerosteon*, *Neovenator* and derived allosauroids (length:width = 2–2.5) (Serenio et al., 2008; Benson et al., 2010a; Novas et al., 2013).

#### 4.4. Fibula

Two incomplete bones are tentatively interpreted as parts of the shaft and distal end of the (?)left fibula. Despite uncertainty regarding the identification of these bones, they are briefly described here to supplement the description. The largest fragment, broken both proximally and distally, measures 9.5 cm long. Medially an elongate concavity extends along the entire length of the bone (Fig. 6B), which may correspond to the longitudinal groove on the fibula of *Australovenator* (Hocknull et al., 2009). The lateral surface forms a convex V-shape in cross-section. The second fragment appears to represent the distal tip of the fibula. In distal view, the lateral margin is convex, the apex of this convexity lying cranial of the midpoint. The medial margin is flat,



**Fig. 4.** Megaraptoridae gen. et sp. indet. left or right manual ungual (?)-2 in (A, E) proximal; (B, F) right lateral; (C, G) left lateral, and; (D, H) ventral aspects; (I) reconstruction of ungual showing known part in white (not to scale). Outline based on *Megaraptor*. Grey in A–H = broken bone surface; grey in I = reconstructed areas; cross-hatching = matrix. su, sulcus; dp, depression; et, extensor tubercle; gr, vascular groove; mr, median ridge; r, ridge and tr, transverse ridge.

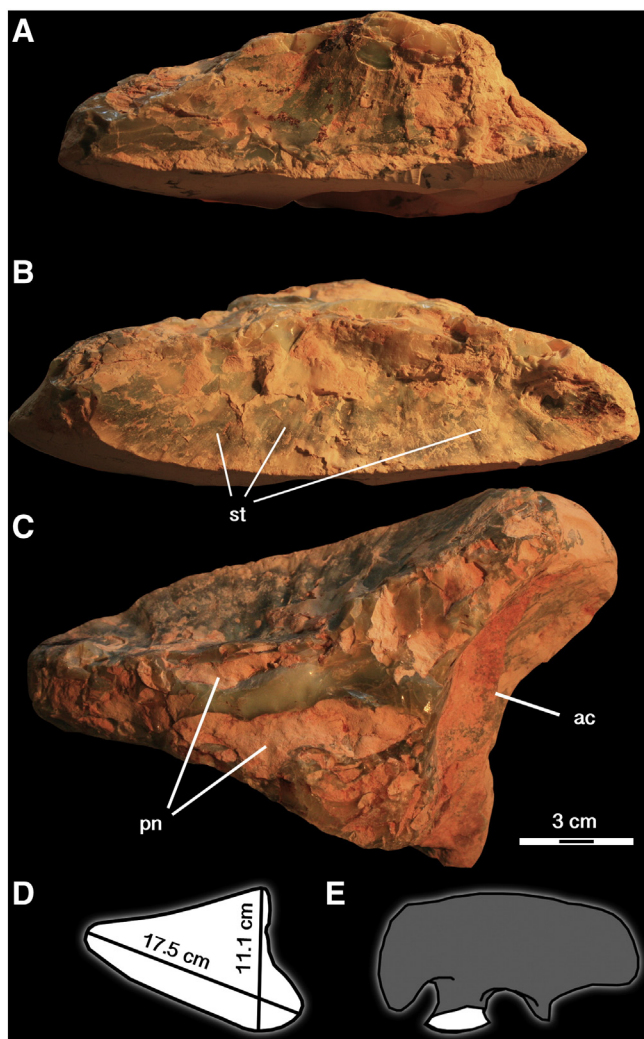
where it presumably formed an articulating facet for the distal tibia (Fig. 6E).

#### 4.5. Metatarsal III

The left metatarsal III is the most complete element of LRF 100–106 (Fig. 7). In general, it is elongate and transversely narrow, typical of most coelurosaur (including megaraptorans), *Mapusaurus*, but contrasting with the more stout proportions in *Neovenator* and basal tetanurans (Novas, 1998; Coria and Currie, 2006; Hocknull et al., 2009; Novas et al., 2013). It is straight in both mediolateral and craniocaudal views and measures roughly 9% longer than the equivalent element on the holotype of *Australovenator* (Table 1). In mediolateral view, the proximal end of the metatarsal is asymmetrically expanded craniocaudally (Fig. 7C); the cranial process is trapezoidal and extends farther distally than the roughly cuboidal-shaped caudal (palmar) process. This configuration gives the proximal metatarsal the overall appearance of a ball-peen hammer, which strongly contrasts with the fan-shaped profile that is otherwise widespread among Theropoda (e.g. Currie and Zhao, 1993; Azuma and Currie, 2000; Coria and Currie, 2006; Fig. 7L, M) and is here considered a potential autapomorphy of the new specimen. The cranial process in *Neovenator* approaches the condition in LRF 100–106; however, *Neovenator* differs in that the cranial margin of the cranial process (when viewed medially) is parallel to the shaft of the metatarsal (Brusatte et al., 2008, pl. 42) whereas it is oblique in LRF 100–106. The caudal process in *Neovenator* is broken; therefore a full comparison cannot be made. Medially, the flat contact for metatarsal II is divided into cranial and caudal halves by a shallow, longitudinal groove (Fig. 7L) and is demarcated caudally by a curved, raised rim of bone (Fig. 7L). The proximal part of metatarsal III is unknown in *Megaraptor*; however, neither the raised caudal rim nor the longitudinal groove is present in *Australovenator*, *Fukuiraptor*, or *Neovenator* and are thus considered potential autapomorphies of the new megaraptorid. In proximal view, the articular surface is rounded cranially and mediolaterally expanded, constricted at its midpoint,

and mediolaterally expanded caudally, although less so than the cranial half. At the caudal margin of the proximal articular surface, the medial and lateral margins meet to form a right angle in proximal aspect (Fig. 7I). This contrasts with the blunt, roughly square caudal end in *Australovenator*. A prominent craniolateral swelling (in proximal view) continues distally by way of a prominent lateral crest that extends approximately one-quarter the length of the shaft (Fig. 7C, F). The height of this crest diminishes abruptly at its distal end but continues as a low ridge for at least two-thirds the length of the shaft (Fig. 7F, G). This arrangement differs from *Australovenator* in which the transition between the proximal crest and the ridge is gradual rather than abrupt. The distal one-third of the shaft is damaged, so the full extent of this ridge cannot be determined in this specimen. Proximally, this ridge would have braced the medial face of metatarsal IV.

In cross-section, the shaft is teardrop-shaped proximally (the pointed end facing cranially), becoming sub-circular distally. The distal extremity of the metatarsal is weakly expanded both mediolaterally and craniocaudally as in *Fukuiraptor* (Azuma and Currie, 2000) and other megaraptorids for which this element is preserved. The distal articular surface is roughly square in distal view (maximum distal width:maximum craniocaudal length = 1:1) and weakly ginglymoid compared to *Megaraptor* (Novas, 1998) and *Australovenator*, but more so than the megaraptoran *Fukuiraptor* (Azuma and Currie, 2000). The distal part of metatarsal III is missing in *Neovenator*, therefore comparisons are impossible. Deep collateral ligament insertion pits are present on either side of the distal articular surface. Despite damage to the craniolateral portion of the distal metatarsal, the distal articular surface appears to extend proximally onto the cranial face of the metatarsal, which is unusual for theropods but is synapomorphic for Megaraptoridae (Novas et al., 2013). The proximal margin of the articular surface sharply demarcates a broad extensor ligament fossa that extends the full width of the element (Fig. 7A, E). This differs from both *Megaraptor* and *Australovenator* whereby there is only a weakly demarcated transition between the distal articular surface and the extensor



**Fig. 5.** Megaraptoridae gen. et sp. indet. pubic peduncle of the left ilium in (A) lateral; (B) medial; (C) dorsal views showing the highly pneumatic interior; (D) ventral outline with associated measurements, and; (E) left ilium in lateral view showing known region (white) in the new specimen. ac, acetabulum; pn, pneumatic chamber and st, scars for the attachment of connective ligaments between pubic peduncle and pubis.

fossa. The proximal border of this fossa is not visible due to breakage of the specimen.

#### 4.6. Ribs and gastralia

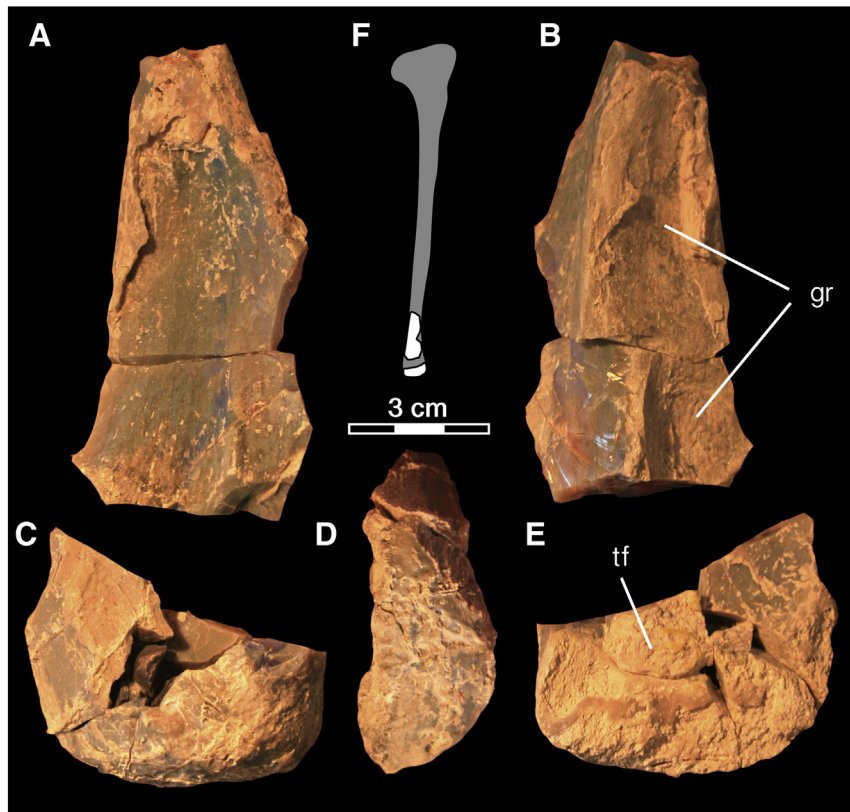
Fragments of several ribs and gastralia were recovered with the holotype. An incomplete rib head (Fig. 8A) comprising the capitulum is craniocaudally compressed with a concave dorsal margin and straight ventral margin (length = 5.5 cm). The proximal articular facet is elliptical; the long axis of which forms an acute angle with the dorsal margin of the capitulum in craniocaudal view. A section of rib shaft measuring 12.5 cm is nearly straight and tapers distally. The cranial surface is convex. Caudally, the rib is broadly concave medially, convex laterally where it is buttressed by a rounded longitudinal ridge. This ridge diminishes distally such that the distal cross-section is more elliptical. A 10 cm section of gastral rib preserves a distinct widening (overtubulation) of the shaft (Fig. 8C). However, surface preservation of this element is poor so it cannot be determined if this widening represents the fusion of two elements (see Sereno et al., 2008), or is pathological or some other artefact. No evidence of pneumaticity was found in any of the gastralia or rib elements.

## 5. Phylogenetic analyses

### 5.1. Parsimony analyses

In order to assess the affinities of the Lightning Ridge theropod, it was scored using modified versions of the most recent and comprehensive character matrices for megaraptorans, provided by Novas et al. (2013) and Zanno and Makovicky (2013), supporting, alternatively, a tyrannosauroid and carcharodontosaurian placement of Megaraptora. Modifications to the Novas et al. (2013) dataset involved the inclusion of the new specimen, two Jurassic coelurosaurians (*Archaeopteryx* and *Zuolong*) and the recently named megaraptoran *Siats* (Zanno and Makovicky, 2013), and the addition of 26 new morphological characters relevant in resolving the positions of the added taxa, resulting in a data matrix of 313 characters and 49 taxa, with *Ceratosaurus* used as an outgroup (see Supplementary information). In both datasets, character scores for *Megaraptor* were updated following Porfiri et al. (2014). Characters 255, 271 and 285 were *a priori* set with weight = 0 as they became redundant with other included characters, respectively, characters 35, 78 and 108 (as outlined by Porfiri et al., 2014). Each dataset was analysed under both parsimony analysis and Bayesian inference, the latter integrating morphological and stratigraphic data following the method described by Lee et al. (2014a,b). Parsimony analyses performed heuristic searches with 100 random addition sequence replicates and tree bisection reconnection using the Hennig Society version of TNT (Goloboff et al., 2008). The search using the modified dataset of Novas et al. (2013) retrieved 448 most parsimonious trees with a length of 1031 steps (Consistency Index = 0.36, Retention Index = 0.64). Unsurprisingly, the overall results are similar to those of the original analysis by Novas et al. (2013). Megaraptorans were recovered among Coelurosauria in a largely unresolved polytomy due to the uncertain position of *Siats*, found, alternatively, as related to ornithomimosaur, as closer to maniraptorans than tyrannosauroids, as a basal megaraptoran, and as closer to tyrannosauroids than *Xiongguanlong*. When *Siats* is pruned *a posteriori* from the results, the reduced strict consensus of the shortest trees recovered a monophyletic Megaraptora, including the new theropod, as sister-taxon of the clade including Tyrannosauridae, *Appalachiosaurus* and *Xiongguanlong* (Fig. S1). The most parsimonious results of the analysis did not support an allosauroid placement for megaraptorans, as measured by step differences between alternative placement of megaraptorans and our preferred topology: forcing megaraptorans among allosauroids (as per Benson et al., 2010a; Zanno and Makovicky, 2013) produced topologies 8 steps longer than the unforced topologies, with *Neovenator* and *Chilantaisaurus* as successive closest relatives of megaraptorans among the basalmost carcharodontosaurian lineage. Nevertheless, this alternative allosauroid hypothesis is not a statistically worse explanation of the data than the tyrannosauroid placement, based on the Templeton test ( $p > 0.7$ ,  $N = 88$ ; Templeton, 1983).

We also analysed the placement of the new Australian theropod and megaraptorans using the dataset of Zanno and Makovicky (2013). Modifications to the original dataset of those authors included the addition of the new specimen and the rescoring of several cranial characters for *Megaraptor* following the findings of Porfiri et al. (2014) (see Supplementary information). The topologies recovered in the second analysis are largely comparable to the original results by Zanno and Makovicky (2013). In all 20,844 shortest trees found (tree length = 1053; CI = 0.41; RI = 0.69), the Lightning Ridge theropod is recovered among megaraptorans, the latter placed among carcharodontosaurian allosauroids (Fig. S1). Since the ingroup of the second dataset lacks both derived tyrannosauroids and representatives of the other main coelurosaur clades, the quantitative support for the tyrannosauroid/coelurosaurian placement for Megaraptora supported by Novas et al. (2013) cannot be tested with the dataset of Zanno and Makovicky (2013). Therefore, based on re-analysis of the most comprehensive datasets published, we consider premature any placement of



**Fig. 6.** Megaraptoridae gen. et sp. indet. partial fibula. Shaft section in (A) lateral and; (B) medial views. Distal end fragment in (C) lateral; (D) distal, and; (E) medial views. (F) Schematic of fibula showing inferred position of present material (white), gr, groove and tf, tibial facet.

Megaraptora beyond *Tetanurae incertae sedis*. We note, however, that wider taxon sampling in the Novas et al. (2013) dataset (compared to that of Zanno and Makovicky, 2013) and the recent discovery of tyrannosauroid features in the skull of *Megaraptor* lends support to the tyrannosauroid hypothesis (Novas et al., 2013; Porfiri et al., 2014). Nevertheless, we discuss the *tempo* and mode of megaraptoran evolution under both the alternative carcharodontosaurian and tyrannosauroid hypotheses.

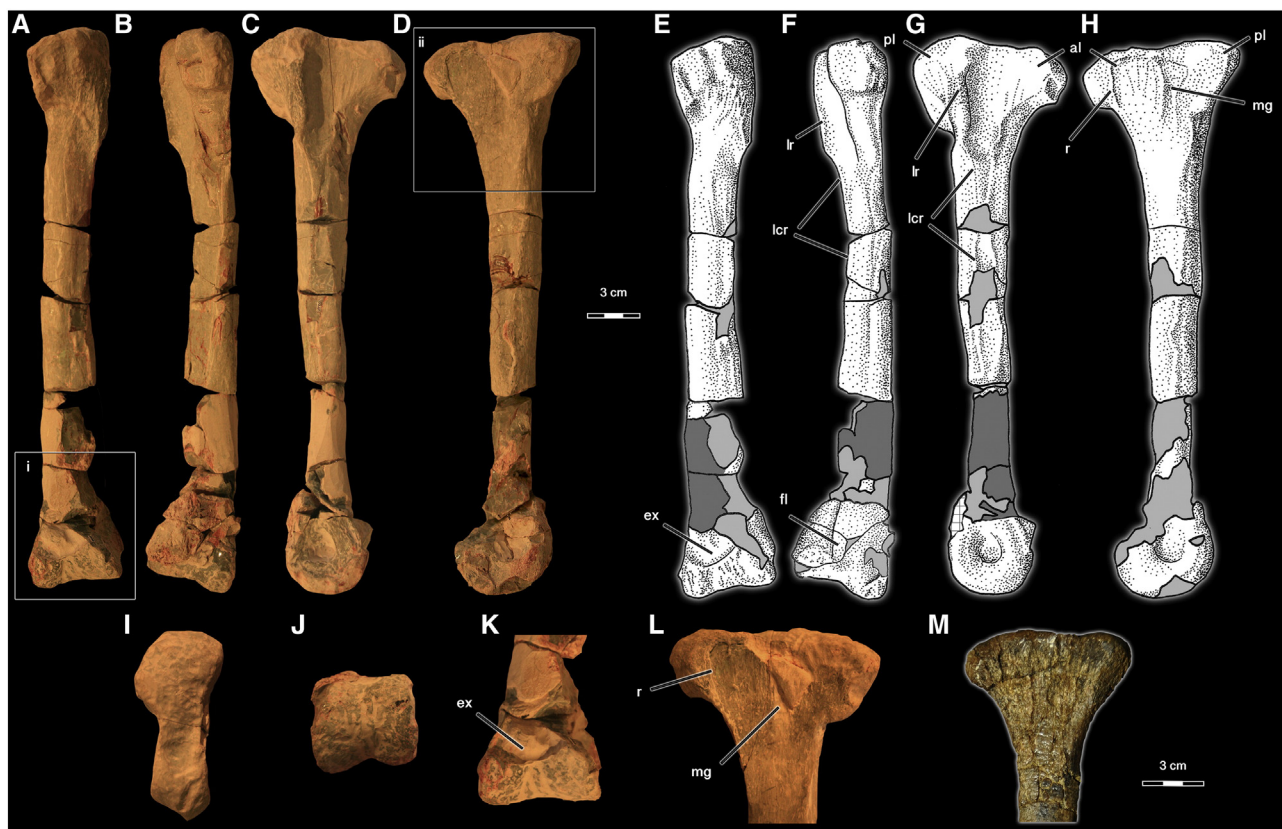
### 5.2. Bayesian and RASP analyses

Bayesian analysis integrating the morphological data (used in the parsimony analyses) and stratigraphic data was performed with BEAST (Drummond et al., 2012) following the method of Lee et al. (2014b). Stratigraphic data and age constraints for each terminal were obtained primarily from the Paleobiology Database (<http://paleobiodb.org/>) and from the literature, using the known geochronological ages for the formations in which the taxa were found or the mean of the geologic stages associated with those formations. In the modified dataset of Novas et al. (2013), root age prior (i.e., the maximum age of the last common ancestor of *Ceratosaurus* and tetanurans) was set along a uniform range between 167 Mya (the age of the oldest terminal included, *Megalosaurus*) and 201 Mya, the latter considered as a 'loose' hard constraint that consistently pre-dates the age of the oldest potential tetanurans and excluding coelophysids from Ceratosauria (as resulted in the parsimony analysis of the dataset of Zanno and Makovicky, 2013). Relevant for the purpose of this analysis, we remark that less restrictive root age assumptions, based on a more inclusive Ceratosauria (e.g., Allain et al., 2007) returned results for the neotetanuran nodes similar to those mentioned above, more restrictive, age assumption. Tetanuran monophyly was forced, following outgroup definition in the parsimony analyses, but no age constraint or internal topologies

for Tetanurae were enforced. In the modified dataset of Zanno and Makovicky (2013), root age prior (i.e., the maximum age of the last common ancestor of *Eoraptor*, *Herrerasaurus* and neotheropods) was set along a uniform range between 233 Mya (the age of the oldest terminals included, *Eoraptor* and *Herrerasaurus*) and 252 Mya (the Permian–Triassic boundary), the latter considered as a 'loose' hard constraint that consistently pre-dates the age of the oldest potential dinosauromorphs. In both analyses, rate variation across traits was modelled using the gamma parameter, and rate variation across branches was modelled using an uncorrelated relaxed clock. The analyses used four replicate runs of 40 million generations, with sampling every 4000 generations. Burnin was set at 20%, and the Maximum Clade Credibility Tree (MCCT) of the four post-burnin samples was used as framework for phyletic reconstruction.

The analysis of the modified dataset of Novas et al. (2013) produced a topology largely consistent with the parsimony analysis (Fig. S2). Megaraptora was recovered as a tyrannosauroid subclade closer to tyrannosaurids than proceratosaurids. *Fukuiraptor* was placed as the basalmost megaraptoran and sister taxon of Megaraptoridae, and the Lightning Ridge theropod as the oldest and most basal member of the latter clade. Although some of the included megaraptoran taxa are based on very fragmentary remains, the phyletic placement of the new Australian taxon was robust, with posterior probability (pp) values of Megaraptora, Megaraptoridae, and of the megaraptorid subclade excluding LRF 100–106 that resulted, respectively, 0.78, 0.89 and 0.71. *Siats* was recovered as closer to ornithomimids than other coelurosaurs as in one of the alternative topologies found in the parsimony analysis, although this placement is weakly supported (pp = 0.29). Cladogenetic timing inferred by the Bayesian analysis placed the megaraptoran divergence from other tyrannosauroids at about 150 Mya, and the origin of the lineage leading to the Gondwanan megaraptorans (Megaraptoridae) at about 130 Mya.





**Fig. 7.** Megaraptoridae gen. et sp. indet. left metatarsal III in (A, E) cranial, (B, F) caudal, (C, G) lateral, (D, H) medial, (I) proximal, and (J) distal aspects. (K) Close-up of distal cranial surface identified by boxed area (i) in A showing broad extensor fossa. (L, M) Comparison of proximal part of metatarsal III in medial view between (L) Lightning Ridge theropod and (M) *Australovenator* (right element reversed for clarity). Region of close-up in L indicated by boxed area (ii). Light grey = broken bone surface; dark grey = plaster; cross-hatching = matrix. al, cranial process of proximal metatarsal; ex, extensor fossa; fl, flexor fossa; lcr, lateral crest; lr, lateral ridge; mg, medial groove; pl, caudal process of proximal metatarsal and r, rim demarcating cranial limit of contact with metatarsal II.

The BEAST analysis of the modified dataset of Zanno and Makovicky (2013) also produced a topology largely consistent with the parsimony analysis (Fig. S2b). Megaraptorans are placed as a basal carcharodontosaurian lineage, diverging from the *Neovenator* lineage at about 135 Ma ( $pp = 0.62$ ). Both *Chilantaisaurus* and *Siats* are recovered as megaraptorans more derived than *Fukuiraptor*, although this result is moderately supported ( $pp = 0.50$ ). The new Australian theropod is found as the basalmost member of the Gondwanan megaraptorids, a result weakly supported ( $pp < 0.50$ ) probably due to the fragmentary preservation of both LRF 100–106 and other basal megaraptorans. The divergence of the megaraptorid lineage from other megaraptorans is placed at about 121 Ma.

The two alternative topologies recovered by the Bayesian analyses were used as phyletic frameworks for palaeobiogeographic reconstruction, inferring ancestral geographic placement of nodes using RASP (Reconstruct Ancestral State in Phylogenies, Yan et al., 2011). The distribution range of the selected theropod taxa was *a priori* divided into six areas: Asia (A), Europe (B), North America (C), Africa (D), South America (E) and Australia (F). Each terminal taxon was scored for the geographic area character state according to the continent(s) it was recovered in (e.g., the new specimen was scored as “F”, whereas *Fukuiraptor* was scored as “A”). Biogeographic inferences on the phylogenetic frameworks were obtained by utilising Statistical Dispersal-Vicariance Analysis (S-DIVA) and Bayesian Binary Markov (BBM) Chain Monte Carlo analysis (Yu et al., 2010). S-DIVA and BBM methods suggest possible ancestral ranges at each node and also calculate probabilities of each ancestral range at nodes. The S-DIVA and BBM analyses performed ten Markov Chain Monte Carlo analyses of 50 million generations, sampling every 100 trees. State frequencies were set as fixed and among-site rate variation was set using the gamma parameter. The first

20% of the recovered trees were discarded and the remaining trees were used to infer ancestral range distribution at nodes. In the S-DIVA analyses, direct range dispersal constraints were forced, excluding those routes considered as not plausible based on Jurassic and Cretaceous palaeogeographic reconstructions (Meschede and Frisch, 1998; Viramonte et al., 1999; Case et al., 2000; Fitzgerald, 2002; Jokat et al., 2003; Macdonald et al., 2003; Cook, 2012; Fanti, 2012; Huston et al., 2012)

### 5.3. Results of palaeobiogeographic analyses

In the following paragraphs, we focus on the results yielded by the palaeogeographic analyses relative to Megaraptora.

#### 5.3.1. *Novas et al. (2013) dataset*

**5.3.1.1. S-DIVA analysis (Fig. 9a).** S-DIVA analysis indicated that the last common ancestor of megaraptorans and other tyrannosauroids was Asian or, alternatively “Asiamerican”. The analysis was unable to infer the ancestral range of the last common ancestor of *Fukuiraptor* and more derived megaraptorans; however, equally robust support was found for an Australian or “Australia–South America” ancestral range for Megaraptoridae. The analysis found an equal support for a South American or an “Australia–South American” range for the last common ancestor of the megaraptorids more derived than the Lightning Ridge theropod

**5.3.1.2. BBM analysis (Fig. 9b).** BBM analysis also indicated that the last common ancestor of Megaraptora and other tyrannosauroids was Asian. An Asian ancestral range for Megaraptora is inferred for the



**Fig. 8.** Megaraptoridae gen. et sp. indet. (A) thoracic rib head, (B) rib shaft, and (C) gastralia fragment. Overtubulation, presumably the result of a healed fracture, indicated by arrowheads.

earliest Cretaceous phase of megaraptoran evolution. A diffusion event from Laurasia to Gondwana is consequently inferred to occur by no later than the early Aptian, with the most plausible ancestral range of the last common ancestor of the Lightning Ridge theropod and more derived megaraptorids (at ca 113 Ma) placed in Australia. The ancestral range of the last common ancestor of the more derived megaraptorids (at ca 103 Ma) is placed in South America. A single dispersal event

from South America to Australia is inferred to have occurred after 96 Ma, leading to *Australovenator*.

### 5.3.2. Zanno and Makovicky (2013) dataset

5.3.2.1. *S-DIVA analysis (Fig. 10a)*. S-DIVA analysis also indicated that the last common ancestor of megaraptorans and other carcharodontosaurians was Eurasian, with an Asia ancestral placement for the megaraptoran node including *Fukuiraptor*. The range of the last common ancestor of the new Lightning Ridge taxon and more derived megaraptorids is inferred as Australian, whereas the analysis was unable to determine the ancestral area of more derived megaraptorids (*Australovenator* and the South American taxa).

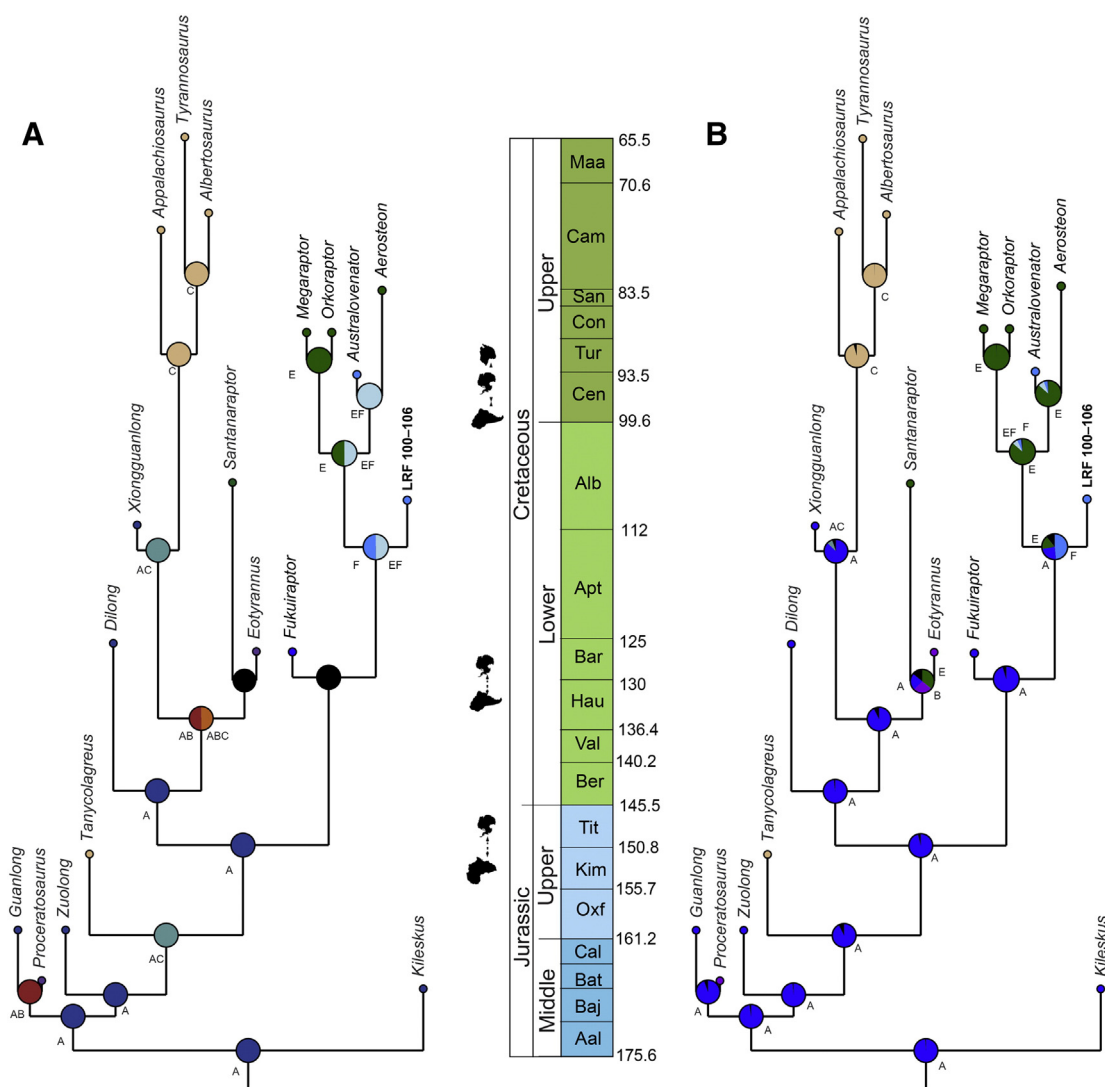
5.3.2.2. *BBM analysis (Fig. 10b)*. BBM analysis indicated that the last common ancestor of Megaraptora and other carcharodontosaurians was European or, alternatively, Eurasian. An Asian root of Megaraptora is also supported, with *Siats* and Megaraptoridae as results of distinct dispersal episodes out of Asia. The last common ancestor shared by the new specimen with more derived megaraptorids is inferred to be Australian. Similarly, the last common ancestor of *Australovenator* and the South American megaraptorids *Aerosteon* and *Megaraptor* is also inferred to be Australian. Accordingly, the South American megaraptorids are interpreted as descendants from a migration event from Australia that occurred between 102 and 92 Ma.

## 6. Discussion

Despite its fragmentary nature, LRF 100–106 is assigned to Megaraptoridae based on the identification of a number of synapomorphies, including: 1. metatarsal III with a distal ginglymoid proximally extended and wide extensor fossa; 2. base of olecranon process mediolaterally compressed suggesting the presence of a sharp caudal crest on proximal ulna (Smith et al., 2008); 3. lateral ridge on the proximal ulna; 4. broad fossa on the caudolateral aspect of proximal ulna (present also in *Baryonyx walkeri* and *Suchomimus tenerensis*; Smith et al., 2008). Furthermore, if our identifications of the pubic peduncle of the ilium and manual ungual I are correct, then two additional synapomorphies may be added to this list: extensive pneumatization of the ilium (present also in *Neovenator*; Benson et al., 2010a), and transversely compressed manual ungual I with dorsoventrally elliptical proximal end. The association and overall morphology of the preserved bones, as well as the presence of derived megaraptoran features consistently agree in referring all specimens to a single taxon. The discovery of this theropod supplements earlier reports based on isolated Australian material (Smith et al., 2008; Agnolin et al., 2010; Benson et al., 2012) that extends Megaraptoridae into the Albian.

### 6.1. Comparison between Australian megaraptorans

Only one named megaraptoran is currently recognised from Australia: *Australovenator*, from the upper part of the Winton Formation (lower Turonian; Tucker et al., 2013) in central-western Queensland (Fig. 1). A nearly complete left ulna (NMV P186076) from the Albian-aged Eumeralla Formation in Victoria represents an indeterminate megaraptoran similar to *Megaraptor* (Smith et al., 2008; Agnolin et al., 2010). Features listed by Hocknull et al. (2009) and Agnolin et al. (2010) that distinguish NMV P186076 from *Australovenator* (presence of a curved caudal margin of the olecranon process, and absence of a longitudinal groove on the lateral surface of the shaft) cannot be observed in the new specimen because it is incomplete. However, NMV P186076 differs from the Lightning Ridge theropod in its smaller size (estimated at two-thirds the length of LRF 100–106 based on the assumption that LRF 100–106 shares similar proportions to *Australovenator*) and a proportionately more slender cranial process that is rounded distally in proximal view (Fig. 3). The same features distinguish *Australovenator*



**Fig. 9.** Palaeogeographic ancestral area reconstruction of Tetanurae, from a Bayesian relaxed-clock analysis based on the dataset of Novas et al. (2013). (A) S-DIVA analysis and (B) BBM analysis. Colours and letters at each node represent the geographic areas of origin (A, Asia; B, Europe; C, North America; D, Africa; E, South America; F, Australia) with relative likelihood of alternate hypotheses represented as a pie graph. Ambiguous geographic areas of origin are indicated by black nodes. (For interpretation of the references to colours in this figure legend, the reader is referred to the web version of this article.)

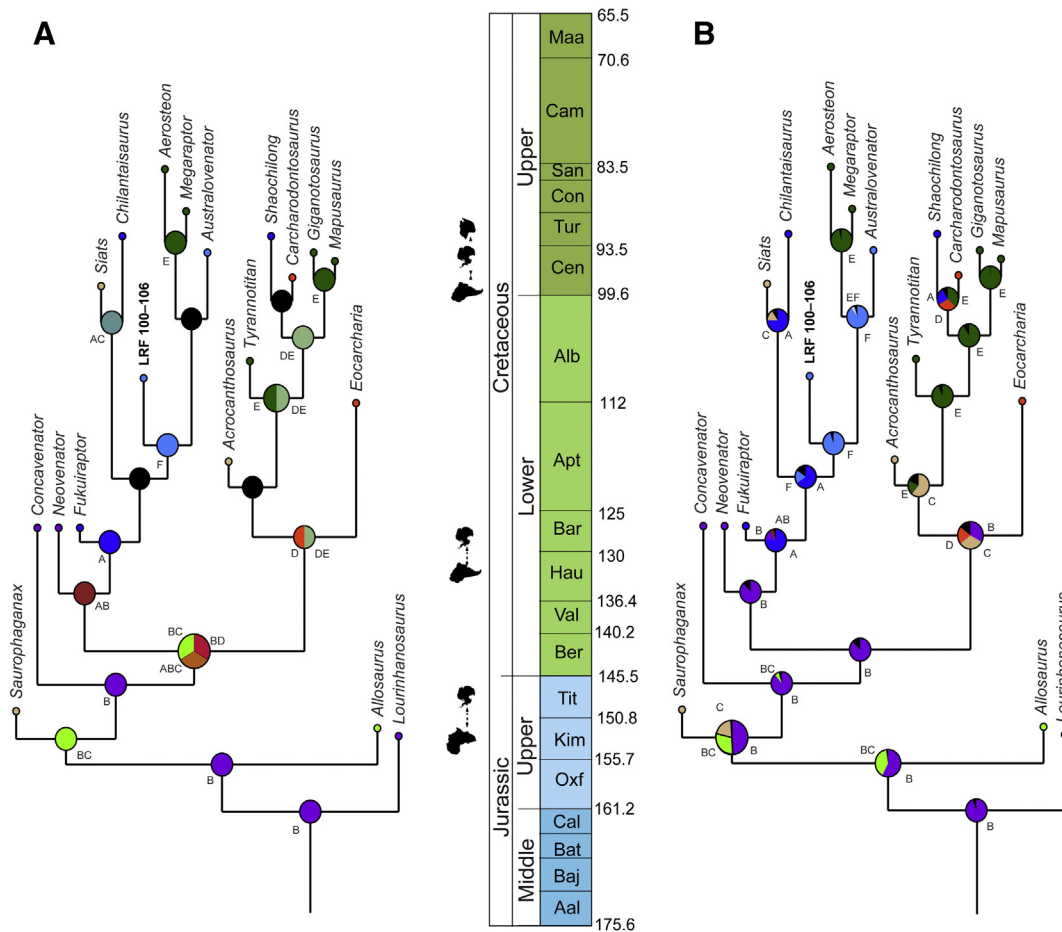
from the new specimen, although *Australovenator* is closer in size to LRF 100–106 than NMV P186076 (Fig. 3). Based on comparative measurements of the available material, the Lightning Ridge theropod was approximately 10% larger than *Australovenator* making it the largest theropod yet discovered in Australia. In addition to its larger size, the Lightning Ridge taxon can be differentiated from *Australovenator* by: 1.) median ridge that subdivides the proximal articular region on manual ungual I (or II) sharp; 2.) boundary between distal articular surface and extensor fossa of metatarsal III sharply demarcated; 3.) proximal metatarsal III asymmetrical and ball-peen hammer-shaped in mediolateral view; 4.) proximal contact for metatarsal II on metatarsal III subdivided by a longitudinal groove, and; 4.) lateral ridge on metatarsal III well developed. Furthermore, the ribs of *Australovenator* display strongly dorso-ventrally constricted “necks” on the capitulum. This contrasts with the comparatively weakly constricted “neck” on the only known capitulum of the Lightning Ridge theropod; however, we concede that this difference may be due to the incompleteness of the new specimen, variation along the dorsal series, or both.

A third putative megaraptoran is represented by an isolated metacarpal I (NHMUK R3718; the holotype of *R. ornitholestoides*) from the same locality as the new specimen. However, as discussed earlier, the validity of *Raptor* is not universally accepted (Hocknull et al., 2009;

Agnolin et al., 2010; White et al., 2013b). Lack of overlapping material precludes comparison or unequivocal assignment of NHMUK R3718 relative to the new specimen, although the possibility that the two are congeneric (or conspecific) cannot be dismissed.

## 6.2. Palaeobiogeography of Megaraptora

The fragmentary and still largely debated theropod record of Australia has led to different interpretations on the tempo and mode of theropod evolution in the continent. Were these taxa mid-Cretaceous immigrants from other Gondwanan landmasses (i.e. Antarctica and South America) or neoendemic taxa that evolved from late Jurassic-earliest Cretaceous forms that were widespread across much of Gondwana and possibly other landmasses? In their recent review, Poropat et al. (2015) remarked on the problematic palaeobiogeographic interpretations of Australia's dinosaurs, which is symptomatic of its highly fragmentary fossil record. Those authors identified two opposing views: one which identifies a fauna of ceratosaurids, dromaeosaurids, neovenatorids, tyrannosauroids, and spinosaurids with Laurasian affinities and an alternative, less-specific interpretation that argues for Gondwanan ties in the Australian fauna. Besides the relatively well-documented affinities between Australian and South American



**Fig. 10.** Palaeogeographic ancestral area reconstruction of Tetanurae, from a Bayesian relaxed-clock analysis based on the dataset of Zanno and Makovicky (2013). (A) S-DIVA analysis and (B) BBM analysis. Colours and letters at nodes represent the geographic areas of origin (A, Asia; B, Europe; C, North America; D, Africa; E, South America; F, Australia) with relative likelihood of alternate hypotheses represented as a pie graph. Ambiguous geographic areas of origin are indicated by black nodes. (For interpretation of the references to colours in this figure legend, the reader is referred to the web version of this article.)

dinosaurs (Molnar and Salisbury, 2005; Smith et al., 2008; Agnolin et al., 2010; Benson et al., 2012; Novas et al., 2013; Poropat et al., 2015), affinities shared by Asian (*Fukuiraptor*) and Australian (the Lightning Ridge taxon, *Australovenator*) megaraptorans with other Asian theropods (e.g., *Chilantaisaurus* and several basal tyrannosauroids) play a pivotal role in this debate. Interestingly, similar Asian–South American affinities have been recently identified for the Australian titanosaur *Diamantinasaurus matildae* (Poropat et al., 2015). *Diamantinasaurus* was recovered as closely related to both a roughly coeval South American taxon (*Tapuiasaurus* from Brazil) but also to a latest Cretaceous Asian (*Opisthocoelicaudia* from Mongolia) taxon (Poropat et al., 2015).

In order to properly discuss the results presented in this study, it is essential to include data for two important clades, tyrannosauroids and carcharodontosauroids. The fossil record of basal tyrannosauroids predates the oldest known megaraptorans and supports a Middle–Late Jurassic radiation of tyrannosauroids prior to a Laurasian–Gondwana break-up (Holtz, 1994; Kellner, 1999; Hutt et al., 2001; Xu et al., 2004, 2006; Brusatte and Benson, 2013). The oldest record of carcharodontosauroids is from the Upper Jurassic of western Africa (Rauhut, 2011), which is consistent with the results of the time-calibrated Bayesian analyses proposed here that places the carcharodontosauroid divergence close to the Jurassic–Cretaceous boundary. Independent of the preferred placement of Megaraptora among Tetanurae, the fossil record of putative megaraptoran sister-taxa supports a Late Jurassic origin of the clade. Palaeobiogeographic implications of both the Novas et al. (2013) and

Zanno and Makovicky (2013) datasets presented here include the primary divergence of megaraptorans from other theropods in the latest Jurassic–earliest Cretaceous (Figs. 9, 10). Our analyses also concur in 1) placing the basal part of the megaraptoran evolution in Asia in the latest Jurassic–earliest Cretaceous; 2) supporting an active diffusion of megaraptorans from Laurasia to Gondwana in the earliest Early Cretaceous, and; 3) suggesting an Early Cretaceous radiation of megaraptorids across Gondwana. Furthermore, S-DIVA and BBM analyses of both the Novas et al. (2013) and Zanno and Makovicky (2013) datasets support Australia as the ancestral area of late Early Cretaceous evolution of Megaraptoridae (Figs. 9, 10). Moreover, this interpretation is consistent with the megaraptoran record from the upper Lower Cretaceous of Australia (Smith et al., 2008; Agnolin et al., 2010; Benson et al., 2012; this paper) even excluding the new taxon from the abovementioned analyses. Significantly, this interpretation challenges earlier claims that Australia played a primarily passive role in the evolution and dispersal of various dinosaur groups (Molnar, 1992a, 1997).

Pending further discoveries from continental Africa and Madagascar, data presented here, calibrated with well-documented palaeogeographic reconstructions concur on a latest Jurassic-to-earliest Cretaceous cosmopolitanism of several theropod groups, including megaraptorans. On the contrary, the Hauterivian–Barremian interval can be inferred as a chronological limit for biogeographical connections between southern landmasses and Europe/northern landmasses following widespread continental break-up and the appearance of vast epicontinental seas (Crame, 1999; Ezcurra and Agnolin, 2012; Fanti, 2012 and references

therein). The survival of theropod taxa in the Australian continent is here interpreted as early dispersal (i.e. Laurasia–Gondwana) followed by vicariance combined with local faunal turnover (see also Agnolin et al., 2010; Benson et al., 2010b, 2012; Novas et al., 2013). These interpretations are mirrored by an increasing number of formerly Gondwanan clades recently discovered in Laurasia, such as rebbachisaurid sauropods, ‘elaphrosaur’, and carcharodontosaurian theropods, which argue for similar latest Jurassic–earliest Cretaceous cosmopolitanism of these respective groups (Brusatte et al., 2009; Hocknull et al., 2009; Xu et al., 2009; Benson et al., 2010b; Barrett et al., 2011; Mannion et al., 2011; Torcida Fernández-Baldor et al., 2011). Furthermore, the apparent proliferation of megaraptorid taxa in the Late Cretaceous coincides with the final stages of the total fragmentation of Gondwana, in particular the separation of South America from Africa. Similar trends have also been observed in abelisaurid theropods and titanosaurid sauropods, which suggest that vicariance played an important role in the later evolution of these groups (Fanti, 2012). However, we note that the fossil record of basal megaraptorans is limited and that future discoveries from the Early Cretaceous of Australia may alter this view.

Contrary to earlier interpretations, Australia was not an evolutionary cul-de-sac for unidirectional dispersal events within Gondwana, nor was it simply a *refugium* for relict taxa (e.g. Rich and Rich, 1989; Rich and Vickers-Rich, 1994; Rich, 1996; Rich and Vickers-Rich, 2003; Rich et al., 2014). Instead, this specimen provides new evidence that Australia played an active role in the evolution and radiation of at least one group of apex theropods. Significantly, the Australian origin of megaraptorid theropods is echoed by eusuchian crocodylomorphs wherein *I. duncani* from the earliest latest Lower Cretaceous of Queensland suggests the origin of this clade also has an Australian root (Salisbury et al., 2006). Evidently, faunal interchange involved complex and multidirectional interplay between the Gondwanan landmasses and it is anticipated that future discoveries from the Cretaceous of Australia will contribute to the increasingly complex picture of dinosaur palaeobiogeography (Upchurch, 2008).

## 7. Conclusions

The new Lightning Ridge megaraptoran is the largest and only the second theropod described from Australia based on a partial skeleton. This new taxon supplements and confirms earlier reports based on isolated Australian material (Smith et al., 2008; Agnolin et al., 2010; Benson et al., 2012; White et al., 2013b) that definitively extends Megaraptoridae into the Albian. Cladogenetic timing inferred by the Bayesian analysis of the two relevant, most recent comprehensive datasets placed the megaraptoran divergence from other theropods close to the Jurassic–Cretaceous boundary (~140 Mya) and the origin of the lineage leading to Gondwanan megaraptorans (Megaraptoridae) at about 130 Mya, approximately 20 Ma prior to the appearance of the Lightning Ridge theropod. Although the phylogenetic position of Megaraptora remains equivocal, these results continue to challenge previous assertions that the Cretaceous of Australia consisted largely of relict fauna derived from elsewhere in Gondwana (e.g. Rich and Rich, 1989; Rich and Vickers-Rich, 1994; Rich, 1996; Rich and Vickers-Rich, 2003; Rich et al., 2014). Instead, these findings provide evidence of complex faunal interchange between Australia and the rest of Gondwana leading to the evolution of Megaraptoridae.

## Acknowledgments

LRF 100–106 was generously donated by Rob and Debbie Brogan and skillfully prepared by Matthew Goodwin. PRB gratefully acknowledges Jenni Brammall, Elizabeth and Robert Smith, Rebel Black and everyone at the Australian Opal Centre (Lightning Ridge) for their hospitality and diligence in preserving the fossils of Lightning Ridge. We thank Scott Hocknull for earlier insights, Roger Benson for the

helpful discussions of European Theropoda and providing photos of *Neovenator* and Matt White for the photo of *Australovenator* in Fig. 7. Detailed reviews from Steven Salisbury, Fernando Novas, and Associate Editor Ian Somerville greatly improved the final version and we thank them for their efforts. PRB was supported by start-up funding from the University of New England.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jgr.2015.08.004>.

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