Opalized archosaur remains from the Bulldog Shale (Aptian: Lower Cretaceous) of South Australia

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Terrestrial reptile remains are very rare in the Lower Cretaceous of South Australia, but include the holotype of the small theropod *Kakuru*. Here, we review this taxon and other archosaur specimens collected from the Bulldog Shale (Aptian) of Andamooka and Coober Pedy. *Kakuru* possesses no unique characters or character state combinations and is regarded as a *nomen dubium*, representing an indeterminate tetanuran theropod. Two other specimens (a left metatarsal and astragalus) can be referred to Dinosauria, but the identity of several other specimens (phalanges and a centrum) can only be resolved to the level of an indeterminate archosaur.

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THE opal fields of Coober Pedy and Andamooka in South Australia have yielded evidence of a diverse Early Cretaceous (Aptian) vertebrate biota, with chimaeroids, actinopterygians, lungfish, dinosaurs, ichthyosaurs and plesiosaurs (e.g. Molnar 1980, Kear 2006). Dinosaur fossils are extremely rare—only four bones from this region have been reported (Alley & Pledge 2000): the holotype tibia (SAM P17926) and referred phalanx (cast P18010: original in a private collection) of the small theropod *Kakuru kujani* Molnar & Pledge, 1980 from Andamooka (Molnar & Pledge 1980, Long 1998) and an incomplete theropod metatarsal (SAM P35321: Long 1998) and ornithopod phalanx (original NMV M23406, cast SAM P24084: Molnar 1980) from Coober Pedy. Two undescribed specimens from Andamooka, an astragalus (cast SAM P36601: original in a private collection, but currently on loan to the SAM) and caudal centrum (SAM P39683), are also held in the collections of the South Australian Museum. Here, we re-evaluate the validity of *Kakuru* and describe, figure and discuss the affinities of the purported dinosaur specimens from South Australia, so that they can be incorporated into broader regional and faunal studies.

Institutional abbreviations. CCG, Chengdu University of Technology, Chengdu, China; NHMUK, Natural History Museum, London; NMV, Museum Victoria, Melbourne, Australia; SAM, South Australian Museum, Adelaide, Australia.

Provenance

All specimens described herein were recovered from the opal fields of Andamooka

(SAM P17926, SAM P18010, SAM P36601, SAM P39683) or Coober Pedy (NMV M23406, SAM P35321), situated within the Eromanga Basin, northeastern South Australia (e.g. Krieg & Rogers 1995, Alexander *et al.* 2006; Fig. 1). Precise locality and stratigraphical details are unavailable for the specimens as they were recovered by opal miners or purchased from private collectors who did not provide such data. Further, some confusion exists regarding the primary source beds of the opaline material. Molnar (1980) listed three formations as the potential opal-bearing units: the Cadna-owie Formation, the Bulldog Shale and the Marree Formation. Subsequently, Molnar & Pledge (1980; see also Molnar 1991) specified that the type and referred specimens of *Kakuru* were obtained from the Marree Formation, a designation followed by most other workers (e.g. Long 1998, Holtz *et al.* 2004, Weishampel *et al.* 2004, Carrano 2008). Weishampel *et al.* (2004) listed an indeterminate ornithopod

(NMV M23406) from the Cadna-owie Formation, but this record is based on selective use of the information provided by Molnar (1980), who mentioned several possible source horizons for this specimen and did not attribute it to any particular unit.

Detailed lithostratigraphic evaluation has now firmly placed the Coober Pedy and Andamooka opaliferous beds within the Bulldog Shale (a constituent of the Marree Subgroup, which was formerly called the Marree Formation: see Krieg & Rogers 1995, Cotton *et al.* 2006); thus, all of the aforementioned archosaurian remains are regarded as pertaining to this unit herein (see Alley & Pledge 2000). Microfossils suggest an Aptian–lower Albian age for the Bulldog Shale (Krieg & Rogers 1995, Alexander *et al.* 2006); however, an Aptian age is usually proposed for the opal-bearing strata on the basis of molluscan remains (see Henderson *et al.* 2000, Alley *et al.* 2006).

Descriptions and comparisons

Many of the specimens described herein are currently mounted and on display in the South Australian Museum. Consequently, they can not easily be photographed. Images of the original specimens are, therefore, supplemented with photographs of high-definition casts in standard views (Figs 2, 3), and by detailed measurements (Table 1).

'Kakuru kujani'. The holotype of *Kakuru* was described in detail by Molnar & Pledge (1980), and most authors have regarded it as a valid taxon (e.g. Long 1998, Holtz *et al.* 2004; Figs 2A–E, 3). Initially, *Kakuru* was considered closely related to *Coelurus* (Molnar 1980, Molnar & Pledge 1980) but, subsequently, it has been compared with avimimids (Molnar 1991, Holtz *et al.* 2004) and abelisauroids (Rauhut 2005). Molnar & Pledge (1980) provided a brief diagnosis of *Kakuru*, based on the morphology of the astragalar facet, the presence of a medial
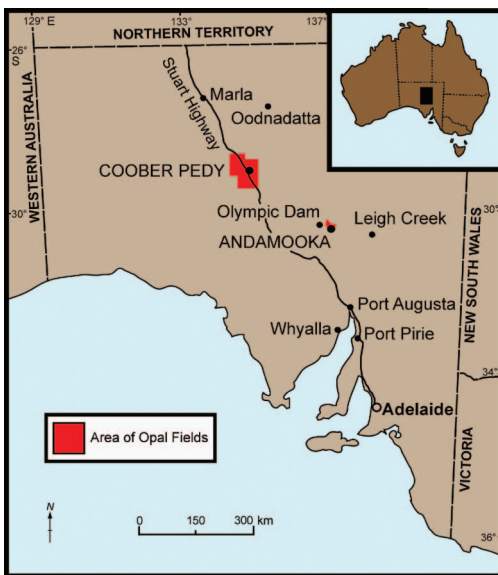

Fig. 1. Map of South Australia showing the opal fields around Coober Pedy and Andamooka (shaded) relative to capital cities (bold) and regional centres (from Robertson & Scott 1990).

Fig. 2. Opalized archosaur remains from the Bulldog Shale (Aptian) of Coober Pedy and Andamooka, South Australia. Original opalized tibia (SAM P17926) of the small theropod '*Kakuru kujani*' purchased by the South Australian Museum (SAM) in 2005; specimen in shown in (**A**) posterior, (**B**) medial, (**C**) anterior and (**D**) lateral views with distal end (**E**) as inset. Archosaurian pedal phalanx (NMV M23406) in (**F**) dorsal, (**G**) lateral and (**H**) ventral views. Archosaurian pedal phalanx (SAM P18010) in (**I**) dorsal and (**J**) lateral views. Proximal end of left metatarsal III (SAM P35321) from an indeterminate dinosaur; opalized original in (**K**) anteromedial perspective (as displayed) with (**L**) proximal articular, (**M**) anterior, (**N**) lateral and (**O**) posterior views of cast. Dinosaurian astragalus (SAM P36601); opalized original (on loan to SAM from private collection) in (**P**) proximal perspective (as displayed) with (**Q**) distal articular, (**R**) anterior, (**S**) posterior, (**T**) medial and (**U**) lateral views of cast. Archosaurian caudal vertebral centrum (SAM P39686) in (**V**) lateral and (**W**) dorsal views. Scale bars = 50 mm in **A–E**, 30 mm in **F–U**, 10 mm in **V**, **W**.
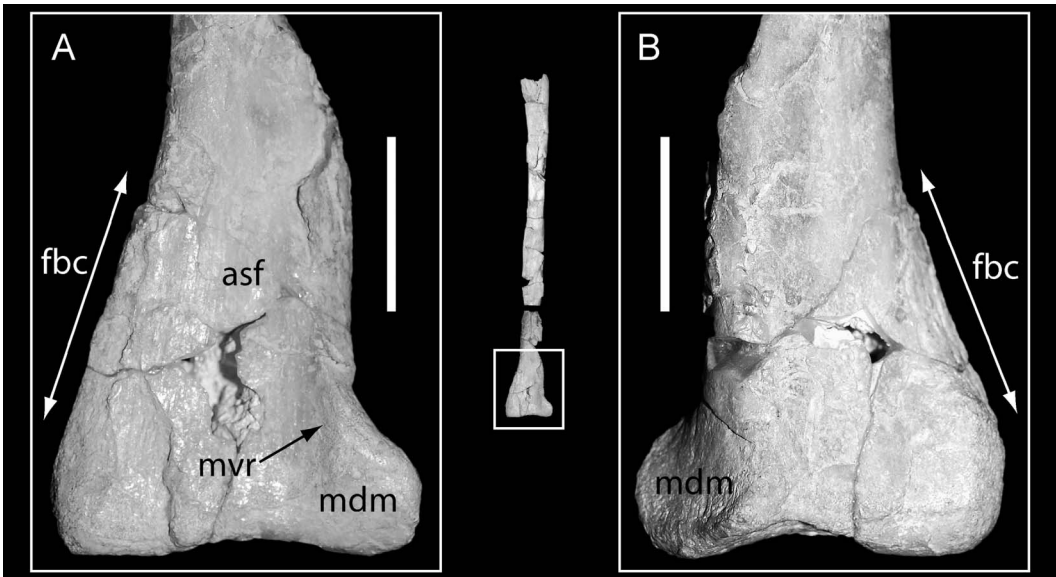
Fig. 3. Enlarged anterior (**A**) and posterior (**B**) views of the original opalized distal tibia (SAM P17926) assigned to the small theropod '*Kakuru kujani*'. Abbreviations: **asf**, astragalar facet; **fbc**, area of fibular contact; **mdm**, medial malleolus; **mvr**, medial vertical ridge. Scale bars = 20 mm.

Specimen	Length	MPH	MPW	MDH	MDW
NMV M23406 (phalanx)	61.0	30.5	38.3	20.5	27.5
SAM P18010 (phalanx)	43.0	16.7	23.0	13.5	17.4
SAM P39683 (caudal centrum)	11.95	7.14	6.4	–	–
SAM P36601 (astragalus)	**Length** (medial) 28.9	**Length** (lateral) 24.8	**Maximum width** 37.7		
SAM P35321 (metatarsal)	**Length** (as preserved) 48.0	**MPL** (along medial margin) 33.0	**MPW** 23.2		

Table 1. Measurements (in mm) of opalized archosaur specimens from South Australia. Abbreviations: MDH = maximum distal height; MDW = maximum distal width; MPH = maximum proximal height; MPL = maximum proximal length; MPW = maximum proximal width.

vertical ridge bounding the facet distally, and a prominent medial malleolus (Fig. 3). However, we do not regard these features as diagnostic and propose that *Kakuru kujani* is a *nomen dubium* for the following reasons. First, it is difficult to trace the extent of the astragalar facet in '*Kakuru*', which is marked only by weak longitudinal striae (Figs 2C, 3A). The anterior surface of the distal tibia is crushed, obscuring details of its geometry, and given its weak expression, the 'facet' may have become more or less

pronounced or extensive during ontogeny. Second, a vertical ridge bounding the astragalar facet medially is also present in the basal tetanuran *Chuandongocoelurus* (CCG 20010), the spinosaurid *Suchomimus* (Rauhut 2003), most neovenatorid allosauroids (Benson *et al.* 2010), some abelisauroids (Rauhut 2005) and basal coelurosaurs such as *Coelurus* (e.g. Galton & Molnar 2005). This morphology seems to be present in taxa with a tall astragalar ascending process that does not extend to the medial surface of the distal tibia, and its convergent acquisition in many lineages (including megalosauroids, allosauroids and coelurosaurs) cautions against its use in taxon diagnosis. Finally, the prominent 'medial malleolus' is constructed primarily from the anteromedially curving medial vertical ridge discussed above and has been illustrated in several basal coelurosaurs and possible abelisauroids (Molnar & Pledge 1980, Rauhut 2005). Unlike all ceratosaurs, '*Kakuru*' lacks a prominent fibular facet. Although Carrano *et al.* (2002) stated that this was present in tetanurans, the fibular facet of tetanurans forms a flat, smooth strip, whereas in all ceratosaurs it forms a flat-topped, rugose ridge that extends distally from the fibular crest (e.g. Madsen & Welles 2000, Carrano *et al.* 2002). Consequently, it is unlikely that '*Kakuru*' represents an abelisauroid (*contra* Rauhut 2005, *contra* Carrano & Sampson 2008). It should instead be regarded as an indeterminate small tetanuran theropod, as it does not uniquely share synapomorphies with any particular theropod clade.

NMV M23406. Molnar (1980) referred this robust ?right pedal phalanx (Fig. 2F–H) to an indeterminate ornithopod, although no justification was provided for the identification. In lateral view (Fig. 2G), the phalanx is dorsoventrally deepest proximally and tapers distally before expanding again slightly to form the distal articular surface. The dorsal and ventral margins are concave, but the latter is more strongly arched. A pronounced rugosity is present on the ventral surface of the phalanx, close to the proximal articular surface and is visible in both lateral and ventral views (Fig. 2G–H). Deep elliptical collateral ligament fossae penetrate both the lateral and medial surfaces of the distal articular expansion. In dorsal view (Fig. 2F), the phalanx has a slender hourglass shape with concave lateral and medial margins: the proximal articular surface is *ca* 1.6 times wider than the distal surface. The ?medial ginglymus of the distal articular surface is slightly longer than the lateral ginglymus, giving the articular region subtle asymmetry. A very shallow pit lies on the midline dorsal to the collateral ligament pits. The distal articular surface is mediolaterally concave and dorsoventrally convex, imparting a saddle-shaped morphology. In ventral view, a small rugosity is present close to the midline, just proximal to the ginglymi. The distal articular surface has a sub-trapeziform outline in distal end view. In contrast, the proximal articular surface is 'D'-shaped, with a straight ventral margin and convex lateral, medial and dorsal margins. The proximal articular surface is surrounded on all sides by a low rim of bone and bears a low, dorsoventrally oriented central eminence. This structure subdivides the proximal articular surface into medial and lateral concavities of roughly equal size.

Although the phalanx is akin to those of some ornithopods (e.g. *Camptosaurus* and *Dryosaurus*: Galton 1981, Carpenter & Wilson 2008), it also has similar features and proportions to phalanges of theropods (e.g. ornithomimids: NHMUK R12609, R12633) and crocodilians (e.g. *Caiman* sp., *Crocodylus* sp.: NHMUK un-numbered Comparative Collection specimens). Consequently, we remove this specimen from Ornithopoda and refer it to Archosauria indet.

SAM P18010. Molnar & Pledge (1980) described this ?first pedal phalanx (Fig. 2I–J), referring it to *Kakuru* 'for convenience' (*ibid*., p. 283). However, no locality data are available to support the association of these specimens. Moreover, as the phalanx cannot be compared directly with the holotype tibia, there is no basis for this assignment. SAM P18010 possesses no features that support referral to Theropoda to the exclusion of other taxa. Indeed, pedal phalanges with similar proportions and deep collateral ligament pits are also found in some crocodilians (e.g. *Caiman* sp., *Crocodylus* sp.: NHMUK un-numbered Comparative Collection specimens) and ornithopod dinosaurs (e.g. *Dryosaurus*: Galton 1981). Further, SAM P18010 possesses no synapomorphies that would permit referral to any particular dinosaur clade (such as the specialized pedal phalanx II-2 present in dromaeosaurids and troodontids: Makovicky & Norell 2004, Norell & Makovicky 2004). Consequently, we regard it as belonging to an indeterminate archosaur.

SAM P35321. Long (1998) mentioned a broken metatarsal from Coober Pedy that he regarded as the distal end of a metatarsal IV from an indeterminate theropod. However, this element actually represents the proximal end of a left metatarsal III. In proximal end view (Fig. 2L), the articular surface has a sub-trapeziform to weakly hourglass shape: the anterior margin is gently concave; the medial and lateral margins are more strongly concave (reflecting the presence of articular surfaces for the proximal ends of metatarsals II and IV, respectively); and the posterior margin is slightly convex. As the articular surface for metatarsal II is longer anteroposteriorly than that for metatarsal IV, the articular surface is asymmetrical in proximal view. The articular surface is flat to gently concave, becoming convex around the margins of the bone (Fig. 2K).

In anterior and posterior views, the articular surface continues ventrally, extending onto the proximal part of the shaft, but separated from the main shaft by a distinct break in slope. This feature is particularly well developed in posterior view (Fig. 2O). The ventral extension of the articular surface, both anteriorly and posteriorly, helps to define shallow fossae on the lateral and medial surfaces of the shaft that would have received metatarsals IV and II, respectively (Fig. 2N). The proximal part of the shaft is slightly narrower than the articular surface, and this width is maintained over the entire shaft length (as preserved). However, in medial or lateral view (Fig. 2K, N), the articular surface is anteroposteriorly expanded with respect to the shaft, by roughly equal distances in both directions. Ventral to the proximal expansion, the shaft has a sub-rectangular cross-section. A shallow furrow, just below the articular surface, extends around the lateral and posterior surfaces of the shaft. However, this feature is a preparation artefact.

SAM P35321 differs from the metatarsals of crocodilians, whose proximal articular surfaces are rotated with respect to the long axis of the shaft (e.g. *Caiman* sp., *Crocodylus* sp.: NHMUK un-numbered Comparative Collection specimens). Although SAM P35321 is similar to the metatarsals of some basal tetanurans (e.g. *Eustreptospondylus*: Sadleir *et al*. 2008), it also strongly resembles those of ornithopods, including *Dryosaurus* (Galton 1981) and *Camptosaurus* (Carpenter & Wilson 2008). Moreover, SAM P35321 is transversely broad relative to the metatarsals of most theropods (e.g. Madsen 1976, Colbert 1989), and although its margins are slightly concave, it lacks the strongly constricted, well-developed hourglass-shaped proximal outline that is characteristic of neotetanurans (Gauthier 1986). The fragmentary nature of the specimen precludes a precise assignment and we regard it as Dinosauria indet.

SAM P36601. This previously undescribed left astragalus from Andamooka (Fig. 2P–U) has a saddle-shaped ventral articular surface that is widest medially and tapers laterally (Fig. 2Q). In dorsal view (Fig. 2P), the body of the bone is excavated by a deep groove for the reception of the distal end of the tibia. The lateral surface is identified by a shallow, lacriform fossa for the articulation of the calcaneum (Fig. 2U). The anterodorsolateral margin of the astragalus is thickened and robust, suggesting the presence of an ascending process (not preserved). There is no trace of an anterolateral process (probably due to poor preservation). A small sub-triangular fibula facet occurs at the laterodorsal corner of the element, immediately dorsal to the calcaneal facet. The dorsomedial corner of the astragalus bears the remnants of a posterior process, although this structure is broken dorsally. The medial surface has a crescentic outline (Fig. 2T).

The lack of well-developed peg-and-socket joints between the astragalus and calcaneum excludes this specimen from Crurotarsi: the probable presence of both a robust ascending process and a groove for reception of the distal tibia indicates referral to Dinosauria (e.g. Langer & Benton 2006). Unfortunately, poor preservation does not permit any further identification.

SAM P39683. This small caudal vertebral centrum lacks fusion with the neural arch (not preserved). Its articular surfaces are amphiplatyan to mildly amphicoelous, of approximately equal size and sub-circular in outline (Fig. 2V–W). In lateral view, the centrum is an elongate cylinder (*ca* 1.67 times longer than the anterior articular surface is wide). Its lateral margins lack ridges and are gently concave anteroposteriorly and dorsolaterally. There is no evidence of transverse processes or any pneumatic features. A small chevron facet is present ventral to the posterior articular surface. The dorsal surface bears a midline groove marking the base of the neural canal: this is flanked by two raised rugose articular contacts for the (missing) neural arch. The presence of a small chevron facet in combination with the lack of transverse processes and the elongation of the centrum suggests that this is a late middle or early distal caudal vertebra.

Numerous dinosaur taxa have caudal centra with similar features and proportions, including basal ornithischians (e.g. *Hypsilophodon*, NHMUK R5830: Galton 1974), small theropods (e.g. *Compsognathus*: Ostrom 1978) and basal sauropodomorphs (e.g. *Thecodontosaurus*: Benton *et al.* 2000). Similar features also occur in some crocodilians (NHMUK un-numbered Comparative Collection specimens). As a result, this specimen is regarded as an indeterminate archosaur.

Discussion

Terrestrial reptile remains are extremely rare in South Australian Cretaceous strata (Molnar 1980, 1991), so documentation of new specimens significantly enhances our knowledge of Mesozoic faunas from this region. Unfortunately, most of the material is fragmentary and undiagnostic, including the holotype of '*Kakuru*', which should be regarded as a *nomen dubium*. It is plausible that some of the abovementioned specimens may ultimately prove to be referable to a single taxon (as posited elsewhere: Molnar & Pledge 1980), but it is also possible that these specimens might represent a diverse range of archosaur clades (e.g. ornithopods, crocodylians) that are otherwise unknown from these sites. More diagnostic material is needed to assess the true diversity of the Coober Pedy and Andamooka opalized faunas. The slow rate of recovery of terrestrial fossils reflects the marine depositional environments of the Bulldog Shale. These South Australian opal-bearing localities might never be as rich in terrestrial

vertebrate remains as the more famous Lower Cretaceous (middle Albian) non-marine deposits of Lightning Ridge, New South Wales (Smith & Smith 1999), but they clearly have the potential to add interesting new information (Molnar & Pledge 1980) with the discovery of further informative fossils.

Acknowledgements

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