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SHORT COMMUNICATION

A "BASAL" TETANURAN FROM THE LOWER CRETACEOUS KIRKWOOD FORMATION OF SOUTH AFRICA

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The Kirkwood Formation is the middle unit of the Uitenhage Group, a sequence of terrestrial and marine rocks that crops out in the Algoa Basin, Eastern Cape Province, South Africa. The Kirkwood Formation is divided into three members: the Swartkops Member, the Colchester Shale Member, and an unnamed, fossiliferous upper member consisting primarily of fluvial sandstones, red-brown and gray-green mudstones, and paleosols (McLachlan and McMillan, 1976; Shone, 1978). Recent dating of the Kirkwood Formation has placed it in the Berriasian-Valanginian ages near the onset of the Cretaceous (McMillan, 2003).

There is a long history of vertebrate fossil collection from the Kirkwood Formation, beginning in 1845 with the discovery of a number of fragmentary bones including a partial skull with teeth now identified as the stegosaur *Paranthodon africanus* (Atherstone, 1857; Galton and Coombs, 1981). Despite more than 150 years of collecting, nearly all vertebrate fossils recovered from the Kirkwood Formation are extremely fragmentary, most commonly consisting of isolated teeth and bones. Nevertheless, a diverse fauna is known.

At least two taxa of sphenodontians have been described from fragmentary jaws (Rich at al., 1983; Ross et al., 1999). In addition, a partial braincase of an unidentified squamate has been recovered (Ross et al., 1999). Other fragmentary remains of lower vertebrates document the presence of lepisosteid and teleost fishes, crocodilians, turtles, and frogs (Rich et al., 1983; de Klerk et al., 1998). In addition to *Paranthodon*, the dinosaur fauna consists of an iguanodontian ornithopod and at least two taxa of sauropods, including the possible camarasaurid *Algoasaurus bauri* (Rich et al., 1983; de Klerk et al., 1998). More recently, de Klerk et al. (2000) discovered and described the first nearly complete and articulated vertebrate remains from the Kirkwood Formation, the small theropod *Nqwebasaurus thwazi* (de Klerk et al., 2000). De Klerk and colleagues suggested *Nqwebasaurus* was a coelurosaurian theropod; this phylogenetic placement has been supported by subsequent authors (e.g., Sereno, 2001; Holtz et al., 2004). *Nqwebasaurus* is the oldest record of a coelurosaurian in Gondwana, and confirms the presence of this derived tetanuran clade on the southern landmass prior to its fragmentation. Isolated teeth from a small theropod, reported by Rich et al. (1983), do not pertain to *Nqwebasaurus*.

In their description of *Nqwebasaurus*, de Klerk et al. (2000) made reference to a second theropod taxon, represented by a proximal femur, from the Kirkwood Formation. This specimen (AM 6041) is described here, and comparisons are made with other theropod taxa to place it in a phylogenetic context. Because of the specimen's incompleteness, we decline to name a new taxon.

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AM 6041 was discovered in 1995 by a group that included CAF, WJD, and CFR at the "Kirkwood Cliffs" (Site 6 of McLachlan and McMillan, 1976, and Rich et al., 1983), the stratotype locality of the Kirkwood Formation, located south of the town of Kirkwood along the Sundays River (Fig. 1). The specimen was recovered from a conglomeratic lens at the base of a thick, yellow, medium-grained sandstone found along the bottom of the cliffs. Neither the upper nor the lower contacts of the Kirkwood Formation are present at the Kirkwood Cliffs site, which exposes nearly 60 m of sediments.

Institutional Abbreviations—**AM**, Albany Museum, Grahamstown, South Africa; **FMNH**, Field Museum of Natural History, Chicago, IL, USA; **QG**, originally catalogued at the Queen Victoria Museum, Dept. of Paleontology, Harare (formerly Salisbury), now curated at the National Museum of Natural History, Bulawayo, Zimbabwe; **UA**, Université d'Antananarivo, Antananarivo, Madagascar.

DESCRIPTION

AM 6041 is an isolated, proximal left femur broken off below the trochanteric shelf and preserving only the dorsal base of the fourth trochanter (Fig. 2). Although missing its distal end and most of the shaft, the remaining portion is complete and well preserved. The size of AM 6041 indicates that, if adult, the femur belonged to a fairly small animal equivalent in stature to the Malagasy noasaurid *Masiakasaurus* (e.g., FMNH PR 2117, UA 8684).

Cortical thickness along the broken margin of AM 6041 varies from 3.1 mm on the lateral surface to 4.8 mm on the anteromedial surface (Fig. 2F). Despite its incompleteness, the preserved portion can be oriented in life position based on a number of morphological features (e.g., position of the fourth trochanter, orientation of the lesser trochanter, etc.) and side-by-side comparison with specimens of *Masiakasaurus*. The femoral head is directed within 20 or 30 degrees of medial, as in most tetanurans (Holtz et al., 2004; Fig. 2E). The proximal end of the femur is compressed (anterolaterally-posteromedially) and notably elongate (posterolaterally-anteromedially), with a maximum length: width ratio of 2.4 (see the Table for measurements). An articular surface, the facies articularis antitrochanterica (Baumel and Witmer, 1993), occupies most of the dorsal surface of the proximal femur. The surface is broadest at its midpoint, constricting significantly towards the greater trochanter, but only slightly towards the femoral head. The facies articularis antitrochanterica itself, as in other theropods (e.g., *Masiakasaurus*, FMNH PR 2108; *Sinraptor*; Currie and Zhao, 1993), is bisected by a very shallow and broad concavity that runs anteroposteriorly across the surface (Fig. 2A, E). The cross-cutting orientation of this concavity with the anteromedially directed femoral head imparts a screw-shaped morphology to the articular surface.

A well-defined, non-articular sulcus runs dorsomedially along the posterior surface of the femoral head (posterior sulcus of Carrano et al., 2002; Fig. 2C). The posteromedial femoral head

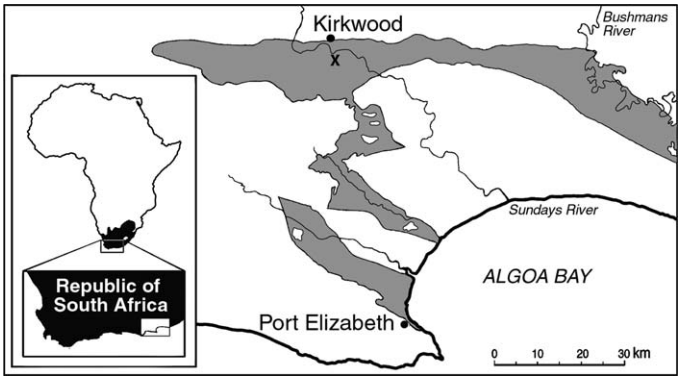

FIGURE 1. Map detailing "Kirkwood Cliffs" site (marked with an 'X'), the stratotype locality of the Kirkwood Formation, where AM 6041 was discovered. The shaded area defines the surface and subsurface extent of the Lower Cretaceous (Berriasian-Valanginian) Kirkwood Formation, the middle member of the Uitenhage Group, within the Algoa Basin, Eastern Cape Province, South Africa.

hooks backward in a distinct process that forms the deep medial margin of this sulcus, as in other theropods. In anterolateral view, the dorsal margin of the femur is very slightly concave, with the femoral head at the same level as the greater trochanter (Fig. 2D). This contrasts with the short, convex dorsal margin and downturned femoral head seen in non-tetanuran theropods (e.g., *Staurikosaurus,* Galton, 1977; *Syntarsus*, QG/1; *Carnotaurus*, Bonaparte et al., 1990; *Masiakasaurus*, FMNH PR 2108). A horizontal dorsal margin has been hypothesized to be a tetanuran synapomorphy (Carrano et al., 2002), and it occurs in basal (non-avetheropod) tetanurans such as *Szechuanosaurus* (Peng et al., 2005), *Sinraptor* (Currie and Zhao, 1993), and *Baryonyx* (Charig and Milner, 1997).

The surface of part of the greater trochanter is damaged. Nevertheless, the lateral margin of the greater trochanter forms nearly a 90-degree angle with the facies articularis antitrochanterica, resulting in a square shoulder on the proximal femur (Fig. 2C, D). The greater trochanter is narrow and melds distally with the femoral shaft. A distinct notch clearly separates the greater and lesser trochanters (Fig. 2C). Together, the lesser trochanter and accessory trochanter (72% and 28%, respectively) form a large, mediolaterally compressed aliform process whose anteroposterior width nearly equals the shaft diameter (Fig. 2D). A large, aliform or blade-like lesser and accessory trochanter occurs in tetanurans and in abelisauroids (Carrano et al., 2002; Allain et al., 2007). Nonetheless, the lesser trochanter is proportionately much thinner than seen in *Masiakasaurus* (e.g., UA 8685). The crest of the lesser trochanter rises above the level of the ventral femoral head in AM 6041, nearly to the midpoint, as in most tetanurans and unlike the condition in abelisauroids (Fig. 2A). The crest terminates well below that of the greater trochanter, as in most non-maniraptoran theropods. The crest is oriented anteroposteriorly and at a 45 degree angle to the femoral head in dorsal view (Fig. 2E). The accessory trochanter is shorter than the lesser trochanter, and a slight notch and sulcus separate the two in lateral view (Fig. 2D).

A small, very slightly raised prominence that likely represents the trochanteric shelf (Hutchinson, 2001) occurs on the posterolateral surface of the proximal femoral shaft, approximately 2.5 cm below the crest of the lesser trochanter (Fig. 2D). A reduced trochanteric shelf has been suggested to characterize non-maniraptoran tetanurans (Hutchinson, 2001; Holtz et al., 2004). However, a reduced or mound-like trochanteric shelf is also seen in some abelisauroids, including *Masiakasaurus* (e.g., UA 8685) and *Berberosaurus* (Allain et al., 2007), although the shelf in these taxa is not reduced to the level seen in AM 6041. A short segment of a compressed ridge, representing the proximal base of the fourth trochanter, arises from the posteromedial femoral shaft (Fig. 2B). The shaft is broken immediately below this short segment, and is sub-cylindrical at this point.

DISCUSSION

Although only consisting of the proximal end of a femur, AM 6041 preserves a number of significant morphological features that help place it within a phylogenetic context. De Klerk at al. (2000) reported the presence of a fragmentary proximal femur

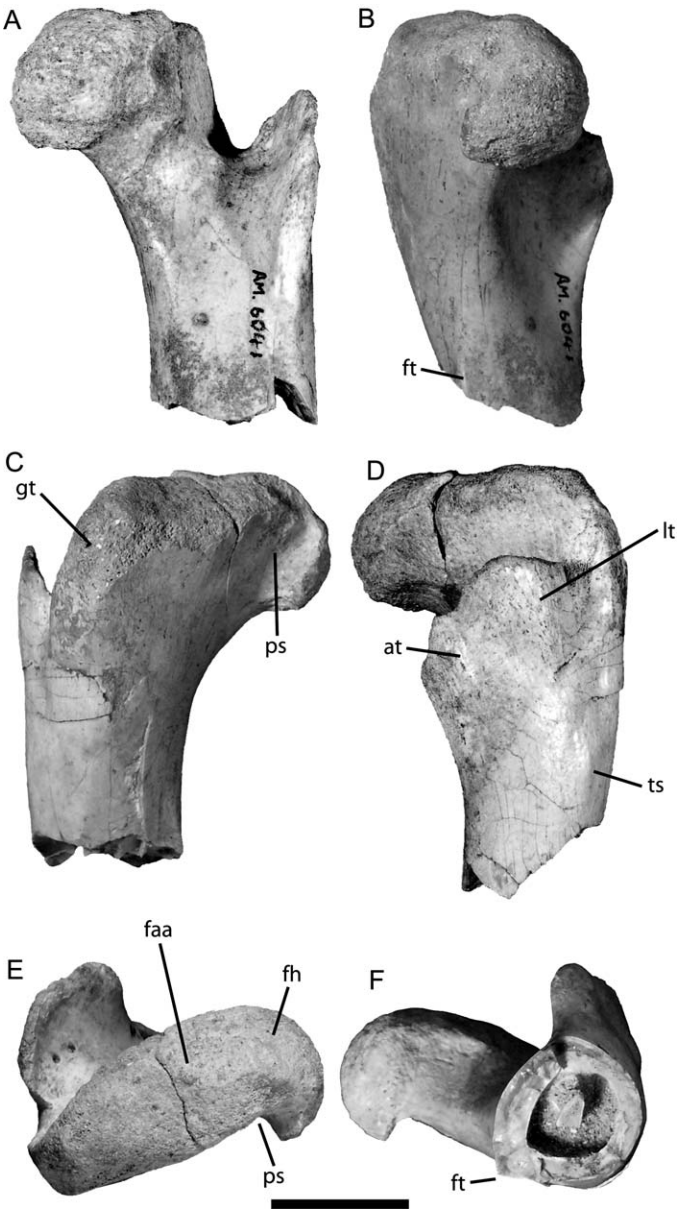

FIGURE 2. Proximal femur of AM 6041 in multiple views. **A**, anterior; **B**, medial; **C**, posterior; **D**, lateral; **E**, proximal; **F**, distal. For proximal and distal views, the anterior direction is towards the top of the figure. **Abbreviations**: **at**, accessory trochanter; **faa**, facies articularis antitrochanterica; **fh**, femoral head; **ft**, fourth trochanter; **gt**, greater trochanter; **lt**, lesser trochanter; **ps**, posterior sulcus; **ts**, trochanteric shelf. The scale bar equals 2 cm.

TABLE. Measurements of proximal left femur (AM 6041) in mm.

Parameter	Measurement
Maximum length (as preserved)	62.5
Maximum length proximal end (including head)	41.5
Maximum width proximal end (excluding head)	17.6
Maximum width femoral head	22.7
Maximum depth femoral head	19.5
Width across greater trochanter	9.8
Width across proximal femur including lesser trochanter	36.0
Height lesser trochanter (above notch)	4.25
Height greater trochanter (above notch)	17.8
Width lesser + accessory trochanters	23.6
Anteroposterior diameter of shaft (at break)	24
Mediolateral diameter of shaft (at break)	20

from the sympatric *Nqwebasaurus*; we have recently determined this proximal femur is too small to be part of the holotype specimen, and its taxonomic identity is unknown. However, *Nqwebasaurus* is firmly lodged within Coelurosauria based on numerous skull and postcranial characters; AM 6041 lacks derived features that would be expected if it pertained to a coelurosaur (e.g., a reduced lesser trochanter). The presence of small theropod teeth, which differ significantly from those of *Nqwebasaurus,* confirm the presence of a second Kirkwood theropod (e.g., Rich et al., 1983). As suggested by de Klerk et al. (2000), we are confident that AM 6041 represents a second small theropod taxon within the Kirkwood fauna.

AM 6041 exhibits two unambiguous features that suggest it is a tetanuran and not an abelisauroid. These include a femoral head lacking any downturn and a lesser trochanter that projects above the most distal point on the femoral head (Hutchinson, 2001; Carrano et al., 2002; Holtz et al., 2004). These synapomorphies, along with the elongate nature of the proximal femur, also suggest that AM 6041 is neither a neoceratosaur nor a coelophysid. As described above, the enlarged lesser trochanter excludes identification as a coelurosaur. Additionally, AM 6041 shows a nearly (but not completely) medially directed femoral head, suggesting (but not completely conclusively) it is a non-avetheropod tetanuran (Rauhut, 2003; Holtz et al., 2004). Again, this latter character contrasts with the condition seen in abelisauroids.

Non-avetheropod tetanurans are known from Gondwana and include forms from South America (*Condorraptor* [Middle Jurassic], *Piatnitzkysaurus* [early Late Jurassic], *Irritator* and *Angaturama* [late Early Cretaceous]), and northern Africa (*Afrovenator* [Early Cretaceous], *Suchomimus* and *Cristatusaurus* [late Early Cretaceous], and *Spinosaurus* [early Late Cretaceous]). The presence of a probable basal tetanuran in the Kirkwood Formation is not surprising, but nevertheless provides a record of this clade in southernmost Africa at the onset of the Cretaceous.

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