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High diversity in the sauropod dinosaur fauna of the Lower Cretaceous Kirkwood Formation of South Africa: Implications for the Jurassic–Cretaceous transition

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ABSTRACT

The Kirkwood Formation of South Africa has long been recognized as having the potential to fill an important gap in the Mesozoic terrestrial fossil record. As one of the few fossil-bearing deposits from the lowermost Cretaceous, the Kirkwood Formation provides critical information on terrestrial ecosystems at the local, subcontinental (southern Gondwana), and global scale during this poorly sampled time interval. However, until recently, the dinosaurian fauna of the Kirkwood Formation, especially that pertaining to Sauropoda, has remained essentially unknown. Here we present comprehensive descriptions of several relatively well-preserved sauropod vertebrae collected from exposures throughout the formation. We identify at least four taxonomically distinct groups of sauropod, comprising representatives of Diplodocidae, Dicraeosauridae, Brachiosauridae, and a eusauropod that belongs to neither Diplodocoidea nor Titanosauriformes. This represents the first unequivocal evidence of these groups having survived into the earliest Cretaceous of Africa. The taxonomic composition of the Kirkwood Formation shows strong similarities to Upper Jurassic deposits, and raises questions regarding the taxonomic decline across the Jurassic/Cretaceous boundary that has been previously inferred for Sauropoda. Investigation of the sauropod fossil record of the first three geological stages of the Cretaceous suggests that reconstruction of sauropod macroevolutionary patterns is complicated by a combination of sampling bias, an uneven and poorly dated rock record, and spatiotemporal disparity in the global disappearance of certain sauropod groups. Nonetheless, the close ecological relationship consistently observed between Brachiosauridae and Diplodocidae, as well as their approximately synchronous decline, suggests some equivalence in response to the changing faunal dynamics of the Early Cretaceous.

1. Introduction

The Jurassic/Cretaceous (J/K) boundary (145 Ma) represents an important transitional period in the evolution of sauropod dinosaurs. Following a period of apparent peak diversity and species-abundance in the latest Jurassic (as exemplified by the sauropod-rich deposits of East Africa and North America), the earliest Cretaceous is conspicuously under-represented in terms of well-understood sauropod taxa (e.g., Upchurch and Barrett, 2005; Barrett et al., 2009). Although this decline has generally been interpreted as the result of genuine biotically-mediated processes (e.g., Mannion et al., 2011), it is also a period characterized by a dearth of sauropod-bearing localities and a general lack of focused sampling across the southern continents (Upchurch et al., 2015).

In terms of dinosaur-bearing units, South Africa is best known for the Upper Triassic–Lower Jurassic Elliot Formation and its assortment of basal sauropodomorphs and ornithischians (e.g., Yates, 2003, 2007; Butler, 2005; Yates et al., 2010; McPhee et al., 2014, 2015). Although geographically more restricted and with appreciably less accessible rock-outcrop, the Lower Cretaceous Kirkwood Formation of the Eastern Cape has also produced a

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number of isolated dinosaurian remains over the past century and a half, the majority resulting from collection efforts over the past twenty years by WJdK and colleagues. Amongst this material is a number of relatively well-preserved sauropod vertebrae collected from exposures throughout the formation. These remains provide valuable insight into the sauropodan faunal composition of the southern regions of Gondwana in the very earliest Cretaceous—a fauna that up until now has remained largely unknown.

Here we provide a short summation of the geology and hypothesized temporal range of the Kirkwood Formation. This is followed by a brief review of the previous palaeontological work conducted within the formation, with special focus on the—rather scant—sauropod literature. We then present full morphological descriptions of the new sauropod material that has come to light in recent years. Based on these anatomical considerations we attempt to assign as accurate a taxonomic position to this material as is possible. This latter goal is of particular pertinence to questions relating to the biogeography and dispersal/extinction patterns of Sauropoda across the J/K boundary.

1.1. Geological and palaeontological context of the Kirkwood Formation

The Kirkwood Formation is one of the three major constituent formations that make up the Uitenhage Group, a middle–upper Mesozoic sedimentary mass that weaves its way intermittently throughout the small, fault-controlled basins that extend for approximately 500 km along the coastal areas of the Eastern Cape and Western Cape provinces, South Africa (Reddering, 2010). Uitenhage Group exposures are best represented within the Algoa Basin, which of all the Uitenhage basins preserves the most diverse and vertically extensive range of sediments (see Muir et al., 2015 for a recent review) (Fig. 1). The coarse conglomerates of the Enon Formation represent the lower/proximal-most deposits within the Uitenhage Group. The interbedded sandstones and mudstones of the Kirkwood Formation appear to conformably overlie the Enon Formation (McLachlan and McMillan, 1976; Reddering, 2010), although Shone (1978, 2006) has cautioned that the palaeo-flow directions between the two formations are demonstratively different, and thus a regional unconformity cannot be ruled out. The siltstones, sandstones, and mudstones of the estuarine–marine Sundays River Formation either conformably overlie the Kirkwood Formation (Shone, 1978) or represent temporally equivalent facies of a marine transgressive event (Ross et al., 1999; McMillan, 2003), although these two scenarios are not mutually exclusive (Rogers and Schwarz, 1901; McLachlan and McMillan, 1976). In either scenario, there is no evidence of any unconformity or erosional break between the Sundays River Formation and the Kirkwood Formation (Shone, 1978, 2006; Reddering, 2010). Taken together, the general Uitenhage succession depicts a depositional scenario whereby a series of alluvial piedmont fans (the Enon Formation) provided the source sediment for the fluvial point-bars and overbank mud accumulations of the Kirkwood Formation, which in turn grade distally from estuarine into the more marine-based sediments of the Sundays River.

Two members have been recognized within the Kirkwood Formation (McLachlan and McMillan, 1976: figs 2, 3; Joubert and Johnson, 1998). The lowest, known as the Swartkops Member, is recognized as a sandstone unit directly overlying the Enon and generally only detectable in boreholes (Atherstone, 1857; Haughton, 1928; Winter, 1973; Reddering, 2010). Immediately above the Swartkops, the Colchester Member consists of marine

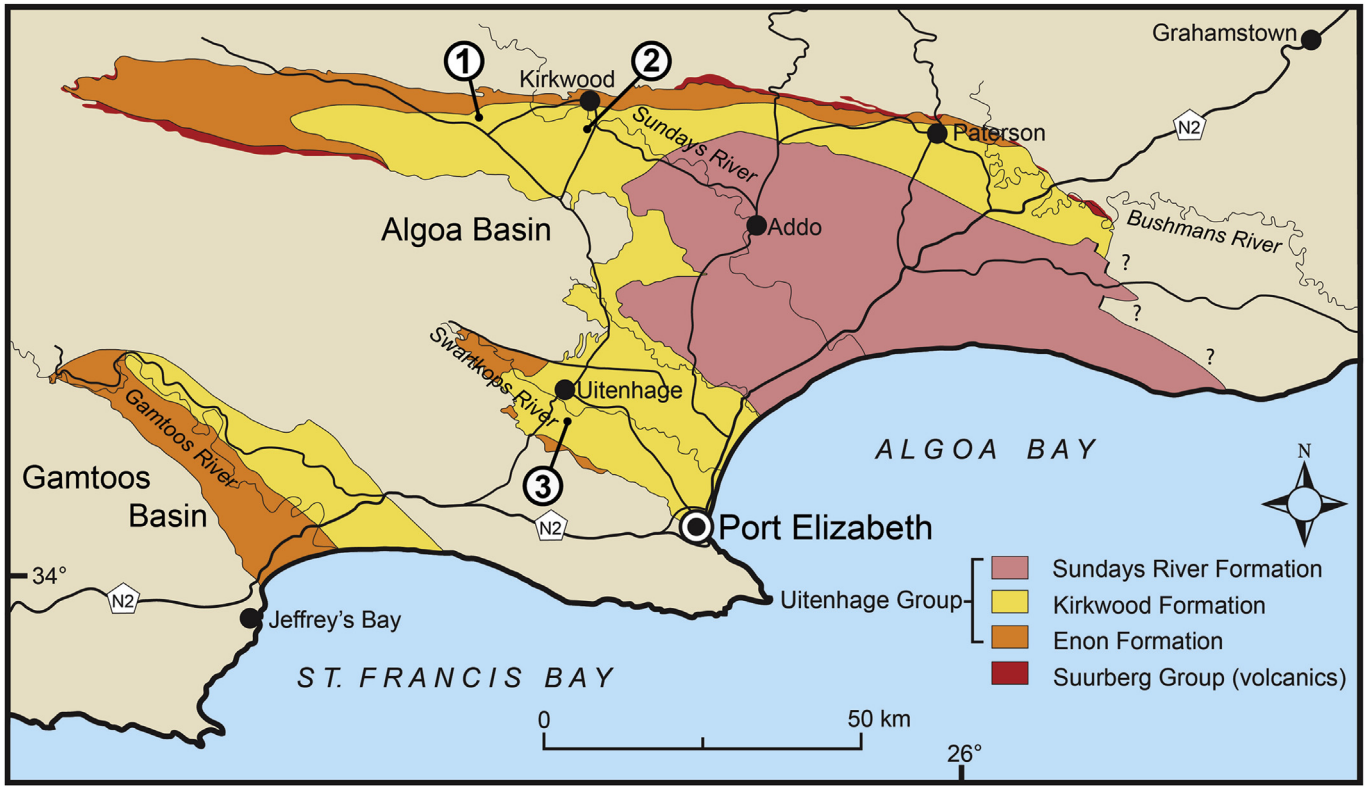

Fig. 1. Geology of the Uitenhage Group, Algoa Basin, Eastern Cape, South Africa. Numbers indicate localities of the specimens described herein. 1, Umlilo Game Park (AM 6125, AM 6128, AM 6130); 2, Kirkwood Cliffs (AM 6000, AM 6004); 3, KwaNobuhle Township (AM 4755).
Figure modified from Muir et al. (2015).