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 recognised 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 at 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 characterised 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 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 Schwartz, 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 clays with oil-storage potential (Reddering, 2010). No vertebrate fossils have been discovered in either of these lower members, but the Colchester Member does contain microfossils (Shone, 2006). The remaining, stratigraphically higher sediments of the Kirkwood Formation have not been formally named, but they contain all of the vertebrate fossil material so far discovered. Traditionally referred to as the 'wood beds', they generally consist of olive-grey to yellow-buff, medium-to-coarse-grained sandstones interbedded with variegated red, pink, grey and pale green mudstones and siltstones up to 30 m thick (McLachlan and McMillan, 1976; Muir et al., 2015). Strongly bioturbated palaeosols that appear to have undergone consistent subaerial exposure during deposition also characterize many of the Kirkwood exposures.

As the original name suggests, chunks of fossilized wood and silicified tree trunks are extremely common throughout the Kirkwood Formation. In addition to this, other plant material is known (e.g., ferns, bennettitaleans, cycads, conifers), as well as several species of freshwater bivalves, gastropods, and crustaceans (see McLachlan and McMillan [1976] for a

comprehensive review). Vertebrate fossils are represented primarily by fragmentary, often abraded fish, turtle, crocodyliform, lepidosaur and dinosaur remains (Rich et al. 1983; Ross et al., 1999; Forster et al. 2009), although recent years have witnessed the discovery of a modest-sized ornithopod nesting site and the nearly complete skeleton of perhaps the basal-most ornithomimosaur theropod currently known (*Nqwebasaurus thwazi*: de Klerk et al., 2000; Choiniere et al., 2012). The Kirkwood Formation has also produced one of the historically earliest stegosaur finds—*Paranthodon africanus* (Galton and Coombs, 1981).

Dating the Kirkwood Formation has proven problematic, especially given the absence of chronometric age determinations. However, the preponderance of the evidence points to an Early Cretaceous age. Based on biostratigraphic evidence from invertebrates and, more recently, Foraminifera, current consensus indicates that the Sundays River Formation is approximately Valanginian to Hauterivian in age (~139–131mya; McLachlan and McMillan, 1976; Ross et al., 1999; Gomez et al., 2002; McMillan, 2003; Shone, 2006; Walker et al., 2012). Whereas it is possible that the Swartkops and Colchester members of the Kirkwood Formation underlie the Sundays River Formation (Rogers and Schwartz, 1901; Rigassi, 1968; Stewart, 1973; McLachlan and McMillan, 1976), nearly all authors concur that the vertebrate fossil-bearing sediment of the Kirkwood Formation occupies a relatively high stratigraphic position, being laterally equivalent to the upper parts of the Sundays River Formation. It would appear therefore that the fossiliferous sections of the Kirkwood Formation most reasonably date tothe early Early Cretaceous.

1.2. *Previous work on Sauropoda in the Kirkwood Formation*

Broom (1904) was the first (and, thus far, only) worker to name a sauropod dinosaur from the Kirkwood Formation. '*Algoasaurus bauri*' was recovered from a clay quarry of the Port Elizabeth Brick and Tile Company at Despatch, southeast of Uitenhage, Eastern Cape Province. Reported as coming from "clayey rock" (Broom, 1904:445), a number of bones were unfortunately processed as bricks before Broom could salvage the incomplete vertebrae, scapula, femur and ?pedal ungual phalanx that comprise the material used to name this taxon. Although some workers have considered '*Algoasaurus*' to possess titanosaurian, diplodocoid (including rebbachisaurid), or camarasaurid affinities (Huene,

5

1932; Romer, 1956; Jacobs et al., 1996; Canudo and Salgado 2003), most recent accounts of this poorly known taxon have regarded it as a nomen dubium (McIntosh, 1990; Upchurch et al., 2004). Unfortunately, the material figured by Broom (1904) was lost at some point during the 20th century, precluding any additional refinement of its taxonomic relationships. However, the recent rediscovery of elements possibly pertaining to the original assemblage (SAM-PK-K1500, a caudal vertebra located within the collections of the Iziko Museum, Cape Town, and AMNH 5631, an ungual phalanx inexplicably housed at the American Natural History Museum, New York), confirms the position of '*Algoasaurus*' within Eusauropoda based on the laterally deflected pedal ungual (inferred from the bevelled proximal end, relative to the long axis of the element; see Wilson and Upchurch 2009: p. 228). However, neither the observable remains nor the figures in Broom (1904) reveal diagnostic features that might allow it to be assigned to a less inclusive grouping, and we therefore regard '*Algoasaurus*' as Eusauropoda indet. pending the relocation of the missing material and/or additional fossil discoveries.

Rich et al. (1983) reported on a number of sauropod teeth (SAM-PK-K-5229–5254, 6137, 6141) from a series of locations close to the town of Kirkwood that they tentatively referred to 'Camarasauridae', '*Astrodon*' sp., and '*Pleurocoelus*' sp., an assignment which is broadly accepted here insofar as all of the teeth figured in that study appear to be of non-titanosaurian titanosauriform origin (i.e., "brachiosaurid-type" *sensu* Barrett and Upchurch [2005]). However, without additional morphological data, taxonomic assignment of this material to anything lower than Titanosauriformes indet. remains difficult.

In addition to the above two studies, other putative sauropod material is known informally from finds by non-palaeontologists. For example, McLachlan and McMillan (1976:202) mentioned a display in the now non-operational Port Elizabeth Museum that featured an "enormous femur and humerus of a "*Brontosaurus*" found at the Kirkwood bridge outcrop... The femur end measures 0.6 m across the top. Quite an amount of bone has been found at this outcrop but it is now dispersed in private and institute collections around the country." This semi-formal approach to the palaeontological record of the Kirkwood was not uncommon—those with a geological interest have long been aware of the existence of 'gigantic reptiles' within the wood beds of the Algoa Basin, but this material was seldom

afforded more than a passing mention in a provincial magazine or geological report (e.g., Atherstone, 1857; Rogers and Schwarz, 1901; Haughton, 1928).

This study aims to expand on the work of Rich et al. (1983) in attempting to establish a more in-depth understanding of the diversity and composition of the sauropod fauna occupying southern Africa at the outset of the Cretaceous. This analysis will primarily draw on an assemblage of sauropod vertebral material that has been added to the collections of the Albany Museum, Grahamstown over the past two decades.

The nomenclature for vertebral laminae employed in this study is taken from Wilson (1999), along with the modifications suggested by Carballido and Sander (2012). We also use the nomenclature for vertebral fossae proposed by Wilson et al. (2011).

Institutional abbreviations: **AM**: Albany Museum, Grahamstown, South Africa; **AMNH**: American Museum of Natural History, NY, USA; **CM**: Carnegie Museum of Natural History, Pittsburgh, PA, USA; **SAM-K**, Iziko-South African Museum, Cape Town, South Africa; **SNGM**: Sernageomin, Santiago, Chile.

Anatomical abbreviations: acl: accessory lamina; **ACDL**: anterior centrodiapophyseal lamina; **afp**: aliform process; **aSPDL**: anterior spinodiapophyseal lamina; **CDF**: centrodiapophyseal fossa; **CPOL**: centropostzygapophyseal lamina; **CPRF**: centroprezygapophyseal fossa; **CPRL**: centroprezygapophyseal lamina; **dof**: dorsal fossa; **dp**: diapophysis; **laf**: lateral fossa; **mdCPRL**: medial division of the centroprezygapophyseal lamina; **mtp**: metapophysis; **nc**: neural canal; **ns**: neural spine; **PCDL**: posterior centrodiapophyseal lamina; **PCPL**: posterior centroparapophyseal lamina; **pnp**: pneumatic pitting; **POCDF**: postzygapophyseal centrodiapophyseal fossa; **PODL**: postzygodiapophyseal lamina; **POSL**: postspinal lamina; **poz**: postzygapophysis; **pp**: parapophysis; **PPDL**: paradiapophyseal lamina; **PRCDF**: prezygapophyseal centrodiapophyseal fossa **PRDL**: prezygodiapophyseal lamina; **PRSL**: prespinal lamina; **pse**: prespinal eminence; **prz**: prezygapophysis; **pSPDL**: posterior spinodiapophyseal lamina; **SPOL**: spinopostzygapophyseal lamina; **SPRL**: spinoprezygapophyseal lamina; **SPDL**: spinodiapophyseal lamina; **sTPOL**: single interpostzygapophyseal lamina; **sTPRL**: single interprezygapophyseal lamina; **TPOL**: interpostzygapophyseal lamina; **TPRL**: interprezygapophyseal lamina; **vex**: ventral excavation; **vk**: ventral keel

2. SYSTEMATIC PALAEONTOLOGY

2.1.   SAURISCHIA Seeley, 1887

SAUROPODOMORPHA von Huene, 1932

SAUROPODA Marsh, 1878

EUSAUROPODA Upchurch, 1995

Eusauropoda indet.

Material: AM 6125, an anterior dorsal vertebra (Fig. 2, Fig. 3).

Locality and Horizon: Kirkwood Formation (lowermost Cretaceous, ?Berriasian–Hauterivian) on Umlilo Game Farm, Eastern Cape, South Africa. Found within a medium to coarse-grained channel sandstone.

Description: The vertebra is missing the distal termini of the prezygapophyses, the postzygapophyses, the diapophyses, most of the neural spine, and the majority of the left side of the neural arch. It is probably either a D2 or D3, based on the position of the parapophysis on the anterodorsal corner of the lateral surface of the centrum.

Although the cortical surface of the anterior articular facet has been mostly eroded away, the facet nevertheless preserves its original hemispherical, anteriorly convex shape. Evidence for this lies in the presence of trabecular bone throughout the hemisphere, as is present on the internal surfaces of vertebrae generally. It is therefore probable that this vertebra was opisthoceolous, as in the anterior dorsal vertebrae of all eusauropods (Wilson and Sereno, 1998; Upchurch et al., 2004). The posterior articular facet has unfortunately been entirely eroded away, precluding assessment of the length-to-height ratios of the centrum. A deep lateral pneumatic fossa ('pleurocoel') is present on the posterior half of the lateral surface of the centrum. It is possible that the lateral fossa might have been more extensive, potentially expanding as a broader fossa towards the anterior edge of the centrum (based on the semi-depressed appearance of this part of the centrum), but this cannot be confirmed because of poor preservation. Although the posterior margin of the opening is partially obscured due to incomplete preservation (right side) and crushing (left side), it is nonetheless clear that it was more rounded than the comparatively acute anterior margin. The cross-section of the missing posterior end suggests a relatively solid internal structure for this region of the centrum, although sediment in-filling obscures a more

detailed assessment of its internal morphology. However, areas of the centrum show 'pocket'-like excavations that likely indicate the presence of pneumatic camerae, as in most eusauropods (Wedel 2003). The parapophyses are present on the anterodorsal corner of the centrum as raised, rugose areas of bone directly anterodorsal to the lateral fossa. The lateral opening is roofed dorsally by a poorly developed ridge that runs posteriorly from the parapopohysis – here interpreted as an incipient posterior centroparapophyseal lamina (PCPL). The ventral surface of the centrum is strongly convex transversely, but relatively flat anteroposteriorly; the latter is an atypical condition for Sauropoda and is possibly due to diagenetic processes (although see *Tehuelchesaurus* [Carballido et al., 2011a: fig 3]).

The neural arch is set back from the anterior edge of the centrum, although the prezygapophyses extend beyond the condyle. The general proportions of the neural arch are likely to have been similar to that of *Tehuelchesaurus* (Carballido et al., 2011a), being subequal-to-lower than the dorsoventral height of the centrum when measured from the neurocentral suture to the hypothesised dorsal margin of the transverse process.

The prezygapophyses are strongly extended anterodorsally and appear to have been widely separated mediolaterally. This morphology, although typical of anterior-most dorsal vertebrae in most derived sauropods, appears to have been especially marked in basal neosauropods (or taxa close to Neosauropoda) such as *Haplocanthosaurus* (CM 572) and *Tehuelchesaurus* (Carballido et al., 2011a). The centroprezygapophyseal lamina (CPRL) is a robust strut that extends from the anterolateral corner of the centrum (where it abuts the ventral corner of the anterior centrodiapophyseal laminae [ACDL]) before turning into a broad, dorsally oriented, laminar sheet braced on either side by the prezygapophyses. Although the dorsal margins of the prezygapophyses are not preserved, it is unlikely that the CPRL would have divided dorsally into lateral and medial components that both contact the prezygapophysis, as occurs in all diplodocids (Upchurch, 1998; Tschopp et al. 2015; although this feature is generally characteristic of middle–posterior dorsal vertebrae).

The small, circular neural canal is bracketed on both sides by pronounced laminar structures that extend dorsomedially from the base of the CPRL. These are interpreted as the medial division of the CPRL (= mdCPRL *sensu* Carballido and Sander, 2014), a feature generally only present in the cervical vertebrae of a number of sauropods (e.g., *Camarasaurus*;

Europasaurus). There appears to have been a distinct, dorsoventrally elongate, elliptical centroprezygapophyseal fossa (CPRF) located between the mdCPRL and the CPRL, although incomplete preservation and matrix infill obscure the full development of this fossa. A small, delicate accessory lamina branches off the CPRL and extends posteroventrally into the prezygapophyseal centrodiapophyseal fossa (PRCDF), bounded by the CPRL and the ACDL. The absence of preserved bone dorsal to the neural canal precludes determination of whether a vertical lamina (the single interprezygapophyseal lamina [sTPRL] of Carballido and Sander, 2014) extended between the interprezygapophyseal lamina (TPRL) and the anterior neural canal opening, such as that observed in the anterior dorsal vertebrae of *Europasaurus* and *Camarasaurus* (Carballido and Sander 2014).

The ACDL is thin and more finely developed than the comparatively robust posterior centrodiapophyseal lamina (PCDL). The PCDL is angled at about 45 degrees (extending anterodorsally to posteroventrally), whereas the ACDL is angled only slightly anteriorly from the vertical. The centrodiapophyseal fossa (CDF) bounded by these laminae appears to have been of considerable depth, impacting deeply into the neural arch. The only preserved portion of the diapophyses is the base of the right side. This is present as a sinuous course of cortical bone that is laterally eroded so as to expose the trabecular bone and matrix preserved within. This geometry extends from the ACDL–PCDL apex to just short of the prezygapophysis, with the anterior portion preserved as an eroded cavity within the lateral surface of the prezygodiapophyseal lamina (PRDL). Although incomplete, it seems that the diapophyses projected mainly laterally.

The postzygapophyses are missing from the posterior surface of the neural arch, although a laterally expanded ridge at the base of the preserved portion of the neural spine possibly represents the remnants of the interpostzygapophyseal lamina (TPOL). Below this ridge the periosteal bone gives way to an amorphous furrow (roughly 2cm in height) containing numerous pits and divots of possible pneumatic origin (see below). Although the anterior extent of this furrow preserves some cortical bone, it cannot be determined if this is a natural or collapsed surface. Immediately ventral to this furrow on the posterior surface of the arch is a mediolaterally narrow, Y-shaped ridge that appears to have extended to the dorsal margin of the neural canal. The dorsolaterally forking arms of this 'Y' are interpreted as the ventral continuation of the TPOL, whereas the median strut below them is likely the

sTPOL (*sensu* Carballido and Sander, 2014), which is present in the anteriormost dorsal vertebrae of a wide range of eusauropods (e.g. *Apatosaurus*, *Camarasaurus*, and *Rapetosaurus* [Curry Rogers, 2005; Carballido and Sander, 2014]). This process is placed centrally within a narrow pillar of bone that separates ventrally so as to buttress either side of the neural canal. These lateral ridges are likely homologous to the centropostzygapophyseal laminae (CPOLs), although they are not as sharply delineated as in the majority of sauropod taxa.

The prezygapophyseal component of the spinoprezygapophyseal lamina (SPRL) is well preserved and extends anterolaterally as a strongly-developed, semi-concave strut of bone from the base of the neural spine to the posterior edge of the prezygapophysis. Unfortunately, the poor preservation of the neural spine means that the morphology of the spinal component of the SPRL is unknown. Just posterior to the SPRL, the base of a major diapophyseal lamina is present as an irregularly-preserved ridge that runs parallel to the SPRL before possibly joining with the SPRL at the base of the neural spine. Because the dorsal terminus of this lamina is not preserved, it cannot be determined if it represents the postzygodiapophyseal lamina (PODL: in which case the spinodiapophyseal [SPDL] would represent the smaller, anteriorly branching lamina, e.g., *Apatosaurus*; *Diplodocus*) or the spinodiapophyseal lamina (SPDL: in which case the situation is reversed, e.g., *Camarasaurus*, *Europasaurus*). The relatively anterior placement of this diapophyseal lamina so close to the SPRL results in a large expanse of relatively featureless bone on the posterior face of the neural arch that grades steeply from the lamina to the posterodorsal edge of the centrum. However, bordering the medial edge of this expanse (where it would have otherwise merged with the neural spine within the infrapostzygapophyseal space) is an elaborate, pneumatic(?) fossa-subfossae complex that is composed primarily of a shallow postzygapophyseal centrodiapophyseal fossa (POCDF) divided by two thin laminae that join at the anterior margin of the fossa so as to broadly resemble a wishbone in dorsal aspect. This pneumatic complex, which appears to have been natural, may have communicated with the irregular series of pits and depressions that penetrate the dorsal summit of the CPOL, as described above.

2.1.1. Possible taxonomic affinities of AM 6125:

The incompletely preserved neural spine and pophyseal facets of AM 6125 make an assessment of its taxonomic affinities difficult. This doubt is exacerbated by a paucity of representative vertebral material from the anterior-most dorsal series of taxa bordering the eusauropod–neosauropod and macronarian–titanosauriform transition. These concerns aside, the possible taxonomic position of AM 6125 is discussed here.

In addition to the prominently developed anterior condyle, the presence of a deep pneumatic opening on the lateral surface of the centrum indicates that AM 6125 is a eusauropod close to the neosauropod radiation (Upchurch 1998), but suggests that it is unlikely to represent a dicraeosaurid, which tend to have only very shallow excavations (Whitlock 2011a). Diplodocids, in contrast, tend to display lateral openings that occupy a much greater proportion of the centrum than that observed in AM 6125 (Tschopp et al., 2015). The unusual, anteroposteriorly flat ventral surface of the centrum shows some similarities with the dorsal vertebrae of the basal macronarian *Tehuelchesaurus* (Carballido et al. 2011a), but in both taxa the vertebrae have experienced crushing that might have contributed to this morphology. A position more derived than basal Macronaria (i.e. Titanosauriformes) for AM 6125 is considered unlikely given the absence of unequivocally camellate air-spaces within the centrum, although our identification of such internal structures might be obscured by matrix infilling and poor preservation.

A diplodocoid position for AM 6125 can be further ruled out primarily with respect to the laminar configuration of its posterior surface, as well as its possession of a clearly defined, laterally flaring SPRL. This latter lamina is either only minimally developed in the anterior dorsal vertebrae of most diplodocoids or situated much closer to the anterior midline (generally in combination with a distinct ventral-dip immediately posterior to the prezygapophyses), e.g., *Apatosaurus* (AMNH 550). The CPOL and TPOL of both diplodocoids and *Haplocanthosaurus* are generally posteriorly-expansive, finely delineated processes which are both anteroposteriorly deep and mediolaterally compressed. In sharp contrast to these taxa, the low, column-like CPOLs of AM 6125 are essentially non-laminar, whereas the sTPOL is only weakly developed. In addition to the posterior laminae, AM 6125 can further be distinguished from *Haplocanthosaurus* with respect to its well-developed ACDL.

The weakly developed CPOL (i.e., the posteroventral portion of the neural arch above the neural canal) of AM 6125 is reminiscent of the anterior dorsal vertebrae of basal macronarian taxa such as *Camarasaurus* and *Europasaurus* (Carballido and Sander, 2014), as well as a number of more derived macronarians (e.g., *Sauroposeidon* and *Malawisaurus*), which also display similarly undeveloped CPOLs. However, *Camarasaurus* is distinguishable from AM 6125 with respect to the broad, mediolaterally extensive area of bone bounding the neural canal, as well as the absence of a clearly defined sTPOL. In comparison, this same region in *Europasaurus* is comparatively mediolaterally constricted (although not to the degree observable in AM 6125), while also presenting a low sTPOL similar in development to AM 6125 – a feature uncommon in the anterior dorsal vertebra of a number of sauropods (D'Emic and Foreman, 2012). It is also worth noting that a number of derived non-neosauropod eusauropod taxa (e.g., *Mamenchisaurus* [Ouyang and Ye, 2002]; *Bellusaurus* [Mo, 2013]) have CPOLs that, while perhaps more finely laminate than the condition of AM 6125, are not as widely separated as observed in most neosauropod taxa (e.g., *Camarasaurus*; Diplodocidae).

Although the absence of unambiguous camellae within the vertebra suggests a non-titanosauriform position for AM 6125, the retention of a mdCPRL beyond the cervical series is currently only recognised within the anterior dorsal vertebrae of the somphospondylan *Chubutisaurus* – a putative autapomorphy of that taxon (Carballido et al. 2011b; see Carballido and Sander, 2014). However, the deep CDF is characteristic of more basal neosauropods, with derived somphospondylans displaying comparatively shallow CDFs (e.g., *Malawisaurus*: Gomani, 2005). Furthermore, although the lateral orientation of the diapophyses in AM 6125 is characteristic of the anterior dorsal vertebrae of most eusauropods (Upchurch 1998; Mannion et al. 2013), it is clearly distinguishable from the dorsally deflected processes of numerous relatively derived neosauropods, including dicraeosaurids, rebbachisaurids (Whitlock 2011a), and a number of titanosauriforms, e.g. *Euhelopus*, *Giraffatitan* and *Malawisaurus* (Mannion et al. 2013). The comparatively large dorsoventral height of the transverse processes also indicates non-brachiosaurid affinities for AM 6125 (see Taylor 2009; D'Emic 2012).

Although a position on the macronarian stem close to Titanosauriformes would therefore appear a reasonable suggestion for AM 6125, the combination of a mediolaterally restricted

CPOL region and a deeply excavated CDF could also be taken as evidence of a slightly more basal position outside of Neosauropoda. Furthermore, the complex of ?pneumatized pits and ridges at the arch-spine juncture also closely matches at least one figured representation of an anterior dorsal vertebra of *Omeisaurus* (He et al., 1988: fig. 25; c.f. Tang et al., 2001). However, Upchurch et al. (2004) have pointed out that such features might simply relate to the extensive musculature required to anchor the bones of the shoulder girdle to the axial column, and therefore are not strictly indicative of phylogeny. Additionally, the low proportions of the arch between the diapophysis and centrum (especially when compared to the relative height of the centrum), while ostensibly similar to 'basal' taxa such as *Tehuelchesaurus*, *Bellusaurus* and *Omeisaurus*, is also highly variable throughout Sauropoda, with similarly basal forms (e.g., *Shunosaurus* [Zhang, 1988], *Haplocanthosaurus* [Hatcher, 1903]) showcasing comparatively tall anterior dorsal neural arches, whereas the relatively derived *Sauroposeidon* (D'Emic and Foreman, 2012) and *Malawisaurus* (Gomani, 2005) have proportions closer to AM 6125.

Although it has not been possible to determine the precise taxonomic affinities of AM 6125 within Eusauropoda, we are able to exclude it from Diplodocoidea as well as (more tentatively) Titanosauriformes. As such, AM 6125 either represents a eusauropod just outside of the neosauropod radiation, or a basal (probable non-titanosauriform) macronarian.

    2.2.   NEOSAUROPODA Bonaparte, 1986

          MACRONARIA Wilson and Sereno, 1998

            TITANOSAURIFORMES Salgado et al., 1997

             BRACHIOSAURIDAE Riggs, 1904

Brachiosauridae indet.

Material: AM 6128, a partial middle-to-posterior dorsal neural arch (Fig. 4).

Locality: Kirkwood Formation (lowermost Cretaceous, ?Berriasian–Hauterivian) on Umlilo Game Farm, Eastern Cape, South Africa.

Description: The element is from the middle–posterior end of the dorsal series, probably from around D8–D10. It preserves almost the entirety of the neural spine, the posterior portion of the right prezygapophysis, the bases (but not the articular facets) of the postzygapophyses, most of the right transverse process and some of the left transverse process.

The neural spine is dorsoventrally higher than anteroposteriorly long, suggesting a position closer to the middle of the posterior half of the dorsal vertebral series. In lateral view the neural spine is mainly vertically-oriented, lacking the distinct posterior inclination of somphospondylan taxa (Wilson, 2002; Mannion et al., 2013). Although the posterior surface is imperfectly preserved, the lateral profile appears to have been relatively constant in anteroposterior depth, differing from the more dorsally-tapering morphology that characterizes the dorsal neural spines of many titanosauriforms (Mannion et al. 2013), including *Brachiosaurus*. The condition in AM6128 is therefore more similar to that observed in *Giraffatitan* (Taylor, 2009). The anterior surface of the neural spine is dominated by the paired SPRLs. These laminae are narrowly separated and run parallel to each other along the spinal midline. Within the dorsal half of the neural spine the SPRLs change abruptly from well-delineated ridges, converging and expanding to form a rugose, prespinal eminence that resembles an inverted triangle in outline. A rugose, sub-triangular area at the anterior summit of the neural spine is common in a number of derived eusauropod taxa (e.g., *Haplocanthosaurus* [Hatcher, 1903]; *Camarasaurus* [Osborn and Mook, 1921]); however, a well-defined, projecting triangular process restricted to the dorsal third of the neural spine and supported from below by robustly developed SPRLs is most readily observable in the brachiosaurid *Giraffatitan* (Janensch, 1950).

There are anterior and posterior branches of each SPDL, a feature generally restricted to derived titanosaurs (Salgado and Powell, 2010). The anterior SPDL (aSPDL) merges with the SPRL a short distance above the base of the neural spine. The posterior (=primary) SPDL (pSPDL) is near-vertical and runs sub-parallel to the aSPDL-SPRL in lateral view. At roughly the dorsoventral midpoint of the neural spine, the pSPDL merges with the SPOL, as occurs in

the majority of eusauropods (Upchurch and Martin, 2003; Upchurch et al., 2004; Carballido et al. 2012). Taylor (2009) suggested SPDLs that continue to the apex of the spine, at no point merging with the SPOLs, as one of the features distinguishing *Giraffatitan* from *Brachiosaurus* (the latter displaying the typical condition). However, examination of the dorsal vertebrae figured in Janensch (1950) suggests that this is not the case for all dorsal elements.

Immediately dorsal to the convergence of the pSPDL and the SPOL, the neural spine undergoes a prominent lateral expansion, adopting the striking 'aliform' morphology typical of non-somphospondylan macronarians, i.e. *Camarasaurus* and brachiosaurids, whereby the lateral tips of these processes extend further laterally than the postzygapophyses (Upchurch 1998; Wilson 2002; Mannion et al. 2013). Although the postzygapophyses are not fully preserved in AM 6128, enough is preserved of the left process to indicate that the strong lateral expansion of the neural spine would have clearly exceeded the lateral terminus of the postzygapophysis. As in *Giraffatitan*, the lateral expansion occurs exclusively within the upper half of the neural spine, differing from the more gradual expansion observed in *Brachiosaurus* (Taylor, 2009).

The lateral margin of the dorsal half of the neural spine is anteroposteriorly expansive and shelf-like, with a highly rugose and irregular surface texture. Due to the expanded nature of the spine apex, the anterior and posterior surfaces of the neural spine are distinctly concave transversely.

The SPOLs are slightly anteriorly inclined and much more strongly developed than the SPDLs. The SPOLs appear to have been asymmetrical insofar as the base of the left lamina shows an additional strut branching off in the direction of the poorly preserved postspinal lamina. The presence of SPOLs divided into lateral and medial branches was recovered as a potential local synapomorphy of Brachiosauridae by Mannion et al. (2013), although this morphology is also present in an array of other sauropods (Wilson 2002).

The postspinal lamina (POSL) is imperfectly preserved and present as an irregular osseous mass that extends dorsoventrally along the posterior surface of the neural spine, with a sinistral bias, almost certainly caused by taphonomic displacement. A sharp, almost fenestral, rim of bone can be seen within the postspinal mass at around the dorsoventral

midpoint, suggesting the presence of a fossa within the POSL, although this might just be the result of the aforementioned deformation of this lamina.

The transverse processes display a distinct laterodorsal orientation, as in *Giraffatitan*, but contrasting with the sub-horizontal processes of *Brachiosaurus* (Taylor, 2009). The diapophysis of the better-preserved transverse process (the right) appears to be mainly complete, although it is possible that the articular surface is slightly eroded. The transverse process adheres to the brachiosaurid condition of being dorsoventrally narrow (D'Emic, 2012), albeit not appreciably more than taxa such as *Camarasaurus* (Osborn and Mook, 1921). A series of small divots or depressions extend mediolaterally along the length of the transverse process, beginning in the space bracketed by the ventral origins of both SPDLs. As a result, the dorsal margin of the transverse process is gently concave, whereas the broad anterior area is flat to convex. The PCDL is a stout buttress of bone that braces the transverse process along the entirety of its length along the ventral surface. On the ventral surface of the preserved lateral tip of the transverse process, saddled between the PCDL and the paradiapophyseal lamina (PPDL), three small fossae can be observed forming an anteroposteriorly-directed row. These features are potentially related to the pneumatic diverticula known to invade the dorsal ribs of titanosauriforms (Wilson and Sereno 1998)

The parapophysis is located on the anteroventral margin of the transverse process slightly medial to mid-length. Therefore, the lamina extending from the parapophysis to the lateral tip of the transverse process is the PPDL, whereas the short strut of bone connecting the parapophysis to the prezygapophysis represents the prezygoparapohyseal lamina (PRPL). A thin, sheet-like lamina extends ventrally beneath the parapophysis, interpreted here as the PCPL. Unfortunately, the ventral incompleteness of this lamina precludes assessment of whether or not it bifurcated, as in the PCPL of most other titanosauriform taxa (D'Emic, 2012; Mannion et al., 2013). The dorsal terminus of the well-developed CPRL supports the preserved portion of the prezygapophysis from below.

In summation, the overall morphological similarities with *Giraffatitan* indicate brachiosaurid affinities for AM 6128. However, none of the proposed autapomorphies of *Giraffatitan* (see Wilson 2002; Upchurch et al., 2004; Taylor 2009; D'Emic 2012) are identifiable in the limited material comprising AM 6128. Although it remains possible that AM 6128 is referable to

Giraffatitan, the lack of shared autapomorphies, coupled with minor differences in the morphology (see above), cautions against such a referral, and we therefore regard AM 6128 as an indeterminate representative of Brachiosauridae.

2.3.   TITANOSAURIFORMES Salgado et al., 1997

?BRACHIOSAURIDAE Riggs, 1904

Material: AM 6130, a partial dorsal centrum (Fig. 5).

Locality: Kirkwood Formation (lowermost Cretaceous, ?Berriasian–Hauterivian) on Umlilo Game Farm, Eastern Cape, South Africa.

Description: AM 6130 is a large dorsal centrum missing most of its dorsal half. Both articular facets are poorly preserved, although the partial remains of the well-developed anterior convexity and the ventral rim of the posterior cotyle can still be observed. Given the moderate anteroposterior length of the centrum, in addition to the absence of any clearly discernible parapophysis, it is likely that this element comes from somewhere within the anterior–middle portion of the dorsal vertebral series, excluding the anteriormost dorsal vertebrae. The most notable feature of the element is the pronounced median keel that extends along the posterior two-thirds of the ventral surface. A ventral keel is known in the dorsal vertebrae of some basal eusauropods and several diplodocids, but also characterises *Brachiosaurus* and *Giraffatitan*, as well as a small number of titanosaurs, e.g. *Opisthocoelicaudia* (Upchurch et al. 2004). The base of a robust strut of bone (probably an ACDL), extending posterodorsally from within the anterior half of the centrum, appears to roof the anterior margin of a large lateral pneumatic opening. Unfortunately, the incomplete state of preservation precludes determination of camellate structures within the centrum. The retention of prominent opisthocoely beyond the anteriormost dorsal vertebrae, coupled with the presence of a ventral keel, suggests titanosauriform affinities (Wilson, 2002; Upchurch et al., 2004; Mannion et al., 2013), and it is possible that AM 6130 represents a brachiosaurid.

2.4.   NEOSAUROPODA Bonaparte, 1986

DIPLODOCOIDEA Marsh, 1884

FLAGELLICAUDATA Harris and Dodson, 2004

DICRAEOSAURIDAE Janensch, 1929

Dicraeosauridae indet.

Material: AM 4755, a partial middle dorsal neural arch (Fig. 6).

Locality and Horizon: Kirkwood Formation (lowermost Cretaceous, ?Berriasian–Hauterivian), on the outskirts of KwaNobuhle Township, 3.3 km south of Uitenhage.

Description: A medium sized dorsal vertebra missing the centrum, zygapophyseal facets, and left transverse process. Due primarily to the markedly high and vertically bifid neural spine, we can be reasonably confident of the assignment of this neural arch to that of a dicraeosaurid diplodocoid. In fact, in general appearance it is near-identical to D6–7 of *Dicraeosaurus hansemanni* (Janensch, 1929: pl. I, figs 17–18).

The neural spine is dorsally bifurcated for approximately 0.4 times its total height. Although the left metapophysis is incomplete at the tip, it appears that the right one is essentially intact (with, at most, a very small amount of material missing), rendering the proportions of the neural spine generally equivalent to D6–7 of *Dicraeosaurus hansemanni*. Both metapophyses are only minimally offset laterally from the sagittal plane, a morphology consistent with the narrowly forked neural spines of dicraeosaurids, but differing from the more widely-diverging metapophyses that characterize other sauropods with bifid presacral neural spines, including *Diplodocus* and *Apatosaurus* (Rauhut et al. 2005; Whitlock 2011a). The persistence of well-developed bifurcation beyond the sixth dorsal vertebra also distinguishes dicraeosaurids from most diplodocid taxa (Whitlock 2011a).

The SPRL is a well-developed sheet of bone that extends with a laterally-sigmoid curvature from a point dorsal to the (not preserved) prezygapophyses, before flattening several centimetres ventral to the tip of the neural spine. In comparison, the SPOL appears to have been a much more mediolaterally narrow process, lacking any pronounced curvature while

also contributing less to the gross structural morphology of the neural spine than the SPRL. The prespinal lamina (PRSL) is a dorsoventrally elongate, mediolaterally thin process that is situated centrally on the deeply inset sheet of bone, bracketed by both SPRLs. Although relatively high, the PRSL does not project as far anteriorly as the SPRL, and grades smoothly into the neural spine several centimetres ventral to the base of the fork. In *Dicraeosaurus hansemanni* the seventh and eighth dorsal neural arches are the only elements to possess a dorsoventrally extensive PRSL while still displaying a clearly bifid neural spine (Janensch, 1929). As this morphology is clearly present in AM 4755, this reinforces our interpretation that this occupied a similar position within the dorsal series. The POSL is slightly more developed than the PRSL, and merges with the emarginated edges of the neural spine at the base of the metapophysis. The effect is that the ventral half of the posterior surface of the neural spine is deeply concave in the spaces delimited by the POSL and the SPOL.

The right transverse process is partially preserved, missing its lateral extent – and hence the diapophyseal articular surface. It is directed dorsolaterally at approximately 30° to the horizontal, as is the case in the dorsal vertebrae of other dicraeosaurids (as well as several other sauropods), but contrasting with the sub-horizontal transverse processes of nearly all diplodocids (Upchurch 1998; Whitlock 2011a; Mannion et al. 2012, 2013). A thin, laminar bridge of bone extends anteriorly from the dorsal margin of the transverse process. This appears to represent the basal remains of the sheet of bone from which both the PPDL and PRDL would have originated. The flange of bone observed directly beneath the transverse process is thus interpreted as a piece of this sheet that has become dislodged and ventrally displaced. The PODL is preserved as a robust, rounded rod of bone that buttresses the transverse process posteriorly. The postzygapophyseal region appears to have been eroded in its entirety, exposing the internal, acamerate body of the neural spine.

2.5.　　　　FLAGELLICAUDATA Harris and Dodson, 2004

　　　　　　DIPLODOCIDAE Marsh, 1884

　　　　　　　　DIPLODOCINAE Marsh, 1884 (*sensu* Taylor and Naish, 2005)

Diplodocinae indet.

Material: AM 6000, an anterior middle caudal vertebra (Fig. 7).

Horizon and Locality: Kirkwood Cliffs 'Lookout', stratotype locality of the Kirkwood Formation (lowermost Cretaceous, ?Berriasian–Hauterivian). Found within grey siltstone above the prominent channel sandstone and the overlying pink palaeosols.

Description: The centrum is approximately 1.5 times as long as high, suggesting that this element comes from somewhere within the anterior portion of the middle caudal series. This is corroborated by the absence of distinct transverse processes, which are usually absent from approximately the 14–15th caudal vertebrae within most neosauropods (Upchurch, 1998; Wilson, 2002), in tandem with the retention of relatively deep lateral pneumatic openings (see below). Tschopp et al. (2015) recovered middle caudal centra in which the anteroposterior length is over 1.7 times the dorsoventral height as a potential synapomorphy of Diplodocinae, which might indicate a more basal position for AM 6000. However, this character uses the highest value for middle caudal vertebrae, and therefore is generally scored for caudal vertebrae of a more posterior position than that occupied by AM 6000.

The anterior articular surface of the centrum displays a more pronounced concavity than the comparatively flat posterior articular surface. This concavity is primarily expressed by a moderately deep, transversely elongate furrow that excavates the centre of the centrum, just dorsal to midheight. Procoelous-to-distoplatyan anterior-to-middle caudal vertebrae are common throughout Flagellicaudata (Tschopp et al., 2015). Both articular faces are approximately as high as they are wide and, although slightly eroded on the right-hand margins, appear to have been more circular in general outline than trapezoidal (see Tschopp et al., 2015: fig. 82).

The ventral surface is deeply concave both anteroposteriorly and transversely, resulting in an expansive ventral excavation. This fossa is bounded laterally by emarginated walls of bone that extend ventrally from the lateral surfaces of the centrum. Thus, excluding the mediolaterally expanded anterior and posterior articular facets, the ventral surface of the centrum is roughly rectangular in ventral aspect, as in other diplodocid taxa (e.g., *Diplodocus longus* YPM 1920). Although Tschopp et al. (2015) questioned the validity of a ventral longitudinal hollow as a diplodocine synapomorphy, being incipiently present in some

apatosaurine and rebbachisaurid specimens, as well as some non-neosauropods and many somphospondylans (Upchurch 1998; Wilson, 2002; Mannion and Barrett, 2013), deep, thinly-walled excavations extending to the middle caudal series are nonetheless only observed in diplodocine taxa (e.g., *Barosaurus*, *Diplodocus*, *Tornieria*). The articular faces are less ventrally extensive than that observed in several diplodocine taxa (i.e., *Tornieria*; *Barosaurus*; *Diplodocus*), resulting in a relatively gently curved ventral margin in lateral view. A similarly shallow ventral arch is observed in a middle caudal vertebra of the Argentinean diplodocine *Leinkupal* (Gallina et al., 2014: fig. 3). The remains of a chevron facet can be observed on the posteroventral corner of the left side of the centrum.

As mentioned above, there is a deep lateral pneumatic fossa located on the dorsal half of the lateral surface of the centrum. This fossa is dorsoventrally narrow and slit-shaped, increasing in depth at its centre (approx. 3—4cm). Whereas several diplodocoid (and some other) taxa have lateral pneumatic openings in their anterior caudal vertebrae (Upchurch 1998; Whitlock et al. 2011; Mannion and Barrett 2013), only diplodocines retain these into their middle caudal vertebrae (Gallina et al. 2014). In the caudal vertebrae of the majority of diplodocine taxa, the disappearance of lateral fossae tends to coincide with the gradual reduction of the transverse processes, with only *Diplodocus* retaining excavations beyond the 16th caudal vertebra, and transverse processes until at least caudal 18 (Tschopp et al., 2015). However, a lateral fossa is present in a diplodocid specimen from the Tendaguru Formation that appears to have largely lost its caudal rib (Remes, 2009: fig. 3d), and a comparatively shallow fossa is present in a similarly rib-less middle caudal centrum of *Tornieria* (MB.R.2956.13 [dd 119]). A recently described diplodocine middle caudal vertebra from the Late Jurassic of Chile (SNGM-1979) also appears to have retained a shallow lateral fossa past the disappearance of the transverse processes (Salgado et al., 2015). Nonetheless, the retention of a lateral fossa beyond the clear presence of a transverse process in AM 6000 suggests either a position posterior to the 16th caudal vertebra, or the atypically anterior loss of caudal ribs. The lateral pneumatic opening is dorsally roofed by an anteroposteriorly elongate, sharp ridge that is situated on the arch-centrum junction. There are no ridges on the lateral surface of the centrum, contrasting with the diplodocids *Apatosaurus*, *Diplodocus* and *Supersaurus*, as well as several other eusauropod taxa (Upchurch and Martin 2002; Mannion et al. 2012), although such ridges are also absent in

the middle caudal centra of the Gondwanan diplodocines *Leinkupal* and *Tornieria* (Remes 2006; Gallina et al. 2014).

The prezygapophyses are slightly dorsally raised (as is typical of more anterior caudal vertebrae) and project well-beyond the anterior edge of the centrum for almost the entirety of their length. The close proximity of the prezygapophyses to the anterior margin of the centrum, in association with their marked anterior projection, is more similar to the condition observed in *Diplodocus hallorum* (AMNH 223) than to any other known diplodocid specimen (with the possible exception of the Chilean specimen SNGM-1979). Nonetheless, the prezygapophyses of *Diplodocus hallorum* are proportionally slender compared to the relatively robust processes of AM 6000. The prezygapophyseal articular facets of AM 6000 are set at an angle of approximately 40 degrees from the horizontal and display a sharp lip of bone that extends ventromedially beyond the main prezygapophyseal process.

The postzygapophyses are large and widely spaced, separated from one another by a deep incision that is almost level with the anterior margin of the neural spine (although it is possible that a thin bridge of bone may have lessened the anteroposterior extent of this gap in life). Given the dorsoventral compression of the neural spine, the SPOLs are reduced to short, thick struts that display a laterally oblique expansion that supports the mediolaterally wide neural spine from below.

SPRLs are present as well-developed horizontal ridges that extend along the length of the neural spine, ultimately contributing to the laterally expanded, table-like morphology of the latter. A shallow fossa is situated at the base of the neural spine, bounded laterally by the SPRL, and floored by the TPRL. Interestingly, the presence of a "triangular fossa" formed by the SPRL and a transverse ridge posteriorly interconnecting the prezygapophyses was suggested as a possible autapomorphy of the problematic *Diplodocus* type species *D. longus* by Tschopp et al. (2015: character 338). This posterior ridge is only weakly present in AM 6000.

The most remarkable feature of the vertebra is the neural spine, which is dorsoventrally flattened and mediolaterally widened so as to appear almost square-shaped in dorsal view. The 'toothed' posterior margin of the neural spine only marginally exceeds that of the centrum and is posteriorly confluent with the postzygapophyses. This latter feature was

described by Tschopp et al. (2015: character 343) as being unique to the middle caudal vertebrae of *Diplodocus hallorum* within Diplodocinae, but also appears to characterize the posterior middle caudal vertebrae of *Tornieria* (Remes, 2006). Diplodocids display a variety of neural spine morphologies within the anterior–middle caudal series, ranging from the high, posteriorly-inclined neural spines of *Apatosaurus* (Gilmore, 1936), to the vertical orientation of *D. hallorum* (AMNH 223). However, within Diplodocidae, only *Leinkupal* appears to have possessed similarly dorsoventrally short neural spines within the middle caudal vertebrae, although these lack the marked mediolateral expansion evident in AM 6000. The anterior middle caudal neural spines of all diplodocid taxa adhere to the plesiomorphic dinosaurian condition of being transversely compressed relative to the sagittal axis. It is only in the anterior (to anterior to anterior-middle) caudal vertebrae of certain diplodocid taxa (e.g., *Supersaurus*, *Tornieria*) that the dorsal summit of the neural spine becomes relatively mediolaterally expanded, although never to the extent seen in AM 6000.

The neural spine morphology expressed by AM 6000 is therefore highly distinctive, being unique within Diplodocidae, and contrasting with most other sauropods too. Although it is possible that this morphology has been accentuated by taphonomic or pathological influences, the fine, ligamentous striations running longitudinally along the dorsal surface of the spine, as well as the uniform, symmetrical manner of preservation, argues against both of these influences. Although the neural spine morphology of AM 6000 is potentially autapomorphic, we refrain from naming a new taxon because of serial variation in vertebral morphology and the incompleteness of the material.

2.6.   DIPLODOCINAE

Diplodocinae indet.

Material: AM 6004, a posterior caudal vertebra (Fig. 8).

Locality: The Kirkwood Cliffs ('lookout'), Kirkwood Formation, lowermost Cretaceous, ?Berriasian–Hauterivian.

The element was found within coarse-grained sandstone and is relatively well preserved, although both the prezygapophyses are missing.

The centrum is roughly twice as long as high, with subsquare-to-subcircular shaped articular facets (although the margins are imperfectly preserved). As in the caudal vertebrae of many diplodocids, the centrum is amphicoelous/distoplatyan, with the anterior articular facet more deeply concave than the relatively flat posterior facet. The internal margin of the posterior articular facet is embossed with a circular ring of bone that protrudes along its ventral margin beyond the posterior extent of the articular facet itself.

The ventral surface of the centrum is concave along both its transverse and sagittal axes, an indication of probable dipolodocine affinity. Unlike the condition in AM 6000, the ventral surface is straight (in lateral view) for over half its length before expanding ventrally towards the articular facets. However, this difference might simply reflect its more posterior position in the caudal series. No obvious chevron facet can be observed and it is likely that this element is posterior to the chevron-bearing vertebrae.

The neural spine is preserved as a dorsoventrally low, sharply pointed process that extends as far posteriorly as the posterior articular surface of the centrum, a morphology common to posterior caudal vertebrae in diplodocid dinosaurs (e.g., Gilmore, 1936).

3. DISCUSSION

3.1. *Sauropod diversity across the Jurassic/Cretaceous boundary*

The fossil material described above demonstrates that the Kirkwood Formation preserves at least four morphologically distinct forms of sauropod dinosaur: a diplodocine, a dicraeosaurid, a brachiosaurid, and a eusauropod that is neither diplodocoid nor titanosauriform (Fig. 9). The additional diplodocine and likely titanosauriform material presented here, as well as teeth described by other researchers (Rich et al. 1983), further attests to the diversity of the sauropodan fauna that inhabited south-eastern South Africa in the Early Cretaceous. These remains represent: (1) the first unequivocal evidence for these groups in the Cretaceous of Africa; (2) additional evidence for the survival of

Brachiosauridae into the Cretaceous outside of North America; and (3) tentative evidence for the survival of a basal neosauropod (or even non-neosauropod) into the Cretaceous. The relevance of each taxon to the biogeography and diversity of Gondwanan Sauropoda at the outset of the Cretaceous is discussed below.

The Cretaceous survival of Diplodocidae was recently confirmed by the discovery of the diplodocine *Leinkupal* from the lowermost Cretaceous Bajada Colorada Formation of Argentina (Gallina et al., 2014). This taxon, in addition to representing the first unambiguous evidence of Diplodocidae outside of the Jurassic, also extended the observed geographic distribution of the group to include South America (previously having only been known from Europe, North America, and East Africa). That observation was recently augmented by diplodocine material from the Tithonian of Chile (Salgado et al., 2015), as well as diplodocid material from the Kimmeridgian of Argentina (Rauhut et al., 2015). The confirmation of additional diplodocine material from southern Gondwana (AM 6000 and AM 6004) suggests that *Leinkupal*, instead of representing a relictual population, was part of a potentially diverse array of diplodocine diplodocids occupying the southern continents at the outset of the Cretaceous. Together with *Tornieria* (Remes, 2006) from the Late Jurassic of Tanzania, the presence of as many as four distinct forms of Gondwanan diplodocine highlights questions pertaining to the regionalisation and biogeographic differentiation of Diplodocidae within the broader Pangaean context.

The palaeobiogeography of diplodocoid dinosaurs has been discussed extensively recently (e.g. Harris, 2006; Remes, 2006; Upchurch and Mannion, 2009; Whitlock, 2011a; Carballido et al., 2012; Mannion et al., 2012; Gallina et al., 2014; Fanti et al., 2015; Rauhut et al., 2015). Although most authors favour a vicariance model of dispersal for the group (whereby the major diplodocoid groups originated by the late Middle Jurassic or early Late Jurassic, establishing themselves in their respective Pangaean 'territories' prior to the global transgression that saw oceanic floor spreading rapidly throughout the Americas [Golonka et al., 1996]), there is currently little phylogenetic support for unambiguous endemism in either Gondwana or western Laurasia. Gallina et al. (2014) alluded to a possible Gondwanan clade of diplodocids based on the close relationship they recovered between *Tornieria* and *Leinkupal*; however, the more comprehensive analysis of Tschopp et al. (2015: fig. 120) failed to recover a sister-taxon relationship between those two taxa, with both taxa

distributed amongst a paraphyletic grade of North American diplodocines (although this might have been affected by the latter authors' exclusion of non-holotypic elements from their *Leinkupal* OTU).

The confirmation of diplodocid material in the Lower Cretaceous Kirkwood Formation invites comparison with these previously known Gondwanan specimens. As illustrated in the description above, AM 6000 is closer in general morphology to *Leinkupal* and the Chilean diplodocine SNGM-1979 than to *Tornieria* (based on the retention of the lateral pneumatic fossa beyond the caudal ribs, and the low neural arch in middle caudal vertebrae). Although it is tempting to interpret this similarity as evidence of a close taxonomic relationship, especially given the assumed temporal contemporaneity of AM 6000 and *Leinkupal*, the incompleteness of both AM 6000 and SNGM-1979 precludes a more detailed assessment of the possible phylogenetic interrelatedness of these materials. Furthermore, the distinctive neural spine of AM 6000, along with the comparatively taller neural arch pedicles of *Leinkupal*, cautions against the premature grouping of these two specimens. Although it is likely that increased sampling will further demonstrate the influence of palaeogeography on diplodocid phylogeny, the spatial relationships of the group remain enigmatic.

In addition to underscoring the Gondwanan diversity of the Diplodocidae, the Kirkwood Formation also confirms the African survival of their flagellicaudatan sister-taxon, Dicraeosauridae. Following a period of relative geographic breadth in the Late Jurassic (being known from East Africa, and North and South America [Whitlock, 2011a]), Dicraeosauridae appears to have undergone a concerted range retraction in the Cretaceous, whereby they were seemingly restricted to South America (Salgado and Bonaparte, 1991; Apesteguía, 2007; Gallina et al., 2014). Although the presence of dicraeosaurids had been suggested in the mid-Cretaceous of northern Sudan (Rauhut, 1999), it is more likely that these isolated and fragmentary remains represent somphospondylans (Mannion and Barrett, 2013). AM 4755 therefore demonstrates that this geographic range reduction was less marked than previously thought, with Dicraeosauridae also surviving into the Cretaceous in southern Africa.

The Early Cretaceous record of Brachiosauridae resembles that of Dicraeosauridae, with a relatively broad Late Jurassic geographic range followed by a hypothesised withdrawal to an

exclusively North American refugium (D'Emic, 2012; see also below). Furthermore, a lengthy ghost-lineage obscures the evolutionary history of Brachiosauridae within the Early Cretaceous, with no unequivocal brachiosaurid remains prior to the Barremian/Aptian of North America (Chure et al., 2010; D'Emic, 2012; Mannion et al., 2013). Although the recent discovery of *Padillasaurus leivaensis* from the Barremian of Columbia places possible representatives of Brachiosauridae within the Lower Cretaceous of South America (Carballido et al., 2015), the African survival of brachiosaurids was previously only alluded to by the presence of brachiosaurid-like teeth from the Lower Cretaceous of Lebanon (then part of the Afro-Arabian plate [Buffetaut et al., 2006]), with diagnostic skeletal material being unknown prior to the present study.Both dicraeosaurids and brachiosaurids are now confidently recognised as part of the Kirkwood assemblage, and therefore as contributing to African faunal diversity in the earliest Cretaceous. However, broad sampling across the rest of the continent suggests the exclusive presence of somphospondylan titanosauriforms and rebbachisaurid diplodocoids from the mid-Cretaceous onwards (Mannion and Barrett, 2013: fig 3). With respect to the latter group, it is worth noting the absence of any material referable to Rebbachisauridae within the Kirkwood Formation. Although previous authors have suggested that '*Algoasaurus*' might represent a rebbachisaurid (e.g. Canudo and Salgado 2003), no member of this enigmatic clade can be confirmed within southern African rocks, meaning that their ~30 million year ghost record remains unaffected.

Finally, the tentative identification of AM 6125 as neither a diplodocoid nor a titanosauriform suggests the survival of non-titanosauriform macronarians and/or non-neosauropod eusauropod taxa into the earliest Cretaceous of Gondwana. Recently, Upchurch et al. (2015) pointed to the absence of these forms from all known Cretaceous deposits outside of Europe (pending the precise age of the Spanish Villar del Arzobispo Formation; see Royo-Torres et al. 2014) and North America (see D'Emic and Foster, 2015). Whereas it was suggested that the J/K boundary thus coincided with the disappearance of basal macronarians and non-neosauropod eusauropods from Gondwana and Asia, Upchurch et al. (2015) reiterated that the near-absence of sampling from southern Gondwana rendered this hypothesis somewhat tentative. Although the incompleteness of AM 6125 is likely to preclude confident determination of its taxonomic relationships, our current identification suggests that the Early Cretaceous survival of non-titanosauriform/non-

diplodocoid taxa was globally more widespread than previously thought, while also highlighting the staggered, gradual nature of decline in many sauropod groups across the J/K boundary (see below).

3.2.   *Fossil record sampling across the J/K boundary*

In general, the sauropod faunal assemblage of the Kirkwood Formation most closely resembles those of Upper Jurassic formations such as the Morrison (North America), Tendaguru (East Africa) and Lourinhã (southwestern Europe), which in aggregate preserve a diverse array of diplodocoid, basal macronarian and titanosauriform, and non-neosauropod eusauropod dinosaurs (see e.g., Weimpshapel et al., 2004; Remes, 2009; Whitlock 2011a; Mannion et al., 2012, 2013; Mocho et al., 2014; Mateus et al., 2014). Early research suggested that the basal-most deposits of the Kirkwood Formation were perhaps Late Jurassic in age (McLachlan and McMillan, 1976, 1979), which would have clearly explained the taxonomic composition of the sauropod fauna. However, most recently the Sundays River Formation was firmly assessed to date to the earliest Early Cretaceous (McMillan, 2003) based on Foraminifera and invertebrate fossils. Given the apparent lateral equivalency between the Kirkwood and Sundays River formations, another explanation is thus required to explain the diversity present within the Kirkwood Formation, which in turn has implications for our understanding of sauropod diversity across the J/K boundary.

Recent studies of sauropod diversity consistently identify the end of the Jurassic as a period of global decline in species richness. This is most readily attested to by a cursory examination of the most recent time-calibrated phylogenies of taxa spanning the Jurassic–Cretaceous transition (e.g., Whitlock, 2011a; D'Emic, 2012; Mannion et al., 2013). These studies are topologically consistent in their depiction of the end-Jurassic as a sharply demarcated event in which a number of sauropod groups, primarily represented by diplodocid flagellicaudatans and non-titanosauriform eusauropods, are thought to have disappeared, with a taxonomic decline of perhaps 60–80% (Upchurch and Barrett, 2005). Although this signal appears relatively robust with respect to successive analyses (see below), the substantial ghost-lineages recorded for Rebbachisauridae and Somphospondyli (see also above regarding the gap in the fossil record of Brachiosauridae) obscure a more

complete understanding of sauropod taxonomic diversity and decline across the J/K boundary (Mannion et al., 2011).

Recent research on the relationship between the rock record and fossil sampling patterns for the Mesozoic suggests that this drop in diversity is not a function of a poor fossil record (see e.g., Upchurch and Barrett, 2005; Barrett et al., 2009; Mannion et al., 2011; Upchurch et al., 2011a). This view is supported by the relatively high area of available rock outcrop reported for the earliest Cretaceous (Berriasian–Hauterivian) compared to other ages of the Jurassic and Cretaceous (Mannion et al., 2011), in association with the absence of a similar decline in both Theropoda and Ornithischia (Barrett et al., 2009; although see Upchurch et al. [2011a] for a more complex pattern). Although this pattern suggests that the observed decline in Sauropoda at the J/K boundary was potentially affected by genuine biotic processes (see also Benson and Mannion, 2012), there are growing indications that the terrestrial rock record for the earliest Cretaceous is not as well-represented as previously thought. Although they documented a similar richness of fossil-bearing units for the lowermost Cretaceous of most regions excluding North America, Benson et al. (2013) drew attention to the notable lack of fossil sampling outside of the restricted geographical regions of western Europe, Morocco, and Japan. This apparent conflict between a 'good' rock record but poor sauropod record for the earliest Cretaceous was explored in greater detail by Upchurch et al. (2015), who found that Gondwanan deposits were especially underrepresented, with only the Bajada Colorada (Argentina) and Kirkwood formations being located south of the Afro-Arabian plate (the Tiouaren Formation, Niger, from which *Jobaria* [Sereno et al., 1999] was recovered, is likely to be Middle Jurassic, rather than Cretaceous, in age [Rauhut and López-Arbarello, 2009]).

Whereas the terrestrial record of the earliest Cretaceous is concentrated in only a small handful of geographically-disparate deposits (Upchurch et al., 2015), sampling throughout those deposits is nonetheless suggestive of a greater diversity of sauropod taxa than that implied by most recent time-calibrated phylogenies (see also Carballido et al., 2015). In addition to the newly described materials of the present study, as well as the recently named Argentinian diplodocine *Leinkupal* (Gallina et al., 2014), the sauropod record of the first three stratigraphic stages (Berriasian–Hauterivian) of the Cretaceous is represented by a number of forms of variable completeness and taxonomic certainty. Named, valid taxa

include the highly incomplete basal macronarians *Haestasaurus* and *Pelorosaurus* from the Wealden Group of the United Kingdom (Upchurch et al., 2011b, 2015), as well as the basal macronarian *Aragosaurus* from the Spanish Villar del Arzobispo Formation (Royo-Torres et al. 2014). Several additional taxa are known from this formation (comprising the probable basal macronarian *Galveosaurus* [Mannion et al. 2013], as well as the turiasaurs *Losillasaurus* and *Turiasaurus* [Royo-Torres et al. 2006]), but their stratigraphic ages are uncertain, with their proposed range spanning the late Tithonian through to the middle Berriasian (Royo-Torres et al. 2006, 2014). An unnamed diplodocid is also known from this unit (Royo-Torres et al., 2009). Furthermore, our understanding of earliest Cretaceous sauropods is augmented by a small number of occurrences of generically indeterminate material, such as a probable basal macronarian from North America (D'Emic and Foster 2015). However, because the phylogenetic affinities and/or stratigraphic ages of much of this material are uncertain, its contribution to Early Cretaceous diversity estimates remains somewhat limited for the time being (Fig. 10).

This growth in research on the earliest Cretaceous is beginning to showcase a previously unappreciated degree of sauropod diversity, even if the relationships of many specimens remain uncertain. Nonetheless, the degree of sauropod diversity presently observed within the Kirkwood Formation is without parallel compared to contemporaneously sampled deposits. In this respect, the Early Cretaceous of Gondwana (or a subregion thereof) may have been environmentally and/or ecologically suited to the survival of specific sauropodan clades relative to other regions, reflecting regional variation in the staggered global decline of various sauropod groups (see Muir et al. [2015] for a palaeo-environmental reconstruction of the Kirkwood Formation). This possibility recalls Mannion et al.'s (2011) suggestion that the absence of certain sauropod groups from the earliest Cretaceous may simply reflect the lack of preservation of environments amenable to sauropod habitation and/or fossilization. However, with reference to the preceding discussion, this investigation also represents an example of how careful fieldwork and comparative anatomy conducted at a broad scale within our greatly improved understanding of sauropod diversity can inform upon and alter hypotheses of sauropod macroevolution at the J/K boundary.

Finally, the Kirkwood Formation also reinforces previous assessments of the J/K boundary not as a discrete 'extinction event', but as a period of gradually-instantiated ecological

change in which the forms that dominated the Mesozoic at the close of the Jurassic were slowly replaced by narrow-crowned somphospondylan titanosauriforms and rebbachisaurid diplodocoids (Chure et al., 2010; Upchurch et al., 2015). The possibility of a gradual shift in faunal composition is also attested to by upper Lower Cretaceous deposits within Gondwana that preserve a mix of 'Jurassic'-type and 'derived Cretaceous'-type faunas. For example, the Barremian La Amarga Formation of southwestern Argentina has yielded the dicraeosaurid *Amargasaurus* (Salgado and Bonaparte 1991), as well as somphospondylan and rebbachisaurid sauropod remains (Apesteguía 2007). These and other examples suggest the presence of multiple ghost-lineages extending back across the J/K boundary, as well as probable 'zombie'-lineages (see Lane et al., 2005) of 'extinct' clades in the Early Cretaceous, that await substantiation through fossil discoveries. This also underscores the caution required in extrapolating major macroevolutionary trends from a clearly incomplete and uneven rock record, with any given rock area estimate unable to factor in the mathematically intricate interrelationships of differential exposure, fossil richness, geographic extensiveness, and a host of other variables that makes one deposit much better suited for recovering fossils than another. It is therefore probably no coincidence that the apparent height of sauropod diversity should occur in the latest Jurassic, a time interval represented by the famously fossiliferous rocks of the Tendaguru and Morrison formations.

3.3.   *Palaeoecological implications of the Kirkwood Formation sauropods*

The suite of sauropods from the Kirkwood Formation reinforces the close ecological and/or spatial association between flagellicaudatans and basal titanosauriforms. These two groups are now known to have co-occurred within five or more Late Jurassic–Early Cretaceous deposits in Gondwana (Africa and South America) and western Laurasia. This spatial and temporal relationship is mainly manifested by the synformational presence of fossils of Diplodocidae and Brachiosauridae, suggesting a degree of mutual-informativeness with respect to the palaeoecological and palaeobiogeographical histories of both groups.

The functional distinctiveness of diplodocids and brachiosaurids has been discussed extensively (e.g., Stevens and Parrish, 1999; Christian and Dzemski, 2011; Whitlock, 2011b; Button et al., 2014), with the general consensus favouring a low-to-mid browsing height strategy for diplodocids, contrasting with the habitual high-browsing regime inferred for

brachiosaurids. Strong evidence for niche-partitioning between the two groups is thus given further support in their near-identical geographic ranges, extending from the south of Gondwana (South Africa) into western Europe and into the western United States. As has been discussed elsewhere (see Button et al. [2014] and references therein), the divergent dietary preferences displayed by either taxon meant that the Mesozoic biomes favoured by diplodocids and brachiosaurids (plus several other coeval sauropod taxa) could support a wider diversity of bulk-feeding mega-herbivores via the efficacious partitioning of resources.

Whitlock (2011b) suggested a specific ecological scenario in which the Morrison Formation (North America) may have been able to support a greater diversity of diplodocids than the contemporaneous Tendaguru Formation (East Africa) due to the widespread presence of herbaceous flora (i.e., ferns) that are likely to have been targeted by a lower-browsing, non-selective feeder. In contrast, the conifer-dominated Tendaguru Formation is thought to have sustained a larger diversity of higher-browsing, selective feeders (e.g., basal Macronaria, Titanosauriformes) that preferred a more wooded environment (although this inference rests partly on the taxonomic affinities of the problematic genus *Australodocus* [see Remes 2007; Whitlock 2011c; Mannion et al., 2013; Tschopp et al. 2015]). Given the broadly mosaic environment recently elucidated for the Kirkwood Formation (Muir et al., 2015), with both plentiful woodland as well as a diverse fern and bennettitalean component present, it appears that both grades of browser could have been easily accommodated within the palaeoenvironments of the Kirkwood Formation. This observation finds tentative support in the relative numerical equivalence of titanosauriform and diplodocid remains found throughout the formation.

The repeated co-occurrence of brachiosaurids and diplodocids thus introduces a testable set of predictive assumptions as the sauropod-bearing deposits of the Upper Jurassic and (especially) the Lower Cretaceous are further sampled and explored – especially in the instances where only one form is currently known. Nonetheless, at some point prior to the mid-Cretaceous this ecological 'partnership' ended, with brachiosaurids becoming restricted to a narrow range in North America and diplodocids apparently going extinct entirely. Although the precise ecological dynamics at play in the radiation/decline of any palaeontological group is extremely difficult to extrapolate from the fossil record, it is worth noting that the extinction and/or geographic restriction of the Diplodocidae and

Brachiosauridae is broadly coincident with the global radiation of somphospondylan titanosauriforms (see D'Emic, 2012; Mannion et al., 2013).

4. CONCLUSIONS

Our review of the sauropod material collected from the lowermost Cretaceous Kirkwood Formation (?Berriasian–Hauterivian) of South Africa illustrates the presence of Dicraeosauridae, Diplodocidae and Brachiosauridae in the Early Cretaceous of Africa, three clades that were thought to have gone extinct at the J/K boundary on this continent.

Although represented by fragmentary and isolated material, the sauropod diversity presented here suggests that reappraisal of the previously observed decline in sauropod diversity at the J/K boundary is warranted. Specifically, we suggest that the apparent 'diversity trough' is explicable through a combination of sampling bias, an uneven rock record, and spatiotemporal disparity in the global disappearance of certain sauropod groups. In this respect, the disappearance of diplodocids and 'broad-crowned' eusauropods/basal macronarians in the Early Cretaceous can be characterized as a spatiotemporally staggered, gradual process. Examination of palaeobiogeographical trends within Sauropoda in the Early Cretaceous suggests that the decline of these groups, as well as the synchronous geographical restriction of Brachiosauridae, is potentially related to the rapid global radiation of Somphospondyli. However, the scarcity of well-dated sauropod-bearing localities within the earliest Cretaceous continues to obscure a more fine-scaled reconstruction of sauropod palaeobiogeography and palaeoecology at this important time in their evolutionary history.

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Table 1. Dimensions of Albany Museum specimens as preserved. All measurements in cm.

AM 6125

anteroposterior length of centrum	18
dorsoventral height anterior face of centrum	12.5
dorsoventral height posterior face of centrum	11
transverse width of centrum	10.5
maximum length of CPRL	13.5

AM 6128

height of neural arch	47
maximum transverse width nueral spine	23

AM 6130

anteroposterior length of centrum	29
maximum dorsoventral height	22

AM 4755

dorsoventral height neural spine (from base of PRSL)	31

AM 6000

anteroposterior length of centrum	27
dorsoventral height of articular facets	18.5
transverse width anterior face of centrum	22
maximum dorsoventral height of vertebra	30

AM 6004

anteroposterior length of centrum	15
dorsoventral height posterior face of centrum	8
transverse width posterior face centrum	8.5

Figure 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)

Figure 2. AM 6125 in **a**, anterior and **b**, posterior views. See text for abbreviations. Scale bar equals 5 cm.

Figure 3. AM 6125 in **a**, right lateral; **b**, left lateral; and **c**, dorsolateral views. See text for abbreviations. Scale bars equal 5 cm.

Figure 4. AM 6128 in **a**, anterior; **b**, right lateral; and **c**, posterior views. See text for abbreviations. Scale bar equal 5cm.

Figure 5. AM 6130 in **a**, ventral and **b**, right lateral views. See text for abbreviations. Scale bar equals 5cm.

Figure 6. AM 4755 in **a**, anterior and **b**, posterior views. See text for abbreviations. Scale bar equals 5 cm.

Figure 7. AM 6000 in **a**, anterior; **b**, posterior; **c**, left lateral; **d**, dorsal; and **e**, ventral views. See text for abbreviations. Scale bar equals 5 cm.

Figure 8. AM 6004 in **a**, right lateral; **b**, anterior; **c**, ventral; and **d**, posterior views. See text for abbreviations. Scale bar equals 5 cm.

Figure 9. Sauropod diversity present within the Kirkwood Formation. **a**, AM 6128 (after *Giraffatitan*); **b**, AM 6125 (after *Camarasaurus*); **c**, AM 6000 (after *Diplodocus*); and **d**, AM 4755 (after *Amargasaurus*). Scale bars equal 1 m. Images courtesy of Scott Hartman.

Figure 10. Composite cladogram illustrating sauropod diversity across the Jurassic–Cretaceous boundary, with hypothetical positions of Albany Museum specimens. Phylogenetic reconstruction based on the analyses of Whitlock (2011), Mannion et al. (2013), Carballido and Sander (2014), Royo-Torres et al. (2014), and Tschopp et al. (2015).