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The South African Mesozoic: Advances in our understanding of the evolution, palaeobiogeography, and palaeoecology of sauropodomorph dinosaurs

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A dissertation submitted to the Faculty of Science, University of the Witwatersrand, in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

Johannesburg, 2016

I declare that the vast majority of this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University. As this thesis is primarily comprised of multiple-authored published papers, the contributions of each co-author are stated clearly within section five of the introduction.



_____23rd_____day of _____May_____2016_____at_____Wits_____

ABSTRACT

The Palaeontological record of South Africa is remarkable in that it preserves the two major temporal transitions of the Mesozoic: The Triassic–Jurassic boundary (the Elliot Formation) and the earliest depositional stages of the Cretaceous (the Kirkwood Formation).

Work within the Elliot Formation has reiterated the importance of this horizon for our understanding of the early evolution and subsequent radiation/diversification of basal sauropodomorph dinosaurs. Moreover, inextricably contained within this radiation is the early evolution of the columnar-limbed, long necked sauropods, the largest terrestrial animals to have ever evolved. The Elliot Formation therefore imparts vital information on the genesis of the group that would become the dominant dinosaurian herbivores throughout most of the Mesozoic. However, several outstanding issues obscure a full understanding of this important radiation. Of primary concern is the complicated taxonomy of the sauropodomorphs of the Upper Triassic lower Elliot Formation and a lack of current consensus as to what precisely constitutes a true sauropod. The latter issue is further complicated by a lack of well-preserved sauropod material prior to the Toarcian. The discovery of new, associated material from both the lower and upper Elliot Formation has direct relevance to both of these concerns. Specifically, although the genus *Eucnemesaurus* is supported in the current analysis, the *bauplan* diversity of lower Elliot Sauropodomorpha remains relatively conservative save for the stocky pedal architecture of *Blikanasaurus* and the autapomorphically robust morphology of a newly rediscovered ilium that is potentially referable to it. Within the upper Elliot Formation, a recently discovered highly apomorphic bone-bed is diagnosed as a new species of sauropod that, in addition to placing the earliest unequivocal sauropods within the basal rocks of the Jurassic, suggests the underlying ecological factors driving the divergence of the derived sauropodan *bauplan*.

In addition to new information provided by the Elliot Formation, two decades' worth of collecting from the Early Cretaceous Kirkwood Formation affords a long overdue insight into the sauropod fauna occupying southern Gondwana at the outset of the Cretaceous. The surprising diversity of forms recognized from the Kirkwood suggests that the taxonomic decline of Sauropoda previously inferred for the earliest Cretaceous is a product of sampling bias compounded by a generally poor fossil record. However, a lack of absolute dates for the Kirkwood Formation means that the plethora of "Jurassic-type" specimens is potentially explicable via their being contemporaneous with similar Late Jurassic faunas of eastern Africa and North America.

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STUDY TWO: A new basal sauropod from the pre-Toarcian Jurassic of South Africa: evidence of niche-partitioning at the sauropodomorph–sauropod boundary? *Scientific Reports*.

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Kirkwood Formation of South Africa: Implications for the Jurassic– Cretaceous transition.

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STUDY FOUR: A hyper-robust sauropodomorph dinosaur ilium from the Upper Triassic–Lower Jurassic Elliot Formation of South Africa: Implications for the functional diversity of basal Sauropodomorpha.

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1. INTRODUCTION

As per the palaeobiologist's favoured inaugural line when introducing any analysis of the group, sauropodomorph dinosaurs include the largest terrestrial animals to have ever evolved. Although derived (i.e., neosauropod) members of the group have been studied extensively since first being recognised as gigantic, long-necked saurians in the 1870's (Marsh, 1878), basal sauropodomorphs ('prosauropods') have tended to be overlooked by comparison. This is potentially an artefact of the outdated notion that basal sauropodomorphs were relatively morphologically homogeneous compared to more well-known dinosaurian groups, as well as early systematic hypotheses that 'Prosauropoda' and Sauropoda formed mutually exclusive sister-taxa, and hence the former was cladistically removed from the evolutionary history of the latter. However, an influx of interest over the past decade has settled on something of a consensus that the traditional 'prosauropod' assemblage is – at least to a degree – paraphyletic with respect to Sauropoda. The primary upshot of this development is the appreciation that sauropod origins can be traced back to the large array of "semi-bipedal" forms that represented the dominant dinosaurian herbivores of the Late Triassic and earliest Jurassic.

With respect to the terrestrial context, this time period is perhaps best captured by the purple–red mudstones of the Elliot Formation of South Africa. Furthermore, within the Algoa Basin of South Africa's Eastern Cape, the Kirkwood Formation preserves an abundance of fragmentary dinosaur remains that provide information on one of the poorest sampled periods of the Mesozoic – the earliest Cretaceous. Drawing on new fossil material collected over recent years from both the Elliot and Kirkwood formations, this thesis aims to extend our knowledge of both the early evolutionary history of Sauropodomorpha, as well as this under-studied latter period of the group's history – a time in which sauropod dinosaurs were previously thought to have undergone a dramatic drop in taxonomic diversity. Representing at least two new taxa as well as several forms previously unknown from the Early Cretaceous of southern Africa (and possibly Gondwana), the material and analyses presented herein attempts to resolve several outstanding issues pertaining to the evolution of sauropodomorph dinosaurs. This centres primarily on continued taxonomic uncertainties relating to the diversity and interrelationships of the sauropodomorphs of the lower Elliot Formation, the poor fossil record of basal sauropod dinosaurs, and the dearth of fossil sampling pertaining to the earliest stages of the Cretaceous.

The background context of these issues is given further discussion below.

INSTITUTIONAL ABBREVIATIONS: BP: Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa; NMQR: National Museum, Bloemfontein, South Africa; SAM: Iziko Museum, Cape Town, South Africa.

2. RECENT ADVANCES in SAUROPODOMORPH PHYLOGENETICS

The historical background of investigations into sauropodomorph phylogenetics has been recounted in detail elsewhere (e.g., Upchurch, 1995; Pol, 2004; Galton and Upchurch, 2004; Upchurch et al., 2007; Langer et al., 2010; McPhee, 2013), and will therefore only be briefly summarised here. Huene (1932) erected the name Sauropodomorpha in order to group the two previously recognised Suborders of Prosauropoda (Huene, 1920) and Sauropoda (Marsh, 1878). Although the sister relationship of one to the other (and both to 'Carnosauria') was a point of repeated contention within the middle twentieth century (see e.g., Romer, 1956, Colbert, 1964; Charig et al., 1965), the suggested taxonomic arrangement of Huene (1932) nonetheless set the tone for discussions of saurischian interrelationships throughout the latter part of the century. 'Prosauropoda' as originally conceived was informally held to constitute the ancestral stock to Sauropoda, and hence would be considered paraphyletic in the modern parlance (Huene. 1920). However, early cladistic-systematic work shifted consensus towards the idea of mutual monophyly between the two groups (e.g., Galton, 1990; Sereno, 1999; Wilson and Sereno, 1998; Benton et al., 2000; Galton and Upchurch, 2004). This consensus appears to have been short lived, however, as increasingly sophisticated character matrices and increased taxon sampling swung opinion back in favour of 'prosauropod' paraphyly (e.g., Yates, 2003a; Yates and Kitching, 2003; Pol, 2004; Upchurch et al., 2007; Yates, 2007a; Pol et al., 2011).

Although the paraphyly of 'Prosauropoda' now appears uncontroversial, uncertainties remain regarding the precise interrelationships of specific subgroupings amongst the stem (Upchurch et al., 2007 *contra* Yates, 2007a), with support for any given topology generally relatively low (Peyre de Fabrègues and Allain, 2015). However, a period of phylogenetic

quiescence has recently been engendered due to the majority of active workers employing personally modified versions of the matrix originally introduced by Yates (2007a; and Yates et al., 2010) (e.g., Apaldetti et al., 2011, 2014; Otero and Pol, 2013; Otero et al., 2015 McPhee et al., 2014, 2015a). Nonetheless, it remains to be seen how long this period of general consensus will continue for; especially as new discoveries, novel character formulations, and personalized edits to the matrix gradually yield increasingly incongruent results. For the moment this is primarily restricted to the composition of the pectinate stem of basal sauropodiforms/anchisaurians, with several recent analyses recovering incompatible positions for e.g., *Anchisaurus* and *Leonerasaurus* (see McPhee et al. [2015] and Otero et al. [2015]).

The repeated recovery of a pectinate grade of "stem-sauropodiforms" has also introduced problems with respect to the preferred nomenclatural (= phylogenetic) position for Sauropoda – this taxon currently placing amongst this stem. The first popularly-cited phylo-taxonomic definition of Sauropoda was the stem-based definition proposed by Wilson and Sereno (1998), which delimited the group as all taxa closer to *Saltasaurus* than *Plateosaurus*. However, Yates (2007a) recognised that in a paraphyletic arrangement the constituency of Sauropoda as traditionally understood (e.g., Salgado et al., 1997) expands to capture a number of forms never classically regarded as sauropodan (e.g., *Massospondylus*). Yates (2007) therefore introduced a novel stem-based phylogenetic definition (the most inclusive clade not including *Melanorosaurus*) in order to "protect" the traditional content of Sauropoda. This redefinition, while initially popular, has not met with universal application (e.g., McPhee et al., 2014; Peyre de Fabrègues and Allain, 2015). This is primarily due to two factors: 1) the taxonomic validity of *Melanorosaurus* is currently highly doubtful

(see McPhee et al. [2015a] for discussion) and 2) this definition was not erected with respect to a combination of uniquely sauropodan synapomorphies, but rather upon a vaguely intuited sense of this representing the "large-bodied quadrupedal" clade. Although the apparently stepwise transition from basal Sauropodomorpha through Sauropoda complicates the delimitation of unambiguous synapomorphies for the latter (this is discussed in great detail within the literature review of my Master's thesis [McPhee, 2013]), it should be stated that the distribution of quadrupedality throughout the sauropodomorph stem now appears more complicated than previously appreciated (Remes, 2008). This is perhaps best exemplified by specific features (both plesiomorphic and specialised) of the relatively derived *Antetonitrus* that suggest the retention of regular phases of bipedal locomotion (McPhee et al., 2014).

It is for these reasons that some authors prefer to restrict the definition of Sauropoda to the node containing *Vulcanodon* (long regarded as the earliest 'true' sauropodan exemplar [Cooper, 1984; Upchurch, 1998; Wilson, 2002]) and all of its descendants (Langer et al., 2010; McPhee et al., 2014). However, given the incompleteness of *Vulcanodon*, along with the persistent incompleteness of the early sauropod record (with important structures such as the skull and manus effectively maintaining twenty-million-year ghost lineages), it is clear that the question of what exactly constitutes a true "sauropod" will continue to be debated as more evidence comes to light. This question is given explicit attention in the second study of this thesis.

3. THE CURRENT STATE of SAUROPODOMORPH PALAEOBIOGEOGRAPHY

Sauropodomorph dinosaurs are known from every major continent. However, basal representatives of the group are yet to have been recovered from Australia, or from the pre-Jurassic of eastern Laurasia (*contra* Buffetaut et al. [2000], the age of the Nam Phong Formation of Thailand is very poorly constrained, with only the lowermost strata potentially extending into the Triassic [Racey and Goodall, 2009]), continental North America (although see Harris et al. [2002]), nor Antarctica. Although this would appear to suggest a southwestern Pangaean origin for the group, it should be noted that sampling opportunities for the Late Triassic outside of South America, South Africa, and Western Europe, remain relatively limited. Nonetheless, the presence of the basal-most sauropodomorphs currently recognised within the Carnian age Ischigualasto (*Panphagia* [Martinez and Alcober, 2009]) and Santa Maria (*Saturnalia* [Langer et al., 1999]) formations of South America suggests that the initial radiation of the group took place in a southwestern Gondwanan context. This is further supported by the recent reinterpretation of the basal saurischian *Eoraptor* (base of the Ischigualasto Formation) as a one of the basal-most sauropodomorphs currently known (Martinez et al., 2011, 2012).

Following their initial appearance in the lowermost rocks of the Ischigualasto Formation, sauropodomorphs quickly became the dominant large-bodied herbivores in all Late Triassic deposits preserving their remains (see Martinez et al. [2011] for a slightly more complex pattern). This is perhaps best exemplified by the sauropodomorph-rich deposits of Argentina (i.e., the ?middle–late Norian Los Colorados Formation which preserves a morphologically disparate range of taxa comprising *Coloradisaurus* [Apaldetti et al., 2012], *Riojasaurus* [Bonaparte, 1971], and *Lessemsaurus* [Pol and Powell, 2007a]) and South Africa

(the Elliot Formation, see below). Other Late Triassic sauropodomorph-bearing deposits are the Caturrita Formation of Brazil (*Unaysaurus*: Leal et al. 2004; Müller et al., 2016), (possibly) the Laguna Colorada Formation of Patagonia in the south of Argentina (*Mussaurus*: Pol 2004; Pol and Powell 2007b), the Rhaetian Upper Maleri and Lower Dharmaram formations of India (Novas et al., 2010), and the German Keuper Group (*Plateosaurus; Efraasia*: *Ruehleia*; Galton, 2001; Yates 2003b; Moser 2003). The ?Norian–Rhaetian fissure-filling deposits of Western England and South Wales have also produced an abundance of small-bodied, gracile sauropodomorph material (Storrs 1994; Benton et al., 2000; Yates, 2003a). A rare exception to the latter is the large-bodied *Camelotia* from the Westbury Formation near Somerset (Galton, 1998), which is the only European taxon of the Late Triassic (Rhaetian) to resemble the 'melanorosaurid' taxa (e.g., *Melanorosaurus*; *Lessemsaurus*) of the Late Triassic deposits of South Africa and Argentina. Thus, from their small-bodied beginnings in the Carnian, by the end of the Triassic Sauropodomorpha had radiated throughout vast areas of western Pangaea. Given the large body sizes of some specimens of e.g., *Plateosaurus*, *Riojasaurus*, and *Camelotia*, it is evident that this radiation was accompanied by a dramatic increase in maximum body size threshold (see also Brusatte et al., 2010).

The global dominance of basal Sauropodomorpha continued unabated throughout the earliest Jurassic, with the group now unequivocally recognised from deposits in Antarctica (Smith and Pol, 2007) and North America (Galton, 1976; Rowe et al., 2011). Additionally, the Lufeng Formation of China preserves a relatively rich sauropodomorph fauna (comprised of *Lufengosaurus*, *Yunnanosaurus*, *Jingshanosaurus*, *Yimenosaurus,* and several other indeterminate forms [Young, 1941, 1942; Zhang, 1994; see also Upchurch, 1995; Barrett,

1999]), and several forms have recently been described from the Upper Dharmaram Formation of India (Kutty et al., 2007). It is worth noting, however, that there is currently little agreement between the biogeographic distribution of basal sauropodomorphs and the currently favoured hypotheses of their phylogenetic relationships, potentially reflecting the cosmopolitan nature of Pangaean faunas at the time. Although the repeated sister-grouping of (*Riojasaurus* + *Eucnemesaurus*) and (*Lessemsaurus* + *Antetonitrus*) from the Los Colorados and Elliot formations of Argentina and South Africa, respectively, suggests a degree of faunal regionalism between these closely aligned basins, ongoing concerns about the validity and monospecificity of the *Riojasaurus* hypodigm cautions against the over-interpretation of this signal (McPhee et al., 2015a; first study of this thesis). The relatively strongly supported monophyly of the Massospondylidae underscores the apparent lack of vicariant geographic boundaries within Pangaea at the Triassic–Jurassic boundary, with representatives of this taxon distributed across South America (Martinez, 2009; Apaletti et al., 2012, 2014), South Africa (Gow et al., 1990), China (Young, 1941), Antarctica (Smith and Pol, 2007), as well possibly North America (Rowe et al., 2011) and India (Novas et al., 2010). Nonetheless, a more in-depth (ideally specimen-based) analysis of this intriguing monophylum (one of the few on the sauropodomorph stem) remains outstanding, especially given the continued phylogenetic questions surrounding *Coloradisaurus* (Apaldetti et al., 2014) (currently the only massospondylid recognised from the Late Triassic).

Reconstructing the palaeobiogeography of basal Sauropoda has been hampered by both a paucity of early sauropod material as well as a lack of consensus as the what precisely constitutes a “true” sauropod (see above). *Isanosaurus* from the Nam Phong Formation from Thailand has generally been regarded as the earliest (Rhaetian) unequivocal sauropod

since its introduction over a decade ago (Buffetaut et al., 2000). However, recent concerns about the temporal relationships of the Nam Phong Formation (Racey and Goodall, 2009), along with the relatively derived morphology of certain elements amongst the paucity of known *Isanosaurus* material, strongly cautions against its Triassic origin. If the stem-based definition of Sauropoda as all taxa more derived that *Melanorosaurus* is followed, then the earliest sauropods are potentially *Lessemsaurus* and *Blikanasaurus* (Galton and van Heereden, 1985, 1998) from the Norian of Argentina and South Africa, respectively, possibly followed by the English *Camelotia*. However, with respect to studies two (McPhee et al., 2015b) and four (McPhee and Choiniere, in review) of the current thesis, the sauropodan affinities of these taxa cannot be taken at face value. A similar concern obtains for *Antetonitrus* (McPhee et al., 2014 *contra* Yates and Kitching, 2003) which may, nonetheless, derive from the Early Jurassic upper Elliot Formation (see below). Given the apomorphic proportions and morphology of its appendicular skeleton (i.e., as clearly evincing that of an obligate, parasagittal quadruped), the earliest unequivocal sauropod is therefore *Vulcanodon* from the late Early Jurassic of Zimbabwe (Cooper, 1984). The recent discovery of *Pulanesaura* from the earliest Jurassic of South Africa, along with its phylogenetic recovery as sister-taxon to *Vulcanodon* + more derived Sauropoda (McPhee et al., 2015b), further underscores the importance of southern Africa to our understanding of the origins of Sauropoda. However, an extremely poor early sauropod record precludes further analysis of the palaeobiogeography of the earliest members of the group.

The end of the Pliensbachian (or early Toarcian) appears to coincide the extinction of all basal (non-sauropodan) sauropodomorphs and the subsequent radiation and global ascendency of Sauropoda (Barrett and Upchurch, 2005; Upchurch and Barrett, 2005; see

also Allain and Aquesbi, 2008). Basal (non-neosauropodan) eusauropod taxa are known from throughout Pangaea, with representatives known from all Middle Jurassic dinosaur-bearing deposits in Argentina, India, China, England, and north-western Africa (e.g., Dong et al., 1983; Bonaparte, 1986; Sereno et al., 1999; Upchurch and Martin, 2003; Upchurch et al., 2004; Bandyopadhyay et al., 2010). Likewise, with the exception of the persistent Asian absence of Diplodocidae (Whitlock et al., 2011), the neosauropod radiation appears to have been similarly global. The taxonomic diversity of Sauropoda is generally held to have peaked towards the end of the Jurassic, as exemplified by the species-rich deposits of East Africa (the Tendaguru Fomation) and North America (the Morrison Formation). It has been hypothesised that the outset of the Cretaceous thus coincided with a precipitous decline in sauropod taxonomic diversity (e.g., Barrett et al., 2009; Mannion et al., 2011; Upchurch et al., 2015). However, terrestrial fossil sampling opportunities for the earliest Cretaceous are appreciably attenuated outside of restricted geographical regions (Benson et al., 2013), with the first three stages of the Gondwanan Cretaceous represented only by the relatively fossil-depauperate Kirkwood and Bajada Colorada (Argentina) formations. Nonetheless, rare sampling opportunities provided by the former suggest a pattern incongruent with that of an Early Cretaceous drop in sauropod taxonomic diversity. This observation forms the basis of the third study of this thesis (McPhee et al., 2016).

4. GEOLOGICAL and PALAEONTOLOGICAL CONTEXT of the DINOSAUR-BEARING STRATA OF SOUTH AFRICA.

4.1. The Elliot Formation

The Elliot Formation is an Upper Triassic ('Lower' Elliot Formation) to Lower Jurassic ('Upper' Elliot Formation) fluvio-lacustrine succession that crops out along the western side of the Lesotho/Free State border, reaching its thickest (350m) in the south near Jamestown in the Eastern Cape. Together with the underlying Molteno and overlying Clarens formations, it forms part of the Stormberg Group and represents the final depositional stages of the Karoo Supergroup – a large foreland basin to the north of the Cape Fold Belt (Catuneanu et al. 1998; Bordy et al. 2004a, b, 2005).

Traditionally, the lower part of the Elliot Formation was thought to be transitional with that of the underlying Molteno Formation, with the lowermost deposits of the Elliot accordingly referred to as the "Passage Beds" (Charig et al., 1965; Cole 1992; Anderson et al. 1998). However, more recent investigation into the contact between the Molteno and lower Elliot formations suggests that the boundary is non-conformable, possibly relating to a minor loading event in the proximal Cape Fold Belt (Bordy et al., 2005). Although some lithological distinctiveness had long been recognised between various "Red-bed" outcrops throughout the basin (Haughton, 1924), a formalized (bio)stratigraphic subdivision was only introduced by Kitching and Raath in 1984, based primarily on differential faunal compositions between the lower and upper sections of the formation. Thus, the lower Elliot "*Euskelosaurus* Range Zone" was delimited primarily with respect to the presence of large-bodied 'prosauropod' remains,

whereas the middle and upper Elliot "*Massospondylus* Range Zone" is characterised by an abundance of small-bodied *Massospondylus* remains (although see below).

A detailed lithostratigraphic framework was later introduced by Bordy and colleagues (2004a,b; 2005). Citing a marked textural contrast between the lower and upper Elliot Formation, Bordy et al. (2004a: 399) formalised a new arrangement in which Kitching and Raath's "Middle" unit was subsumed into the upper unit; the reorganised lower (LEF) and upper (UEF) Elliot Formation therefore correlating with the '*Euskelosaurus*' and *Massospondylus* Range Zones of Kitching and Raath (1984), respectively. With respect to lithology, the LEF is characterised at its base by olive-grey to bluish silt/mudstones regularly interbedded with cream-coloured sandstones. Thick purplish mudstone units upwards of ~30m thick are found above this, incised by equally thick sandstones with geometries evincing multi-storey, asymmetrical channel-fills. The depositional environment of the LEF is thus characterised as one of perennial meandering river systems with extensive floodplains and overbank areas, evincing a humid to semi-arid climate dominated by riparian forests and inhabited by large bodied animals (Bordy et al. 2004a, 2005, 2006). The LEF, while upwards of 300m thick at its thickest point in the south of the basin, thins dramatically within the northern section of the formation, potentially related to a strengthening of the underlying lithosphere wherein it parallels the southern edge of the Kaapvaal Craton (Bordy et al., 2004a). LEF outcrops are accordingly relatively restricted in the north.

There appears to have been a depositional hiatus of upwards of several million years between the LEF and the UEF due to the final orogenic loading of the Cape Fold Belt (Bordy et al., 2004a). During this time the area embodied by the Elliot Formation became elevated and erosion took place. Once sedimentation resumed it was within a markedly different fluvial environment, characterised by mostly tabular, multi-storey sheet sandstones appreciably thinner than those of the underlying LEF. The lack of significant down-cutting and extensive

pedogenic modification of the UEF mudstones suggest an ephemeral, flash flood-dominated fluvial system whereby lower rates of subsidence enabled more significant pedogenic alterations of the floodplain areas (Bordy et al., 2004b). This is consistent with the the progressive aridification of the Stormberg sequence generally, with aeolian influences becoming increasingly dominant and culminating in the overlying dune systems of the Clarens Formation. In contrast to the relatively heterogeneous olive-grey through purple sediments diagnostic of the LEF, UEF mudstones are primarily a uniform brick-red in general colouring.

Due to the lack of absolute age determinations, dating of the Elliot Formation has generally relied on faunal correlations with other "Liassic" deposits elsewhere. Hence, the assemblage of large 'prosauropods', cynodonts, putative 'rauisuchians', and ichnofossils from LEF are generally held to best correlate with Norian (or potentially Rhaetian) deposits elsewhere in the world (e.g. the Los Colorados Formation, Argentina; Trossingen Formation, Germany) (e.g., Lucas and Hancox, 2001; Knoll, 2004). In contrast, a rich fauna of gracile 'prosauropods', heterodontosaurid and 'fabrosaurid' basal ornithischian dinosaurs, cynodonts, sphenosuchian crocodylomorphs, basal turtles, and at least two species of theropod dinosaur suggests a Hettangian–Sinemurian age for the UEF based upon faunal congruence with early Jurassic deposits elsewhere (e.g., the Glen Canyon Group of the south-western USA and the Lower Lufeng Formation of China) (Olsen and Galton 1984; Smith and Kitching, 1997; Yates 2005; Butler, 2005). However, a continued lack of absolute dates precludes a reliable constraint on the temporal boundaries of the formation.

4.1.1. *Sauropodomorpha within the Elliot Formation*

The taxonomic composition of the sauropodomorph assemblages of both the lower and upper Elliot Formation are currently in a state of flux.

Yates, in a series of influential studies ([Yates and Kitching, 2003] 2003c; 2007a, b), convincingly showed the LEF to be represented by more than the single waste-basket taxon '*Euskelosaurus*' (van Heerden, 1979; Kitching and Raath, 1984), which is now considered to be a *nomen dubium* (due primarily to a lack of diagnostic character traits in the type specimen and a profusion of conflicting character data within the hypodigm). At the outset of this thesis (2013), and with reference to the taxonomic work of Yates (e.g., 2007b), there was generally held to be five valid sauropodomorph genera within the LEF: *Plateosauravus*, *Eucnemesaurus*, *Melanorosaurus*, *Blikanasaurus*, and *Antetonitrus* (see also McPhee, 2013). However, fieldwork conducted over the past two years has established that the *Antetonitrus* topotypic site is located securely within the UEF (McPhee, Choiniere, and Bordy unpublished data). Furthermore, there is growing concern that one of the major specimens associated with the *Melanorosaurus* hypodigm (NMQR 3314: Yates, 2007a) was also collected from within the UEF. However, formalisation of these recent observations awaits publication of a revised, sauropodomorph-based biostratigraphy of the Elliot Formation.

Of the remaining, unequivocally LEF taxa, *Plateosauravus* is generally regarded as the most basal (Haughton, 1924; Yates, 2003c, 2007a; McPhee et al., 2014, 2015a). Nonetheless, although basal, the incongruous presence of relatively derived features within the type assemblage (i.e., high neural spines in the posterior dorsal vertebrae; relatively elongate humerus) suggests a possibly chimerical grouping. However, given the minimal amount of taphonomic information recorded upon its collection in 1918, confirmation of the validity of

Plateosauravus likely awaits the discovery of additional fossil material. *Eucnemesaurus* (van Hoepen, 1920) was resurrected by Yates (2007b) as the senior synonym of the enigmatic "herrerasaurid" '*Aliwalia rex*' (Galton, 1985). Known primarily from fragmentary material collected from throughout the basin over the past century, *Eucnemesaurus* remains a relatively problematic genus. Although the recent naming of a second species of *Eucnemesaurus* (McPhee et al., 2015a; first study of this thesis) bolsters support for its validity, several points of similarity between the new species and the major LEF "*Melanorosaurus*" assemblage (NMQR 1551: Galton et al., 2005) points to ongoing taxonomic questions. With reference to the above stratigraphic concern, the latter genus is now in serious need of revision and, given the non-association of specific elements within the *Melanorosaurus* syntype (SAM 3449, 3450), may potentially be declared a *nomen dubium* in the future. These issues are given explicit discussion in the first study of this thesis. Known primarily by an articulated epipodium of unprecedented robustness, *Blikanasaurus* (Galton and van Heerden, 1985, 1998) represents a rare morphological departure from the relatively conservative *bauplan* of the LEF taxa mentioned above. Unfortunately, the incompleteness of this intriguing genus precludes further assessment of its skeletal anatomy.

Traditionally regarded as containing a taxonomically depauperate sauropodomorph assemblage restricted to otherwise abundant *Massospondylus* remains (Kitching and Raath, 1984; Barrett, 2009), the UEF is now proving considerably more diverse than previously thought (Barrett, 2000). In addition to the recent discovery of the basal sauropodiform *Aardonyx* (Yates et al., 2010) and the highly gracile, potentially relictual *Arcusaurus* (Yates et al., 2011), the diversity of the UEF is also augmented with the stratigraphic realignment of

Antetonitrus and at least one specimen from within the *Melanorosaurus* hypodigm (NMQR 3314). Added to this, the introduction of *Pulanesaura* (second study of this thesis) underscores the importance of the UEF for contextually framing the early divergence of Sauropoda. A primary upshot of these discoveries is the attendant observation that the desiccated floodplain of the UEF could nonetheless support a wide variety of morphologically disparate forms. The significance of this to the guild structuring and ecological partitioning of Sauropodomorpha within the earliest Jurassic should provide a rich avenue of future investigation.

4.2. The Kirkwood Formation

Although outcrops of the Kirkwood Formation yielded some of the first dinosaur fossils discovered in South Africa (Atherstone, 1857), it is understudied relative to the Elliot Formation. The discovery of *Algoasaurus* (Broom 1904) and subsequent work by Tom Rich, Pat Vickers-Rich, and B. de Klerk and colleagues in the 1990s hinted that a diverse fauna of sauropodomorph dinosaurs inhabited this region in the Early Cretaceous. However, no formal study dedicated to this sauropod material has been presented since the description of several isolated macronarian teeth by Rich et al. in 1983. The recent discovery of several relatively well-preserved sauropod vertebrae provides a much needed opportunity to further our understanding of the sauropod fauna of southern Gondwana during this poorly sampled period (the earliest Cretaceous). A comprehensive background of both the geology and palaeontology of the Kirkwood Formation is given in the third study of this thesis (McPhee et al., 2016).

5. AIMS of the CURRENT THESIS and DECLARATION of PERSONAL CONTRIBUTION

With reference to the brief literature review above, the current thesis aimed to contribute additional information to the following problems:

1) A further exploration of the diversity and taxonomic composition of the lower Elliot Formation. This centres primarily on a newly discovered, partial individual from Cannon Rock Farm near Aliwal North. As articulated individuals (even if highly incomplete) are extraordinarily rare within the LEF, this material provides a much needed point of comparison with previously known, historically collected lower Elliot taxa – many of which remain highly problematic with respect to the diagnostic morphology and monospecificity of their respective hypodigms.
   The description, figures, phylogenetic analysis, and discussion of results was primarily conducted by myself with substantive editorial input from my doctoral supervisor Jonah Choiniere. Pia Viglietti undertook the stratigraphic analysis and Adam Yates (previously of the Bernard Price Institute) originally excavated and oversaw preparation of the specimen.
2) The description and phylogenetic analysis of a new species of basal sauropod from the upper Elliot Formation of Heelbo Farm near Senekal. The early evolutionary history of Sauropoda remains complicated due to a number of factors – not least amongst them a paucity of good fossil material and a lack of consensus as to what constitutes a “true” sauropod. Therefore, this material, in presenting a more apomorphic morphology than any other sauropodomorph material previously collected from the formation, represents a substantive increase in our knowledge of the anatomy of transitional sauropodomorphs. Additionally, it provides valuable

insight into the underlying causative and ecological processes potentially driving the evolution of the derived sauropod bauplan in the earliest Jurassic.

The description, figures, phylogenetic analysis, and discussion of results were primarily conducted by myself with substantive editorial input from my supervisor Jonah Choiniere. Johann Neveling undertook the stratigraphic analysis whereas Adam Yates and Matthew Bonnan originally excavated the material (the latter also contributing contextually to the final product).

3) An in-depth anatomical review of the Sauropod material collected from the Early Cretaceous Kirkwood Formation, accompanied by an investigation of sauropod diversity and fossil occurrences throughout the first three stages of the Cretaceous. The earliest Cretaceous represents a relatively enigmatic period in the study of sauropod evolution, with most material restricted to isolated, fragmentary occurrences in geographically disparate locations. The collection of several highly diagnostic sauropod vertebrae from the Kirkwood Formation therefore represents a dramatic increase in the sampling of this poorly known temporal bracket. The descriptions, figures, taxonomic assignments, and Early Cretaceous literature review were primarily conducted by myself. Philip Mannion provided expert assistance in several issues pertaining to the diversity and anatomy of Early Cretaceous Sauropoda. My supervisor, Jonah Choiniere, again contributed substantive edits to the final document and was a motivating force in my taking-up of the project. The material is the product of two decades' worth of collecting expeditions led by William de Klerk of the Albany Museum.
4) The description and functional investigation of a highly autapomorphic and unprecedentedly robust ilium rediscovered in the collections of the National

Museum, Bloemfontein. As body plan diversity is relatively conservative amongst the majority of sauropodomorph dinosaurs of the lower Elliot Formation of South Africa, this element (hypothesized as coming from the lower Elliot) suggests a much larger range of body plan diversity that previously appreciated. This study was primarily interested in investigating the possible functional correlates of this unique morphology. Although I contributed the majority of the writing, this was a combined effort by myself and my supervisor, Jonah Choiniere.

References for the above sections are located after the Synthesis and Concluding remarks.

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A second species of Eucnemesaurus Van Hoepen, 1920 (Dinosauria, Sauropodomorpha): new information on the diversity and evolution of the sauropodomorph fauna of South Africa's lower Elliot Formation (latest Triassic)

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ARTICLE

A SECOND SPECIES OF *EUCNEMESAURUS* VAN HOEPEN, 1920 (DINOSAURIA, SAUROPODOMORPHA): NEW INFORMATION ON THE DIVERSITY AND EVOLUTION OF THE SAUROPODOMORPH FAUNA OF SOUTH AFRICA'S LOWER ELLIOT FORMATION (LATEST TRIASSIC)

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ABSTRACT—The Late Triassic–Early Jurassic Elliot Formation of South Africa is one of the most important geological formations worldwide for understanding the early evolution of sauropodomorph dinosaurs. However, many of the taxa currently recognized as valid within its lower strata remain either poorly understood, vaguely diagnosed, or both. The recent discovery of an articulated partial skeleton of a single individual of the enigmatic lower Elliot genus *Eucnemesaurus* provides an important opportunity to expand our understanding of the anatomy and phylogeny of this poorly known taxon. A comprehensive investigation of the morphological relationships of this new specimen identified key features, pertaining primarily to the femoral shaft and distal tibia, which distinguish it from the only other previously named species of *Eucnemesaurus—E. fortis*. A new species, *E. entaxonis*, is erected within which to accommodate it. A cladistic analysis confirms the monophyly of *Eucnemesaurus*, as well as its continued inclusion within the low-diversity 'Riojasauridae.' Nonetheless, this result highlights continued uncertainties regarding the constituency of the *Riojasaurus* hypodigm. The relatively robust pedal architecture of *E. entaxonis* suggests an unexpectedly early experiment in a slower, subgraviportal form of locomotion within Late Triassic basal Massopoda, whereas the intriguing mosaic of plesiomorphic and derived characters evident in *E. entaxonis* raises questions regarding the hypothesized population dynamics of the basal-most sauropodomorph taxa of the lower Elliot Formation. This latter concern has particular bearing on newly observed inconsistencies in the prevailing hypodigms of other lower Elliot basal sauropodomorph taxa such as *Melanorosaurus*.

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INTRODUCTION

The morphological and phylogenetic significance of the sauropodomorph dinosaurs of the lower Elliot Formation (hereafter LEF; Norian/Rhaetian) of South Africa has been successively reiterated in recent years (Yates, 2003a, 2007a, 2007b; Yates and Kitching, 2003; Yates et al., 2004, 2010, 2011, 2012; McPhee et al., 2014). This fauna is composed of an anatomically and taxonomically diverse set of animals that ranges from 'primitive' taxa occupying basal positions within Sauropodomorpha to relatively derived forms that share some anatomical features with the specialized bauplan of Sauropoda. The morphological breadth of this community not only furthers our understanding of basal sauropodomorph diversity immediately prior to the end Triassic extinction event, but also is of particular significance in tracking the nature and tempo of the character changes that led to the graviportal quadrupedal gait of the gigantic sauropods.

Although our anatomical and systematic knowledge of these lower Elliot taxa has increased dramatically since the late 20th century (when every large-bodied form tended to be lumped within the catch-all taxon of '*Euskelesaurus browni*' [e.g., Van Heerden, 1979]), many genera currently recognized as valid within the LEF remain very poorly understood. Of these, the most enigmatic is undoubtedly *Eucnemesaurus*. Although recently the subject of an updated diagnosis and description (Yates, 2007a), the only previously recognized species within the genus—*Eucnemesaurus fortis*—is only known from sparse, incomplete material. These remains are restricted to a few isolated vertebrae, a coracoid, a fragmentary pubis, three partial femora, and two tibiae (of which only the proximal surface of one is preserved). Unsurprisingly, the majority of diagnostic traits attributed to *Eucnemesaurus* are exclusive to the femur, rendering the taxonomic validity of this genus tentative at best.

The discovery of a largely complete pelvis, hind limb, and partial vertebral column of a *Eucnemesaurus*-like sauropodomorph (BP/1/6234) from the LEF of the Aliwal North district in the Eastern Cape Province of South Africa provides an opportunity to advance our understanding of this rare and poorly defined taxon. We present and describe this material as belonging to a new species in the genus *Eucnemesaurus*. We analyze the phylogenetic relationships of this new species and examine its implications for basal sauropodomorph evolution, especially in regards

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to the interrelationships of other poorly known LEF genera (i.e., *Plateosauravus, Melanorosaurus*).

Additionally, the phylogenetic position of *Eucnemesaurus* is of particular interest because it represents one of the two genera within the taxonomically depauperate 'Riojasauridae' (Yates, 2007a, 2007b, 2010) and thus suggests a close biogeographic relationship between South Africa and South America during the Late Triassic (Bonaparte, 1971). The additional data afforded by the new *Eucnemesaurus* specimen described here represent an opportunity to more stringently test that phylogenetic relationship and to address questions pertaining to the dispersal and biogeography of basal members of Sauropodomorpha within the Gondwana in the Late Triassic.

History of *Eucnemesaurus*

During the 1860s, Alfred Brown sent several shipments of large sauropodomorph bones collected from the Aliwal region (Eastern Cape) of the lower Elliot Formation to several institutions in Europe. Amongst material that ultimately made its way to the Naturhistorisches Museum in Vienna was a distinctive femur (NMW 1889-XV-39) that Huene (1906; see also Cooper, 1980) allocated to '*Euskelosaurus browni*.' This femur experienced a rather confused taxonomic history for the remainder of the century, being ultimately reclassified as the herrerasaurid theropod *Aliwalia rex* (Galton, 1985) based on the assumed interrelatedness of this bone to a carnivorous archosaurian maxilla that Brown had sent in an earlier shipment to the Natural History Museum in London.

In 2003, a femur (BP/1/6111) that closely resembled that of the Viennese '*Euskelosaurus/Aliwalia*' was found in association with vertebrae clearly diagnostic of Sauropodomorpha, leading Yates (2007a) to conclude that this was not the first time an *Aliwalia*-type femur had been recovered from the lower Elliot alongside material referable to Sauropodomorpha. Specifically, the long-forgotten *Eucnemesaurus fortis* Van Hoepen, 1920, was recognized as displaying a similar morphology and subsequently resurrected from its status as one of the many taxa synonymized with *Euskelosaurus browni* by Van Heerden in 1979. Based on the revised understanding of the *Eucnemesaurus* hypodigm afforded by this new material, Yates (2007a) also erected the novel taxon Riojasauridae as a low-diversity (*Eucnemesaurus* + *Riojasaurus*), pan-Gondwanan clade at the base of Massopoda (the history of *Eucnemesaurus fortis* and its associated material is covered in greater detail in Yates, 2007a). The new specimen (BP/1/6234) that we hereby ascribe to *E. entaxonis* was not included in Yates' (2007a) resurrection of *Eucnemesaurus* (due to being both incompletely prepared and excavated at the time).

Institutional Abbreviations—**BPI**, Evolutionary Studies institute, Johannesburg, South Africa (formerly Bernard Price Institute); **GPIT**, Institute for Geosciences, Eberhard-Karls-Universität Tübingen, Tübingen, Germany (Formerly Geologisch-Paläontologisches Institut Tübingen); **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; **MB.R.**, Museum für Naturkunde–Leibniz-Institut für Evolutions und Biodiversitätsforschung an der Humboldt-Universität zu Berlin; **NM QR**, National Museum, Bloemfontein, South Africa; **PULR**, Museo de Ciencias Naturales, Universidad Nacional de La Rioja, La Rioja, Argentina; **PVL**, Paleontología de Vertebrados, Instituto 'Miguel Lillo,' San Miguel de Tucumán, Argentina; **SAM-PK**, Iziko-South African Museum, Cape Town, South Africa; **SMNS**, Staatliches Museum fur Naturkunde Stuttgart, Stuttgart, Germany; **TM**, Ditsong Museum of Natural History, Pretoria, South Africa (previously Transvaal Museum).

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1888
SAUROPODOMORPHA Huene, 1932
MASSOPODA Yates, 2007a
'RIOJASAURIDAE' Yates, 2007a
EUCNEMESAURUS Van Hoepen, 1920

Diagnosis—Yates (2007a) included a diagnosis for both the Riojasauridae and *E. fortis* that centered almost exclusively on features of the femur. Although the issues surrounding the diagnostic validity of *Riojasaurus* are discussed below, many of these features remain relevant to the generic diagnosis of *Eucnemesaurus*. These include: presence of a large posterior proximal tubercle on the femoral head (although the phylogenetic expression of this character has recently come in doubt; see below); proximally abrupt lesser trochanter that is taller than its basal width; fourth trochanter rounded in profile and obliquely oriented so that the proximal half is more medially set than the distal half.

EUCNEMESAURUS ENTAXONIS, sp. nov.

Holotype—BP/1/6234, the articulated remains of most of the hindquarters of a medium-sized sauropodomorph dinosaur. It consists of an articulated vertebral column composed of the posterior-most dorsal vertebrae, sacral vertebrae, and the anterior portion of the tail; partial right ilium; partial pubic apron; left ischium; right femur and fragments of the left; distal epipodium (crus); and almost complete right pes (Fig. 1).

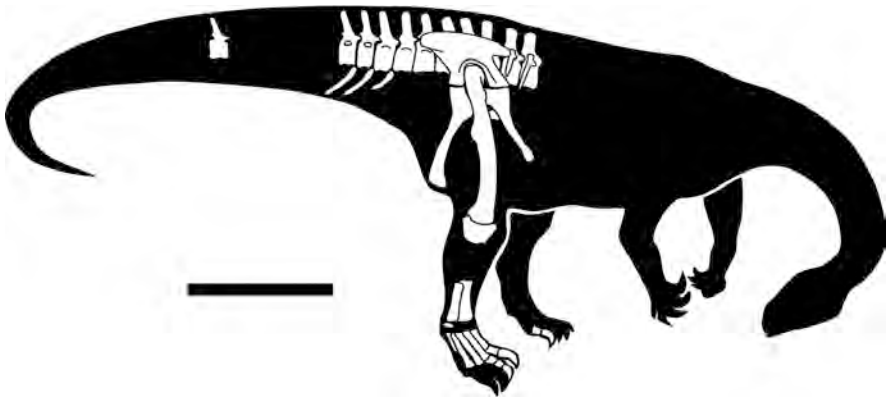


FIGURE 1. Reconstruction of *Eucnemesaurus entaxonis*. Illustrated bones are those preserved in the holotype BP/1/6234. Scale bar equals 50 cm.

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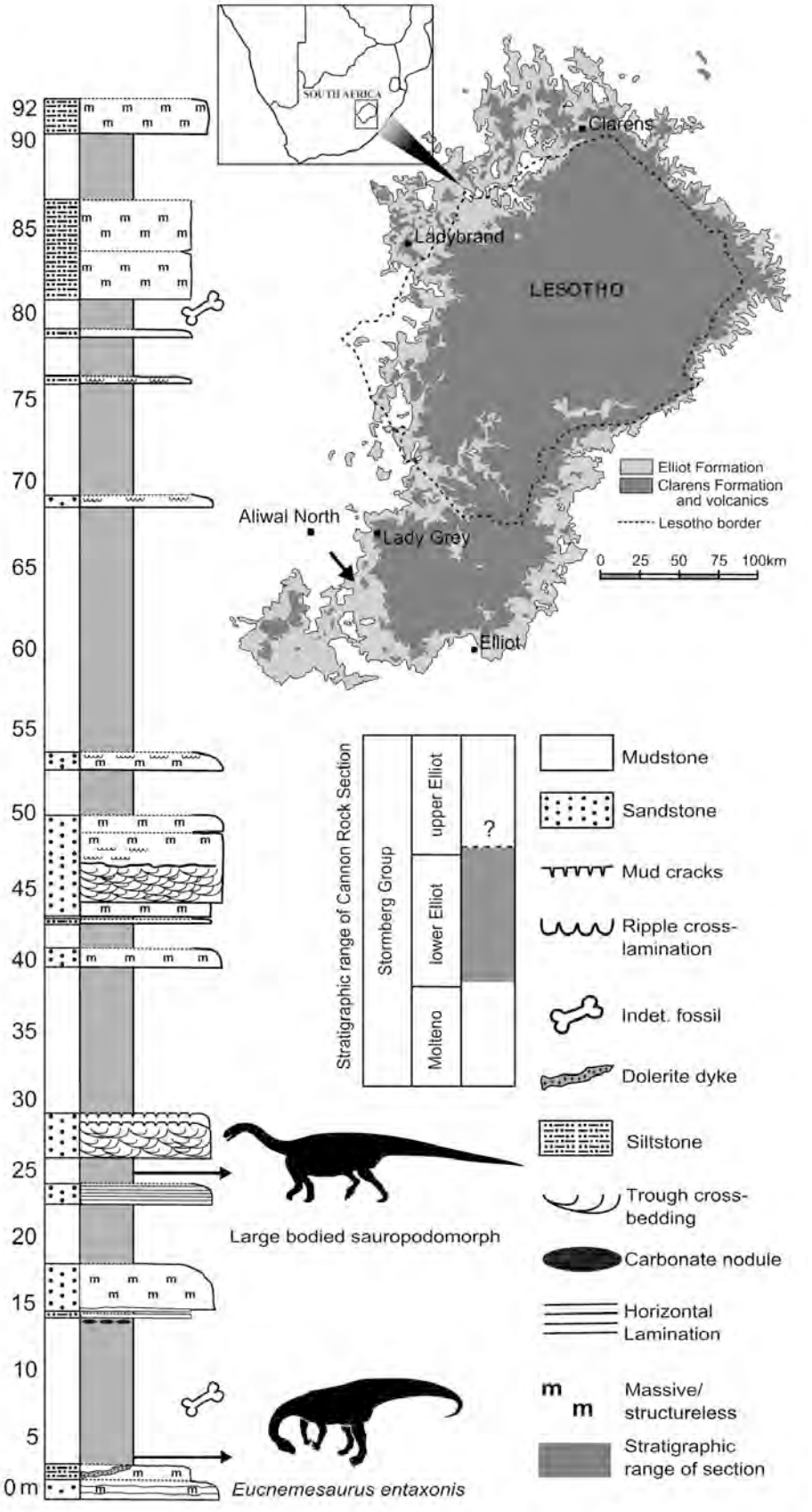


FIGURE 2. Stratigraphic section of the Cannon Rock site. Arrow on map indicates excavation site of BP/1/6234. The large-bodied sauropodomorph is of indeterminate taxonomy and cataloged within the ESI collections as BP/1/7408. The section spans most of lower Elliot and may include the basal-most rocks of the upper Elliot Formation.

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Locality and Horizon—The material was unearthed in 2003 during a survey of Elliot rocks on Cannon Rock Farm (owned by Piet Prinsloo) in the Aliwal North area of the Eastern Cape Province, Republic of South Africa (RSA). The specimen was found in grayish-brown mudstone (Munsell color 5YR 3/2) immediately above a thin crevasse-splay sandstone approximately 10–15 m above the Elliot-Molteno contact at the base of the lower Elliot Formation (Fig. 2). The Elliot Formation, along with the underlying Molteno and overlying Clarens formations, forms part of the Stormberg group, the youngest depositional sequence of the Karoo Supergroup (Catuneanu et al., 1998). Currently considered mid-Norian to Rhaetian in age (Olsen and Galton, 1984; Lucas and Hancox, 2001; Bordy et al., 2005; Irmis, 2010; McPhee et al., 2014), the lower Elliot can be distinguished from the Early Jurassic upper Elliot by its thicker, more laterally persistent mudstone intervals, considerably thicker sandstone bodies, and comparative lack of pedogenic artifacts. These geometries are characteristic of a palaeoenvironment dominated by perennial meandering river systems with extensive floodplains and overbank areas, evincing a humid to semiarid climate dominated by riparian forests that were able to support large-bodied animals (Anderson et al., 1998; Bordy et al., 2004, 2006).

Preservation—Many of the periosteal bone surfaces throughout the assemblage appear to have experienced decay prior to fossilization, and temerarious preparation has in some rare instances erroneously removed cortical bone. Preservational issues stemming from these caveats will be addressed when applicable throughout the following description.

Diagnosis—Two potential autapomorphies diagnose *E. entaxonis*: a deep brevis fossa with relatively thin lateral and medial walls on the ventral surface of the postacetabular process of the ilium (a pronounced brevis fossa is also present in the holotype of *Riojasaurus*, but this can be distinguished from *E. entaxonis* with respect to its expansive mediolateral width and considerably thicker medial and lateral margins); and a sharp ventral keel on the centra of the proximal caudal vertebrae (although this region is poorly preserved).

In addition to these features, *E. entaxonis* can be further diagnosed with respect to a unique suite of local autapomorphies (given its current position within our phylogeny): a small, circular pit ('non-articulating gap') that excavates the sacral rib of the first primordial sacral at midheight (present also in *Melanorosaurus*); femoral shaft beneath the fourth trochanter transversely elliptical in cross-section (present in taxa from *Melanorosaurus* crownwards); posterior descending process of the distal tibia does not extend as far laterally as the anterior ascending process, rendering the latter visible in posterior view (present in *Aardonyx* crownwards; convergently acquired in *Anchisaurus*); and a semi-stout pes in which the maximum proximal breadth of the first metatarsal is approximately 0.6 times its proximodistal length (present in several derived basal sauropodiform taxa).

E. entaxonis differs from *E. fortis* in the following features: (1) *E. fortis* presents a femur that is subcircular in cross-section rather than elliptical, and (2) the holotype of *E. fortis* (TM 119) displays a distal tibia in which the mediolaterally extensive posterior surface extends as far laterally as the anterior ascending process (for articulation with the astragalus). It is possible that the distal embayment present on the fourth trochanter in *E. fortis* is absent in *E. entaxonis*, but poor preservation in the latter taxon precludes confirmation of this. Furthermore, a dorsal neural arch of *E. fortis* possesses a unique accessory lamina within the centrodiapophyseal fossa—a feature that cannot be confirmed in the preserved material of *E. entaxonis*. This feature therefore remains a valid diagnostic character of *E. fortis* for the time being.

Etymology—The novel species name alludes to the surprisingly robust foot architecture of this species. An entaxonic pes (or manus) is one in which the medial digits bear the main weight-resisting forces and are thus the most developed—a trait later developed in the extreme within Sauropoda (see e.g., Carrano, 2005).

Preparation Methods—Exposed in situ bone was consolidated using a dilute solution of Paraloid B-72 in acetone solvent. Once consolidated, the specimen was excavated using hand tools, including rock hammers, chisels, and shovels. It was removed from the ground in several major blocks containing the sacrum and vertebral column, the distal epipodium, and the pes, respectively. These were protected during removal by a layer of newspaper dampened in water, followed by jackets composed of layers of burlap and plaster of Paris. Rock matrix was removed from the specimen in the laboratory primarily with handheld pneumatic air scribes. Fossilized bone was consolidated using an approximately 10% solution of Paraloid B-72 solid-grade thermoplastic acrylic resin (Rohm and Haas Company, 2007) in 100% acetone solvent. Individual pieces of bone (e.g., neural spines of proximal vertebrae) were glued together using either cyanoacrylate (various brands) or a highly concentrated (~30%) solution of Paraloid B-72 in 100% acetone solvent (remainder of specimen).

PHYLOGENETIC METHODS

The data matrix for this analysis was drawn from the data matrix originally introduced by Yates (2007b) and subsequently employed (with various alterations) by a number of other sauropodomorph workers (Smith and Pol, 2007; Ezcurra, 2010; Yates et al., 2010; Apaldetti et al., 2011; Otero and Pol, 2013; Martínez et al., 2012; McPhee et al., 2014). It was further modified in the current study via the alteration of several preexisting characters and the addition of two novel ones (see below). The phylogenetic matrix, comprising 53 taxa and 362 characters, was analyzed with TNT 1.1 (Goloboff et al., 2008) using a heuristic search of 1000 replicates of Wagner trees followed by TBR branch swapping with 10 trees saved per replication. Characters were equally weighted. The following 40 multistate characters were treated as ordered: 8, 13, 19, 23, 40, 57, 69, 92, 102, 117, 121, 131, 144, 147, 149, 150, 157, 162, 167, 170, 177, 205, 207, 222, 227, 234, 242, 251, 254, 267, 280, 301, 307, 315, 335, 348, 351, 353, 358, 362. Additional analyses were performed on the data set in order to assess the robustness of the position of *Eucnemesaurus* and other related taxa. These included implied weighting, constraint analyses, and, in the case of *Riojasaurus*, the a priori removal of a taxon.

The novel character additions are as follows:

Character 180: 'Deep, medially directed pit excavating the surface of the non-articulating gap of the first primordial sacral rib: absent (0); present (1).' This addition is intended to capture a morphology that has now been observed in both *Eucnemesaurus* and *Melanorosaurus*.

Character 335: 'Size of first metatarsal: maximum proximal breadth less than 0.4 times its proximodistal length (0); maximum proximal breadth between 0.4 and 0.7 times its proximodistal length (1); maximum proximal breadth greater than 0.7 times its proximodistal length (2).' There is a crownward tendency within Sauropodomorpha towards a more robust, stout foot architecture in which the transverse width of the first metatarsal increases relative to its proximodistal length (curiously reversed in the basal sauropod genera *Vulcanodon* and *Tazoudasaurus*), a trend that has not been adequately expressed in previous matrices.

Four preexisting characters were altered in order to more fully capture our improved understanding of sauropodomorph evolution and variation. The character 'pneumatic excavation of the dorsal neural arches' (char. 162; Yates, 2007b) was altered to more clearly express the varied nature of invasive pneumaticity

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within both basal and derived sauropodomorphs (see Yates et al., 2012). An additional state was added to the character 'shape of the proximal articular surface of the tibia' (char. 307 [Yates, 2007b:char. 305]) in order to homologize a subset of this ratio feature and better differentiate between the considerable variation of the archosaur proximal tibia, which ranges from being as transversely wide as it is anteroposteriorly long to over twice as anteroposteriorly long as it is wide. An additional state was added to the character 'projection of ventral flange on proximal surface of second metatarsal' (char. 341 [Smith and Pol, 2007:char. 354]). As originally defined, this character only codified for the presence of a laterally directed flange on the ventral surface of the proximal metatarsal II—a feature seen almost exclusively in massospondylids. The additional character state is intended to homologize a ventromedial flange that is significantly more developed than the ventrolateral flange, as is observed in other basal sauropodomorph taxa. Finally, an additional state was added to 'length of the ungual of pedal digit one' (char. 353 [Yates, 2007b:char. 344]). The relative length of this element varies widely across Sauropodomorpha, from shorter than some non-terminal phalanges (e.g., *Anchisaurus*), to longer than the first metatarsal (e.g., *Blikanasaurus*). The additional state homologizes this latter morphology in a range of taxa. See Supplementary Data for the full list of character descriptions and their respective states.

DESCRIPTION OF *EUCNEMESAURUS ENTAXONIS*

Sources of comparative information employed throughout the description are referenced in Table 1. See Table 2 for selected measurements of BP/1/6234.

Axial Skeleton—The axial skeleton of *E. entaxonis* is represented by an articulated series of vertebrae consisting of the two posterior-most dorsal vertebrae (probably D13 and D14), a dorsosacral, two primordial sacrals, and the first five anterior caudal vertebrae (Figs. 3 and 4). An additional, isolated, more posterior caudal (from approximately the middle of the caudal series) is also present. The proximal ends of the ribs associated with the posterior dorsals are preserved in close proximity to the diapophyses on the left side of each vertebra. The distal ends have been displaced ventrally, approximating the lateral side of their respective centra.

Dorsal Vertebrae—Although relatively complete, some aspects of the anatomy of the dorsal vertebrae are obscured due to a combination of postmortem deterioration and the articulated manner of preservation. This applies especially to the morphology of the articular facets of the zygapophyses, the proportions of the hyposphene, and the morphology of the anterior and posterior faces of the neural arches generally.

The amphicoelous centra of the two posterior-most dorsals are both subequal in their relative dorsoventral height and anteroposterior length, the plesiomorphic morphology for non-sauropodan Sauropodomorpha with the exception of the Massospondylidae, which tend to have dorsal centra that are longer than they are tall (Apaldetti et al., 2013). The transverse width of the anterior and posterior articular surfaces is approximately 0.68 times their dorsoventral height, a metric also typical of most basal sauropodomorphs, especially in dorsals of the posterior series (Apaldetti et al., 2013). Although the internal structure of the centra cannot be discerned, it is clear from the absence of any pleurocoelous fossae or foramina on the lateral side of the elements that they are acamerate.

TABLE 1. Sources of comparative data used in this study.

Taxon	Source(s)
Saturnalia tupiniquim	Langer, 2003
Panphagia protos	Martínez and Alcober, 2009
Thecodontosaurus antiquus	Benton et al., 2000
Pantydraco caducus	Yates, 2003b
Plateosauravus cullingworthi	SAM-PK 3341–3356, 3602–3603, 3607–3609
Plateosaurus engelhardti	Huene, 1926; Yates, 2003c; Mallison, 2010a, 2010b
Eucnemesaurus fortis	BP/1/6107, 6110–6115, 6220; TM 119
Riojasaurus incertus	PVL 3808; Bonaparte, 1971
Leonerasaurus taquetrensis	Pol et al., 2011
Massospondylus carinatus	BP/1/4377, 4693, 4924, 4934, 4998, 5000, 5241; Cooper, 1981
Coloradisaurus brevis	PVL 5904 (field no. 6); Apaldetti et al., 2013
Lufengosaurus hueni	Young, 1941
Adeopapposaurus mognai	Martínez, 2009
Glacialisaurus hammeri	Smith and Pol, 2007
Yunnanosaurus huangi	Young, 1942
Jingshanosaurus xinwaensis	Zhang and Yang, 1994
Mussaurus patagonicus	Otero and Pol, 2013
Aardonyx celestae	BP/1/386; various elements cataloged BP/1/5379–6893
Anchisaurus polyzelus	Galton, 1976; Yates, 2004, 2010
Melanorosaurus readi	NM QR1551, 3314; SAM 3449, 3450, 3532
Blikanasaurus cromptoni	SAM-PK 403
Lessemsaurus sauropoides	PVL 4822; Pol and Powell, 2007
Antetonitrus ingenipes	BP/1/4952a, b, c
Vulcanodon karibaensis	Cooper, 1984
Tazoudasaurus naimi	Allain and Aquesbi, 2008

TABLE 2. Selected measurements of BP/1/6234.

Dorsal vertebra ?13	
Dorsoventral height of centrum	~ 95
Transverse width of centrum (may be taphonomically compressed)	~ 68
Anteroposterior length of centrum	~ 91
Anteroposterior length of base of neural spine	~ 65
Dorsoventral height of neural spine	~ 76
Total height of vertebra	230
Dorsosacral vertebra	
Length of base of neural spine	~ 48
Height of neural spine	~ 96
First primordial sacral vertebra	
Length of base of neural spine	~ 69
Height of neural spine	~ 100
Second primordial sacral vertebra	
Length of base of neural spine	77
Height of neural spine	106
First caudal vertebra	
Height of centrum	~ 100
Width of centrum (may be taphonomically compressed)	~ 80
Length of centrum	~ 75
Ischium	
Total length	~ 400
Dorsoventral depth distal end	115
Transverse width distal end	75
Femur	
Total length	535
Transverse width femoral shaft	86
Anteroposterior depth femoral shaft	64
Tibia	
Transverse with distal tibia	117
Anteroposterior depth medial side distal tibia	70
Anteroposterior depth lateral side distal tibia	~ 45
Pes	
Maximum proximal breadth metatarsal 1	60
Total length metatarsal 1	92
Proximal dorsoventral depth metatarsal 2	73
Total length metatarsal 2	149
Transverse width of midshaft metatarsal 2	37
Total length of metatarsal 3	~ 170
Transverse width of proximal surface of metatarsal 5	36
Total length metatarsal 5	74

All measurements in mm.

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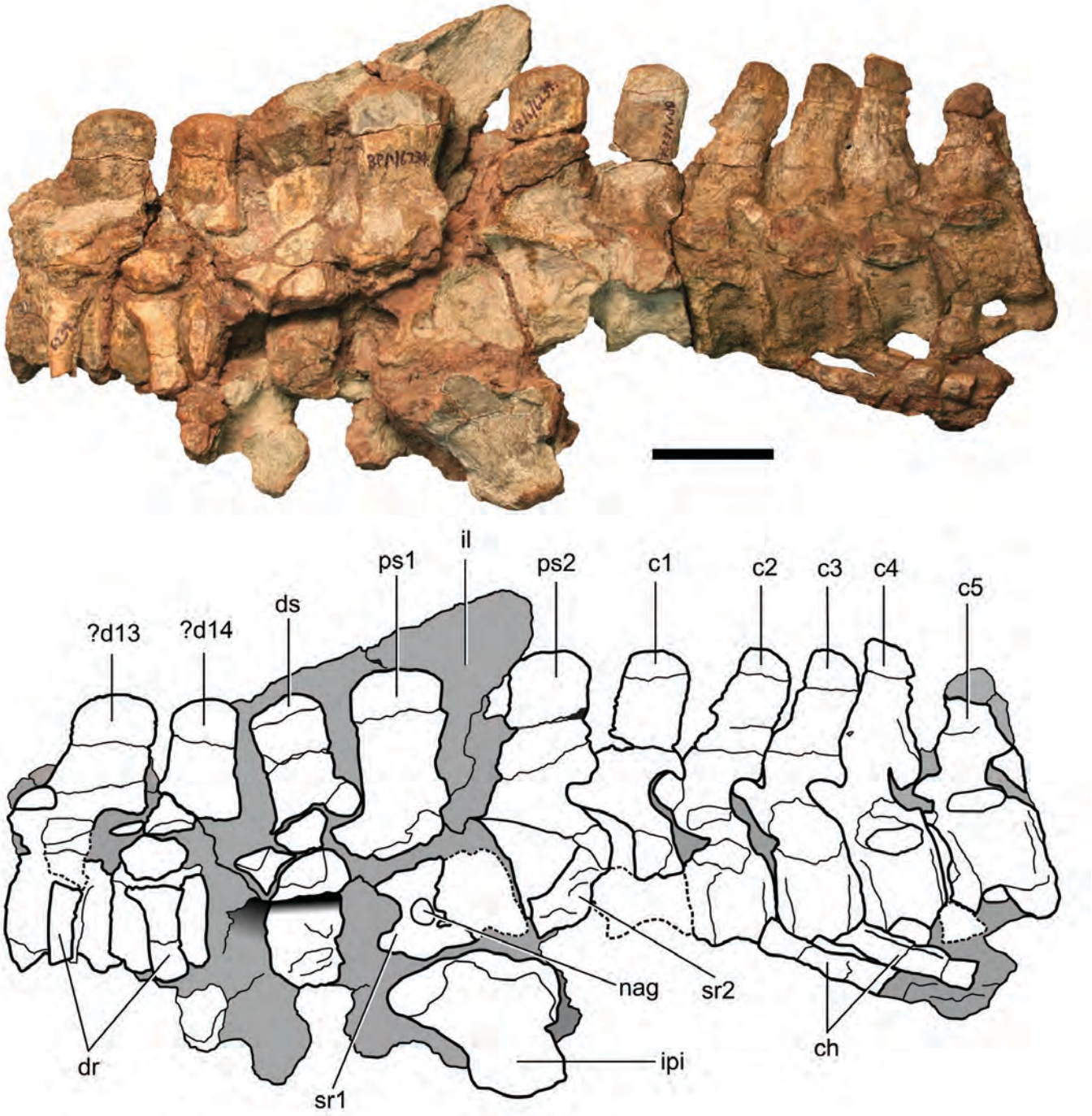


FIGURE 3. Axial column and pelvic elements of *Eucnemesaurus entaxonis* (BP/1/6234) in left lateral view. **Abbreviations: c1**, first caudal vertebra; **c2**, second caudal vertebra; **c3**, third caudal vertebra; **c4**, fourth caudal vertebra; **c5**, fifth caudal vertebra; **ch**, chevron; **?d13**, probable thirteenth dorsal vertebra; **?d14**, probable fourteenth dorsal vertebra; **dr**, dorsal rib; **ds**, dorsosacral vertebra; **il**, right ilium; **ipi**, left ischial peduncle of the ilium; **nag**, non-articulating gap; **ps1**, first primordial sacral vertebra; **ps2**, second primordial sacral vertebra; **sr1**, first sacral rib; **sr2**, second sacral rib. Dashed lines represent uncertainty in natural bone surface. Scale bar equals 10 cm.

The dorsal neural spines of *E. entaxonis* are mediolaterally thin, lacking the transverse dorsal expansion seen in the derived sauropodiform taxa *Antetonitrus* (BP/1/4952) and *Lessemsaurus* (Pol and Powell, 2007). The spines are directed primarily dorsally, and whereas the anterior margin displays a subtle anteroventral inclination, the posterior margin is essentially dorsoventrally straight in lateral view. This distinguishes *E. entaxonis* from a number of basal sauropodomorph taxa that possess dorsal neural spines with a concave posterior margin in lateral view and a projecting posterodorsal corner (e.g., *Riojasaurus*; *Plateosaurus engelhardti* [see Yates, 2003a]). The posterior dorsal neural spines are approximately as long at the base (measured anteroposteriorly) as they are dorsoventrally tall. This contrasts with the dorsal neural spines of the slightly more derived

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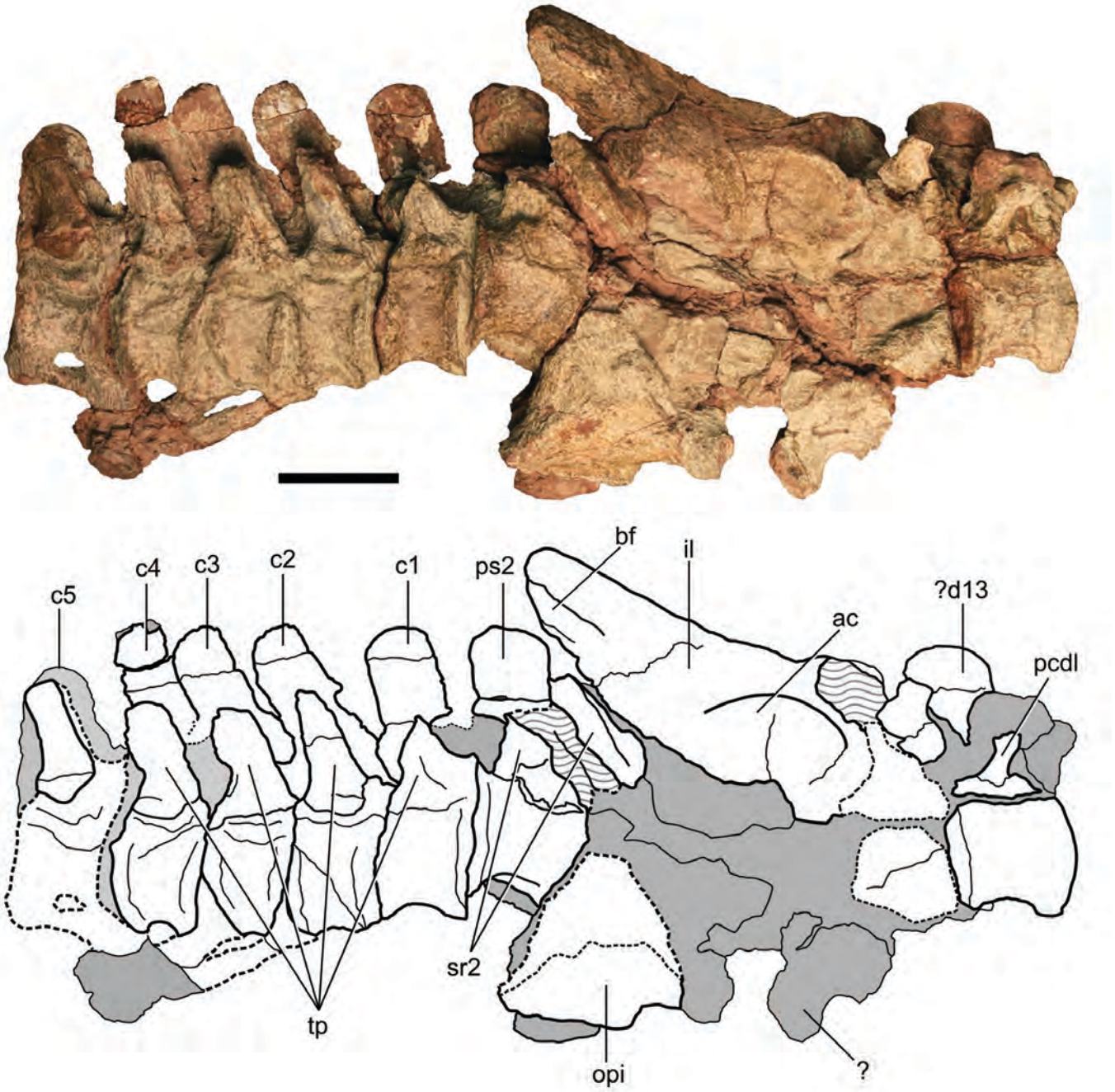


FIGURE 4. Axial column and pelvic elements of *Eucnemesaurus entaxonis* (BP/1/6234) in right lateral view. **Abbreviations: ac**, acetabulum; **bf**, brevis fossa; **c1**, first caudal vertebra; **c2**, second caudal vertebra; **c3**, third caudal vertebra; **c4**, fourth caudal vertebra; **c5**, fifth caudal vertebra; **ch**, chevron; **?d13**, probable 13th dorsal vertebra; **il**, right ilium; **opi**, right ischium obturator plate; **pcdl**, posterior centrodiapophyseal lamina; **ps2**, second primordial sacral vertebra; **sr2**, second sacral rib; **tp**, transverse process. Dashed lines represent uncertainty in natural bone surface. Wavy lines represent exposed, internal bone. Scale bar equals 10 cm.

Melanorosaurus, which exhibits a neural spine base/height ratio of just under 1.5 (Galton et al., 2005; seen also in NM QR3314). However, it is still higher than in other basal sauropodomorph taxa such as *Riojasaurus, Massospondylus*, and the unnamed prosauropod from the LEF (BP/1/4953; see Yates, 2003a), which tend to have dorsal neural spines that are longer at the base than dorsoventrally tall. Poor preservation means that it cannot be confirmed if *E. entaxonis* possesses the incipient keel on the anterior margin of the neural spines observed in the posterior dorsals of *Antetonitrus* and some specimens of *Plateosauravus* (van Heerden, 1979).

The main body of the posterior dorsal neural arches of *E. entaxonis* lacks the pronounced anteroposterior constriction seen in *Aardonyx, Antetonitrus*, and more derived taxa. The pre- and postzygapophyses are preserved in articulation with one another, which obscures many of their morphological attributes.

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The anterior-most projection of the prezygapophyses appears to have been relatively flush with the level of the anterior margin of the centrum in both posterior dorsals. As is typical of sauropodomorph posterior dorsal vertebrae, the parapophyses are not located on the centrum and are presumed to be located directly ventrally to the diapophyses, although this is obscured by the close proximity of the dorsal ribs. The diapophyses of the left side of both vertebrae are poorly preserved but clearly visible slightly below the level of the zygapophyses. The right side of the anterior-most preserved dorsal vertebra bears a centro-infradiapophyseal fossa, which is bounded posteriorly by the posterior centrodiapophyseal lamina, although both have been displaced ventrally during preservation (Wilson, 1999; Yates et al., 2012). A middle dorsal vertebra of the holotype of *E. fortis* was described as possessing a small accessory lamina that branched off of the paradiapophyseal lamina, partially dividing the centro-infradiapophyseal fossa (Yates, 2007a). This was treated as a diagnostic feature of *E. fortis* (another accessory lamina located within the posterior infradiapophyseal fossa was later reinterpreted as the external margin of a putatively pneumatic subfossa; Yates et al., 2012). Unfortunately, the level of preservation, along with the adherent orientation of the dorsal ribs, precludes confirmation of a similar structure in *E. entaxonis*.

The neural canal is low and subcircular in cross-section, and the flanking pedicles are low. In *Aardonyx* and more derived sauropodomorphs, the neural canals are more slot-like in cross-section and are generally accompanied by a concomitant increase of the distance between the diapophyses and the base of the arch. Overall, the neural arches of *E. entaxonis* are approximately 1.4 times the height of their accompanying centra. This ratio approaches the condition observed in *Melanorosaurus* but falls radically short of the ratio displayed by *Antetonitrus*, which has neural arches that are over twice as tall as the associated dorsal centra. Most other sauropodomorph taxa (including *Riojasaurus*) have dorsal neural arches that are roughly subequal to the height of their centra. Two posterior dorsal vertebrae located amongst the *Plateosauravus* assemblage (SAM-PK-3607) are remarkable for displaying neural arches that are approximately 1.57 times the height of their centra. This is a relatively high metric for basal Sauropodomorpha and suggests either the convergent acquisition of a derived vertebral morphology in a taxon for which the majority of remaining character information is rather plesiomorphic, or the presence of more than one taxon within that assemblage (see Yates, 2003a).

The morphology of the head of the ribs (capitulum and tuberculum) cannot be discerned because of their close articulation with the dorsal vertebrae. The shaft of these posterior elements is flat and dorsoventrally compressed, being considerably wider than high. It appears that none of the dorsal vertebrae of *E. entaxonis* were ribless, as has been suggested for the posterior-most dorsals of some taxa (e.g., *Plateosaurus* [Huene, 1926]; Yates, 2007b).

Sacral Vertebrae—Portions of a dorsosacral and two primordial sacral vertebrae are preserved. Although the dorsosacral is missing its centrum and portions of the neural arch (the former is possibly represented as an amorphous block of spongy bone), the position of the dorsosacral in relation to the adherent right ilium argues strongly for its participation in the sacrum. Thus, *E. entaxonis* likely presents the 'typical' basal sauropodomorph arrangement of a dorsosacral plus two primordial sacrals (Pol et al., 2011). The two more posterior sacral vertebrae are relatively more complete, preserving the general morphology of their respective sacral ribs.

The neural spines of the sacral series are markedly taller than the neural spines of the dorsal series, as generally occurs at the dorsosacral transition in sauropodomorph dinosaurs. The height of the dorsosacral neural spine of *E. entaxonis* is approximately 1.60 times the anteroposterior length of its base. Ventral to the neural spine the prezygapophyses can be seen in tight articulation with the postzygapophyses of the posterior-most dorsal, but the deterioration of the transverse process and sacral rib has erased all information pertaining to the remainder of the neural arch and centrum.

Most of the lateral components of the sacral ribs of the first primordial vertebra have been eroded away, and only the base is well preserved. The base extends dorsoventrally as an hourglass-shaped (in lateral view) plateau that is bordered both anteriorly and posteriorly by deep concavities. The anterior concavity is clearly a natural feature of the skeleton, but the posterior concavity may have been produced by over-preparation. This suggests that, when complete, the sacral rib would have housed an anteroposteriorly expanded dorsal process (= transverse process) that likely roofed the intercostal cavity both anteriorly and posteriorly, as seen in a number of basal sauropodomorph taxa (e.g., *Riojasaurus*; *Leonerasaurus*).

A deep circular pit is positioned directly at midheight of this plateau, dividing it into dorsal and ventral halves. A distinct rim of bone bordering this pit suggests that this feature is real, and that it is thus probably homologous to the 'non-articulating gap' observed by Yates (2007a) in referred specimens of *Melanorosaurus* (NM QR1551 and NM QR3314). Although a great many sauropodomorph taxa (e.g., *Riojasaurus*; Yates, 2007b) display some form of intercostal fenestra (sensu Wilson, 2011) between the dorsal and ventral sections of the first primordial sacral rib, this medially directed excavation of the rib itself appears to be a much rarer occurrence (see Discussion below).

Presaging the condition of the neural spines of the caudal series, the neural spine of the second primordial sacral vertebra is more posteriorly inclined than the first, as seen in most non-sauropodan sauropodomorphs (e.g., *Plateosaurus* [Huene, 1926]; *Lufengosaurus*; *Melanorosaurus* [NM QR1551]). The neural arch of this element appears to have been better preserved than in the two anterior sacrals, and although either temerarious preparation or poor preservation has removed the majority of the cortical bone surface, the general morphology nonetheless remains clearly distinguishable. The most distinctive feature of the second primordial neural arch is the strong posterolateral projection of the transverse processes, a geometry seen in the final non-caudal sacral of most basal sauropodomorphs (e.g., *Lufengosaurus, Melanorosaurus, Plateosaurus*). This process partially roofs the same deep, expansive concavity that borders the posterior margin of the first primordial sacral rib. Although most sauropodomorph genera present a large intercostal aperture in the region between the two primordial sacral ribs, it is possible that this aperture in BP/1/6234 has been artificially exaggerated due to poor preservation. The intercostal concavity is bordered ventrally by the second primordial sacral rib, which rises posterodorsally at an oblique angle towards the transverse process, with which it is fused. This 'en echelon' morphology of the second primordial sacral rib is common to basal Sauropodomorpha, also being seen in forms such as *Riojasaurus, Lufengosaurus*, and *Yunnanosaurus*. The dorsal displacement of the ilium has exposed the right sacral rib of the second primordial sacral vertebra, although this same displacement has removed the articulation of the latter with the medial surface of the former. Nonetheless, general agreement in contours between the lateral articular surface of the rib and the posteroventral corner of the ilium suggests that the rib articulated along most of the ventral extent of the postacetabular process (Fig. 4). This would have left only a minimal amount of space in which to accommodate a potential caudosacral rib—an arrangement that we consider unlikely (see below).

Caudal Vertebrae—The first five caudals are present as an articulated series. The anterior-most caudal is in poor condition and most of its cortical surface is missing. The remaining four caudals appear to retain the majority of their cortical bone surface.

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The shallowly amphicoelous centrum of the second anterior caudal vertebra is approximately 1.4 times dorsoventrally taller than wide at the anterior articular facet. It is also taller than it is anteroposteriorly long, with a height/length ratio of approximately 1.6. These ratios are fairly typical for anterior-most caudals in basal Sauropodomorpha, although the mediolateral constriction of the centra is comparatively high. Although it is possible that this is an effect of taphonomic distortion, a mid-anterior caudal from the Spioenkop *Eucnemesaurus* (BP/1/6220; Yates, 2007a) displays a similar height/width ratio of 1.3. The ventral surface of the centra of C2, C3, and C4 (surface not preserved in C1) is sharply delineated into an acute median ridge. Although taphonomic compression cannot be ruled out, if natural, this keel would appear to be the opposite condition of certain derived sauropodomorphs (e.g., *Melanorosaurus* [SAM-PK-3449]; *Vulcanodon*) that exhibit a ventral furrow on the underside of the anterior centra (Yates, 2004). This feature represents a possible autapomorphy of *E. entaxonis*.

The mediolaterally thin neural spines of C1, C2, C3, and C4 are high and posterodorsally sloped, with their posterior projection far exceeding the level of the posterior margin of the centrum. A sharp keel is visible along the anterior margin of the neural spines, but it is possible that this is an artefact of mediolateral compression during diagenesis. If it is indeed present, this would be homologous with the same feature observed in BP/1/6220 (Yates, 2007a).

The neural arches occupy the great majority of the dorsal surface of their respective centra, with the prezygapophyses projecting slightly anterior to the anterior margin of the centrum. However, as with the dorsal and sacral series, the finer details of the zygapophyses of the caudal vertebrae are obscured due to being in articulation with one another. The manner of preservation of the transverse processes in the holotype of *E. entaxonis* is curious. On the left side of C2 and C3, the transverse processes have been displaced ventrally and compressed to the neurocentral suture in such a fashion as to superficially resemble parapophyses (recalling Hatcher's [1903] suggestion that the transverse processes of anterior caudal vertebrae are composed of the coalesced diapophyses and parapophyses; see Wilson, 2011). In the anterior-most caudal vertebra, this same compaction gives the transverse process the appearance of having possibly contacted the ilium as a caudosacral rib. However, on the right side of C1, the transverse process can be seen as a dorsally flattened arm that, in life, most likely exhibited the laterally flared, tapered morphology typical of caudal transverse processes. This dorsally oriented dislocation of the transverse processes is repeated throughout the right side of the preserved caudal series and gives the transverse processes the appearance of not having been fully fused to the neural arch at death. Because the transverse processes of the caudal vertebrae of practically all vertebrates ossify as a single unit with the neural arch, this peculiar arrangement is interpreted here as simply representing a unique breakage pattern.

The fifth caudal in the series most closely resembles the element referred to *Eucnemesaurus* and figured and described in Yates' previous study (2007a; BP/1/6220). Besides sharing a general equivalence in proportions, these elements both have an enlarged chevron facet on the posteroventral corner of the centrum that hangs well below the level of the anteroventral corner of the centrum. Based on observed morphology, it is also possible that, as in BP/1/6220, C5 in *E. entaxonis* exhibited the same shallow, paramedian fossae and associate flanking ridges either side of the base of the anterior margin of the neural spine. However, poor preservation renders this difficult to quantify. It is also possible that this morphology became more prevalent in posterior elements, and because it appears that the Spioenkop *Eucnemesaurus* was a relatively larger individual than *E. entaxonis* (based on the comparative sizes of the distal femora), BP/1/6220 likely derives from a more posterior position in the series—likely ~C6–C8.

Chevrons are present between all the preserved caudal vertebrae with the exception C1–C2. This is consistent with all known basal sauropodomorphs (at least those for which the anterior tail is complete) with the exception of *Plateosaurus*, which, due to the anterior-most caudal vertebra being incorporated into the sacral unit as a caudosacral, possesses a true chevron (i.e., not just a lenticular oval intercentrum between the first and second caudal vertebrae; Huene, 1926; Galton, 1999; Martínez, 2009). The chevrons are preserved articulated to their respective centra, and although obscured distally by adherent matrix, it is clear that they displayed the proximodistally elongate, transversely compressed morphology typical to all basal Sauropodomorpha.

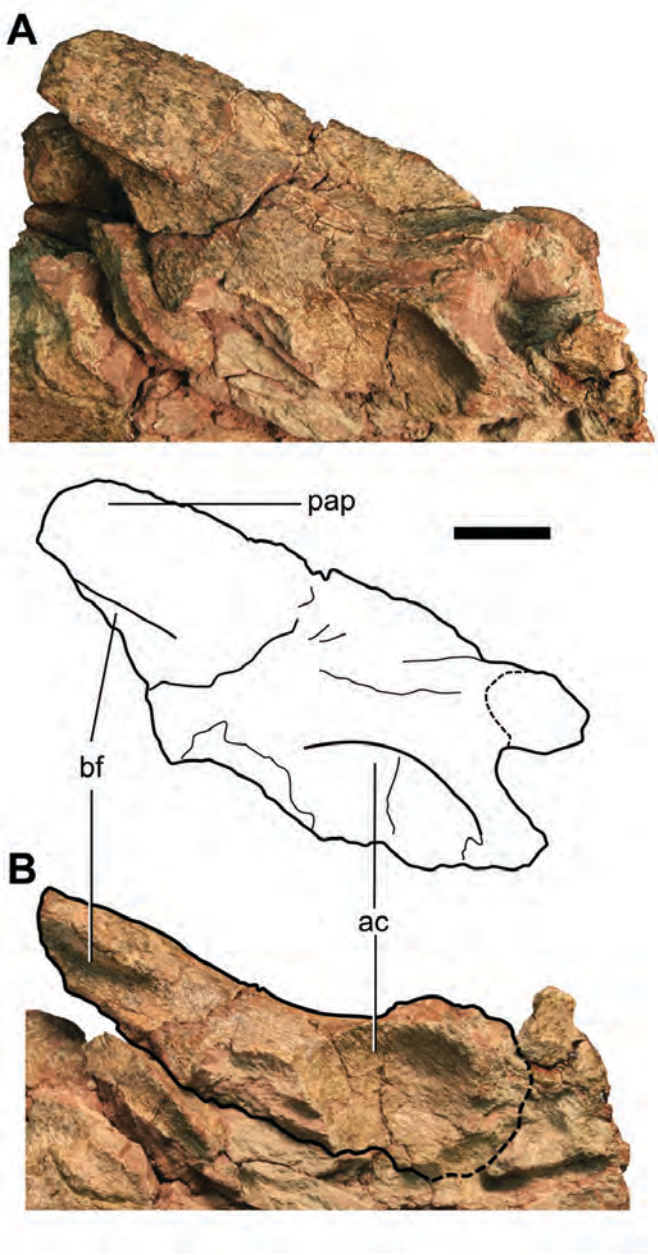


FIGURE 5. Detail of right ilium of *Eucnemesaurus entaxonis* (BP/1/6234) in **A**, lateral view and **B**, ventral view. **Abbreviations: ac**, acetabulum; **bf**, brevis fossa; **pap**, postacetabular process. Scale bar equals 5 cm.

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Ilium—The main body of the right ilium, although preserved in semi-articulation with the first and second primordial sacral vertebrae, has been dislocated dorsally and thus sits at an oblique angle above these elements (Figs. 4, 5). The anterior portion of the preacetabular process and both the pubic and ischial peduncles of the right ilium are missing. Only small portions of the left ilium are preserved—the isolated pubic peduncle was located amongst loose material accessioned under BP/1/6234, and the ischial peduncle is adhered to the opposite side of the block to the right ilium (albeit in a much more ventral position; Fig. 3). Unfortunately, the medial surface of the ilium is too poorly preserved to distinguish sacral attachment scars or other related morphologies.

The ilium of *E. entaxonis* is dorsoventrally low with a straight, non-convex dorsal margin, as in the majority of basal sauropodomorphs. It is possible that the anterior portion of the dorsal margin may have displayed a distinct 'step' similar to that seen in *Riojasaurus* and some specimens of *Massospondylus*; however, its incompleteness makes this difficult to confirm.

Dorsal to the acetabular region the lateral surface of the iliac blade is deeply concave, typical of the condition in most non-sauropodan sauropodomorphs. The posterior margin of the anteroposteriorly elongate postacetabular process is semicircular in lateral view. This contrasts with the morphology of forms such as *Plateosauravus* (SAM-PK-3609) and *Plateosaurus* (Huene, 1926) where the postacetabular process is posteriorly squared in lateral view and bears a sharp posteroventral corner. A subtle protuberance can be discerned in the center of the lateral surface of the postacetabular process, likely related to the origin point of the flexor tibialis musculature (Carrano and Hutchinson, 2002; Langer, 2003).

Perhaps the most notable aspect of the ilium in *E. entaxonis* is the deep, strongly emarginated brevis fossa that extends along the ventral surface of the postacetabular process for the entirety of its length. The lateral wall of this fossa (homologous to the 'brevis shelf'; e.g., Novas, 1996; Martínez et al., 2012) appears to have been more strongly developed than the medial, and at its tallest point measures approximately 2 cm from its ventral margin to the base of the fossa. The morphology of the brevis fossa in *E. entaxonis* differs from the same structure in the holotype of Riojasaurus (PVL 3808), which, although of proportionally similar dorsoventral depth, is mediolaterally expanded to an almost autapomorphic extent for sauropodomorph dinosaurs (see Discussion).

The acetabulum is laterally expanded with a well-developed supracetabular crest along its anterior margin. As in a number of basal sauropodomorphs, this crest (based on the morphology of the dislocated left pubic peduncle) appears to have extended anteriorly along the posterolateral margin of the pubic peduncle until a point just short of its ventral termination. The pubic peduncle is ovoid to teardrop-shaped in cross-section. As in *Coloradisaurus* (Apaldetti et al., 2013), it is possible that a mediolaterally narrow flange of bone may have been present on the posteromedial margin of this peduncle, although the possibility remains that this is simply a product of taphonomic excavation of the posterior surface.

The ischial peduncle is dorsoventrally extensive, as is plesiomorphic for Sauropodomorpha. Although its distal end is poorly preserved, it appears to lack the distinct posteroventral 'heel' seen in forms such as *Plateosauravus* (SAM-PK-2609) and *Plateosaurus*.

Pubis—A poorly preserved proximal portion (the iliac peduncle) of one pubis and scrappy sections of the pubic apron of both pubic blades were recovered with the specimen (Fig. 6). Although poorly preserved, the pubic blades clearly show that *E. entaxonis* retained the mediolaterally wide, transversely oriented apron typical of all non-eusauropodan sauropodomorphs. The lateral margins of the pubic apron appear to have been relatively straight in anterior or posterior views, lacking the concavity present in *Massospondylus* (BP/1/4924) and *Mussaurus* (Apaldetti et al., 2013; Otero and Pol, 2013).

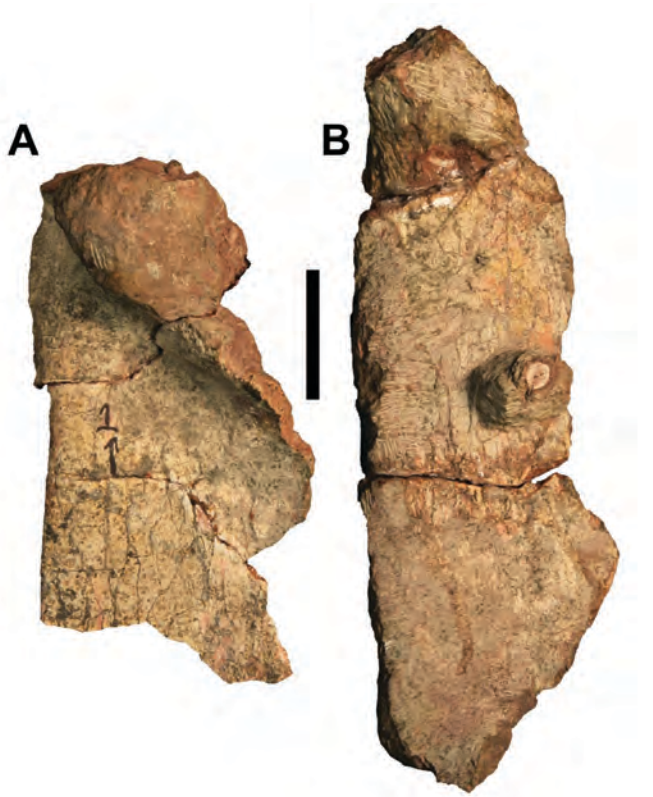


FIGURE 6. Isolated fragments of the pubic apron of *Eucnemesaurus entaxonis* (BP/1/6234). **A**, proximal portion of left pubis in ventral view; **B**, section of the pubic blade of the ?right pubis in dorsal view. Scale bar equals 5 cm.

Ischium—The left ischium is relatively complete except for part of the proximal end (= obturator plate), which, aside from missing most of its proximal articular processes, has also experienced the complete loss of cortical bone (Fig. 7). However, the head of the right ischium is preserved adhered to the main sacral block (Fig. 4).

Although generally better preserved than the same region of the left ischium, the pubic and iliac peduncles of the right proximal end are poorly preserved and the acetabular margin is merely hinted at. Nonetheless, the preserved morphology of the ventral margin of the obturator plate suggests that the distal end was smoothly confluent with respect to the proximal ischial shaft, therefore lacking the distinct notch that ventrally separates the two primary ischial bodies seen in *Plateosaurus* and *Riojasaurus* (Yates, 2003c; Apaldetti et al., 2013; Otero and Pol, 2013). As in the majority of non-eusauropodan sauropodomorphs, the shaft is subtriangular in cross-section with a broad and flat medial symphysis and an acutely convex lateral margin (becoming more obtuse towards the distal end). In contrast, derived members of Sauropoda develop flattened, blade-like ischial shafts that are transversely wider than dorsoventrally deep throughout their length (observed also in *Anchisaurus*; Yates, 2004). An irregular sulcus excavates the dorsal surface of the proximal third of the ischial shaft. This is interpreted as the remains of the proximal ischial groove that is present in the majority of saurischian dinosaurs (Langer and Benton, 2006; Otero and Pol, 2013).

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FIGURE 7. Left ischium of *Eucnemesaurus entaxonis* (BP/1/6234) in lateral view. **Abbreviations: de**, distal expansion; **ip**, iliac peduncle. Scale bar equals 5 cm.

Immediately distal to its connection with the obturator plate the dorsoventral depth of the proximal ischial shaft is approximately 0.74 times its mediolateral width. This value increases throughout the proximodistal length of the shaft, with the dorsoventral height of the subovoid distal end being ultimately 1.4 times its transverse width. However, a number of basal taxa (e.g., *Plateosaurus*; *Massospondylus*) display proportionately narrower distal ischial shafts in which the dorsoventral depth is over twice the mediolateral width.

This expansion of the ischial shaft appears to be conducted primarily along the ventral surface. This imparts a subtle, ventrally oriented deflection to the distal end of the shaft and thus a concave ventral margin of the shaft when viewed laterally. A similar ventral deflection can be seen in the ischia of *Coloradisaurus* (Apaldetti et al., 2013). In contrast, other basal sauropodomorph taxa (e.g., *Massospondylus* [BP/1/4693]; *Mussaurus*) tend to exhibit ischial shafts with a dorsally expanded distal end and thus a concave dorsal margin in lateral view. The dorsal margin of the distal end extends further distally than the ventral—similar to that of a number of basal sauropodomorph forms (e.g., *Plateosaurus*; *Coloradisaurus*; *Massospondylus*).

Femur—A nearly complete right femur and fragments of the left femur (notably including the fourth trochanter) are preserved (Figs. 8, 9). Because femora are known from the holotype of *E. fortis* (TM 119), as well as the referred *E. fortis* specimens NMW 1889-XV-39 and BP/I/6111, this element represents our best means of assessing the degree to which BP/I/6234 can be confidently integrated within the *Eucnemesaurus* hypodigm.

The preservation of the femoral head in *E. entaxonis* is curious, being either heavily eroded or strongly anteroposteriorly compressed (or both). An accreted nodule (possibly left as a preparatory 'control') is adhered to the anterolateral corner of the femoral head. Because this sedimentary mass bears no marked textural difference to the anterior 'surface' of the head, it is likely that this portion of the femur decomposed prior to fossilization. The posterior surface of the femoral head is slightly better preserved, showing some periosteal bone surface. There is a small, posteriorly directed bulge (in either posterior or proximal view) located towards the middle of the head, roughly congruent with the medial margin of the femoral shaft (Fig. 9A). This corresponds to the 'posterior tubercle' of Yates (2007a), a feature that was posited as representing "a reversal to the non-dinosaurian condition" (Yates, 2007a:94; see Discussion below).

Given the poor preservation of the femoral head, it cannot be said with confidence if *E. entaxonis* displayed the same mediolaterally elongate morphology described for specimens of *E. fortis* (Yates, 2007a). Additionally, the sharp mediodistal edge of the femoral head—where the ligaments of the caput femoris would have inserted—appears to be composed primarily of matrix, meaning that caution should be used before attributing to *E. entaxonis* the opposite condition to the rounded, indistinct mediodistal corner of the femoral head seen in *E. fortis* (e.g., BP/1/6111).

Distal to the femoral head there is a ca. 40 mm section of the anterior shaft missing, although the proximal portion of the lesser trochanter is well preserved. The lesser trochanter rises abruptly from the anterior surface of the femoral shaft from a position lateral to the midline, with its proximal termination distal to the distal edge of the femoral head. Both of these features are congruent with *E. fortis*. Additionally, as in *E. fortis* (BP/1/6111), the lateral surface of the lesser trochanter in *E. entaxonis* is considerably deeper (i.e., more anteroposteriorly extensive) than the medial surface (Fig. 9B). It is probable that the trochanter as a whole was much higher than mediolaterally wide, a feature consistent with Yates' (2007a) diagnosis of the Riojasauridae. In contrast, many other basal sauropodomorphs exhibit a lesser trochanter in which the proximal end is more gradually sloped towards the femoral shaft and the main body of the process is wider than it is tall (e.g., *Plateosauravus* [SAM-PK-3602, 3603]; *Aardonyx* [BP/1/6510]; *Melanorosaurus* [SAM-PK-3450]). However, this latter morphology is often observed primarily in the distal half of the trochanter, a section that is poorly preserved in the lesser trochanter of *E. entaxonis*. A small yet distinct notch is located at the proximal-most tip of the lesser trochanter and may be homologous to the trio of small, rounded spurs mentioned by Yates (2007a) in BP/1/6111, although the possibility remains that this is merely an artefact of preservation.

All of the fourth trochanter of the right femur is preserved, but it is slightly eroded and its finer anatomical details are hard to make out. An isolated section of the left femoral shaft presents a very well preserved fourth trochanter (Fig. 9C, D) of equal proportions, and we base our description largely on that element.

Consistent with the primitive sauropodomorph condition, the fourth trochanter in *E. entaxonis* is located almost entirely within the proximal half of the femoral shaft. Its proximal end is positioned on the medial margin of the femoral shaft, whereupon it extends distolaterally so that the distal end terminates slightly medial to the midline of the posterior surface of the shaft. This is accompanied by a slight curvature of the long axis of the fourth

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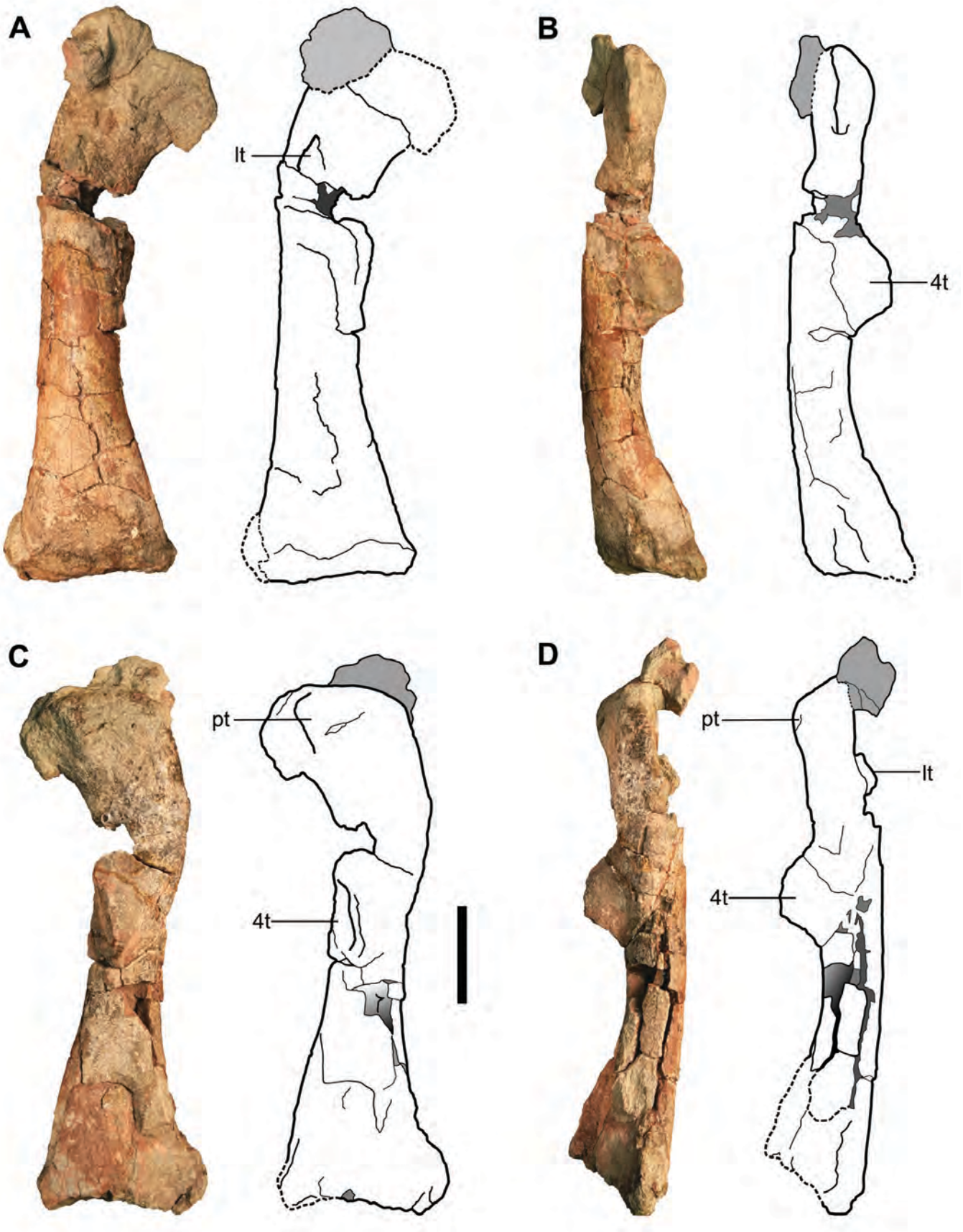


FIGURE 8. Right femur of *Eucnemesaurus entaxonis* (BP/1/6234) in **A**, anterior view; **B**, medial view; **C**, posterior view; and **D**, lateral view. **Abbreviations: 4t**, fourth trochanter; **lt**, lesser trochanter; **pt**, posterior tubercle. Dashed lines represent uncertainty in natural bone surface. Scale bar equals 10 cm.

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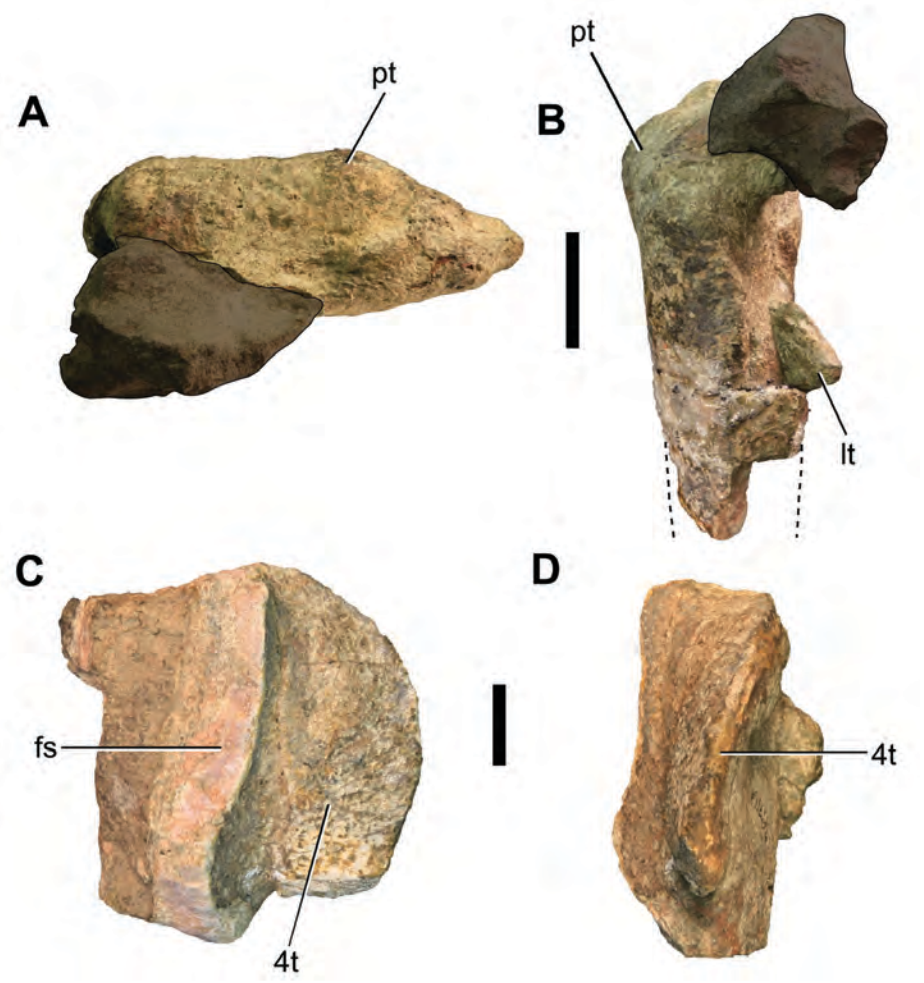


FIGURE 9. Details of diagnostic features of the femur of *Eucnemesaurus entaxonis* (BP/1/6234). Proximal portion of right femur in **A**, proximal view and **B**, posterior view. Isolated fourth trochanter of left femur in **C**, posterolateral view and **D**, medial view. **Abbreviations: 4t**, fourth trochanter; **fs**, femoral shaft; **lt**, lesser trochanter; **pt**, posterior tubercle. Scale bars equal 5 cm (**A** and **B**) and 2 cm (**C** and **D**).

trochanter such that the proximal half is oriented more obliquely than the distal half, whereas the latter is set subparallel to the proximodistal axis of the femoral shaft. Both the oblique orientation of the fourth trochanter and the curvature of its long axis are thus considered diagnostic of *Eucnemesaurus* at the genus level. The profile of the fourth trochanter of the right femur is obscured on account of its outer margin having been eroded; however, the dislocated fourth trochanter of the fragmentary left element clearly displays (when viewed anteriorly) the *Eucnemesaurus*-like rounded profile that distinguishes this taxon from other basal sauropodomorphs, which display a more rectangular-shaped fourth trochanter. Unfortunately, preservation is insufficient to determine if *E. entaxonis* displayed the same distinctly notched, pendant-shaped distal termination of the fourth trochanter to that seen in BP/1/6111.

Distal to the fourth trochanter the anteroposterior depth of the femoral shaft is approximately 0.75 times its mediolateral width. This degree of transverse eccentricity approaches the condition of derived taxa such as *Melanorosaurus* and *Antetonitrus*. In contrast, the well preserved femoral midshaft of a specimen of *E. fortis* (BP/1/6111) displays a depth/width ratio of 0.89, almost identical to that of *Plateosauravus* (SAM-PK-3602). Although repairs to the midshaft of the femur are evident due to the presence of large quantities of glue (potentially resulting in a superficially heightened degree of eccentricity), well-preserved sections of femoral shaft adjacent to the repaired section strongly suggest that the midshaft was moderately eccentric in cross-section, and that this morphology is therefore more variable amongst non-sauropodan sauropodomorphs than previously appreciated.

The posterior components of the distal femoral condyles are not preserved, and although they appear to have been mediolaterally extensive, this is likely an exaggeration due to anteroposterior crushing during diagenesis. The attachments for the extensor musculature can be seen in the very shallow depression positioned centrally on the distal end of the anterior surface of the femur.

Tibia—The tibia of *E. entaxonis* is incompletely represented. The distal end of the right tibia is preserved in articulation with distal limb elements (Fig. 10). A partial proximal end is preserved, but because the anterior portion is missing (including the cnemial crest), it is impossible to say with confidence whether it is of the right or left side. However, one side of the proximal surface is expanded in such a manner that it roofs a shallow depression on the proximal surface of the shaft. It is possible that this morphology is consistent with the large fibular condyle observed in the tibia of TM 119, suggesting that the preserved element in *E. entaxonis* is of the left side. As in the corresponding element in the holotype of *E. fortis*, this condyle is centrally located and does not extend to the posterior margin of the proximal surface. The posterior expansion of the posterior margin of the proximal surface is consistent with a number of derived non-sauropodan sauropodomorphs (*Melanorosaurus*; *Antetonitrus*), whereas basal forms such as *Saturnalia* and *Panphagia* (but also seen in

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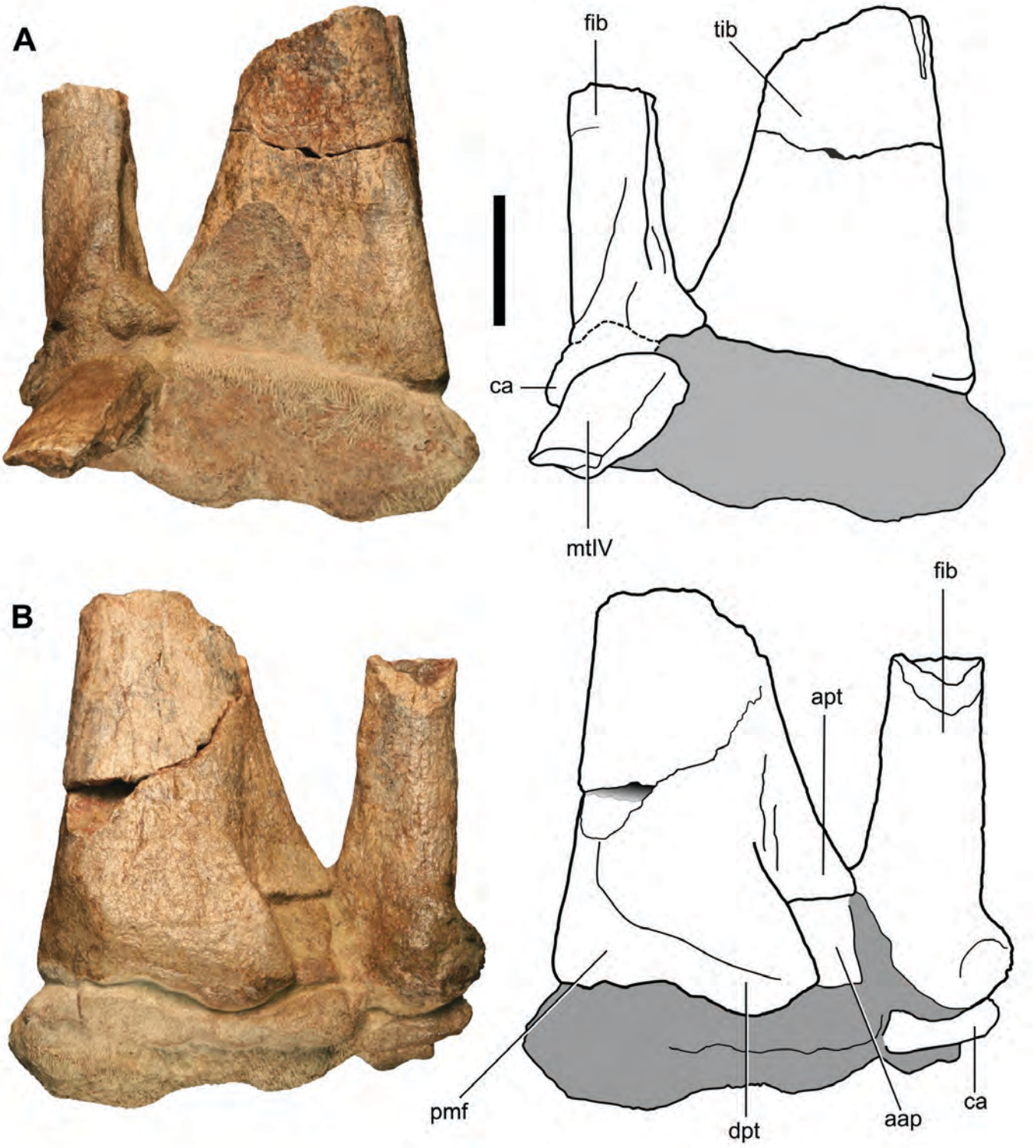


FIGURE 10. Right distal epipodium of *Eucnemesaurus entaxonis* (BP/1/6234) in **A**, anterior view and **B**, posterior view. **Abbreviations: aap**, astragalar ascending process; **apt**, ascending process of the distal tibia; **ca**, calcaneum; **dpt**, descending process of the distal tibia; **fib**, fibula; **pmf**, posteromedial facet of the distal tibia; **tib**, tibia. Gray represents matrix/eroded bone. Scale bar equals 5 cm.

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some large-bodied forms such as *Plateosaurus* and *Coloradisaurus*) tend to have posteriorly flattened, subquadrangular posterior margins.

The distal end of the right tibia, including about 15 cm of its distal shaft and a similar amount of the distal shaft of the adjacent fibula, is preserved in articulation with the astragalus distally and the distal end of the right fibula laterally. The anterior half of an additional 13 cm of the right tibial shaft remains embedded in a block of matrix and articulates precisely with the other preserved tibial material. The shaft is strongly elliptical, being wider mediolaterally than anteroposteriorly. Accordingly, the transverse width of the distal articular surface far exceeds its anteroposterior depth, with the anteroposterior depth of the medial margin exceeding that of the lateral margin, as is primitive for basal Sauropodomorpha. *E. entaxonis* also lacks the anterolateral deflection of the anterior ascending process (= facet for articulation with the astragalus), which, in some derived basal sauropodomorphs (e.g., *Antetonitrus*; *Melanorosaurus* [SAM-PK-3449]), produces a subtriangular distal articular surface of the tibia in which the depths of the medial and lateral margins are rendered relatively subequal.

Nonetheless, the lateral margin of the distal end of the tibia in *E. entaxonis* is notable insofar as the anterior ascending process extends further laterally than the posterior descending process, rendering the former clearly visible in posterior view. This differs from the plesiomorphic condition for Sauropodomorpha, in which the descending process is laterally expanded beyond the level of the anterior ascending process and the anterior ascending process is not visible in posterior view. The condition observed in *E. entaxonis* is, in fact, more similar to the derived condition seen in *Anchisaurus, Aardonyx, Melanorosaurus, Antetonitrus*, and Sauropoda (e.g., Yates and Kitching, 2003; Yates, 2004). This morphology also distinguishes *E. entaxonis* from TM 119 (*E. fortis*), which preserves a mediolaterally expansive posterodistal end in which the ascending and descending distal processes are essentially level with each other (Van Hoepen, 1920; Yates, 2007a:fig. 1). Although the relationship of the distal to the proximal end of the bone is unknown in BP/1/6234, and it is possible that the reduced lateral expansion of the descending process may have been taphonomically exaggerated by an abstruse angle of preservation, the possibility remains that this feature has a more varied distribution than previously recognized within basal nodes of Sauropodomorpha—and possibly even within individual genera. A further distinguishing feature between *E. fortis* and *E. entaxonis* can be seen in the facets that divide the distal edge of the posterior surfaces of the tibia: in *E. fortis* this surface is divided into two broad, subequal facets that are separated by a subtle, centrally located ridge, whereas in *E. entaxonis* this same ridge is located medially, resulting in a considerably reduced medial facet and a greatly expanded lateral one (Fig. 10).

The lateral margin of the descending process is straight, lacking the beveled morphology seen in the distal tibiae of the '*Plateosauravus*' assemblage (SAM-PK-3341, 3349). As in most non-sauropodan sauropodomorphs, the anteromedial corner of the distal end is acute. The morphology of the distal articular surface is obscured because the tibia is in articulation to the main body of the astragalus.

Fibula—The distal fibula is a morphologically simple element that in cross-section has a subcircular shaft and an anteroposteriorly expanded distal end (Fig. 10). There is a distinct swelling evident on the posterodistal corner of the bone, and this connects to a ridge that runs dorsomedially along the anterior face of the shaft about 15 mm from the distal end. However, these latter two features are interpreted as either taphonomic or diagenetic artifacts.

Astragalus—Although the astragalus was clearly articulated with the epipodium at death, most of its cortical bone has not been preserved, with only the ascending process visible beneath the ascending process of the tibia (= facet for reception of the ascending process of the astragalus) (Fig. 10). Given that the ascending process occupies an anterior position upon the astragalus in sauropodomorph dinosaurs, the absence of any bone posterior to this process in *E. entaxonis* is illustrative of the amount of diagenetic attrition experienced by this element. The ascending process appears to have been transversely flat in posterior view, lacking the posterolateral concavity seen in a number of sauropodomorph taxa (e.g., *Coloradisaurus*; '*Aardonyx*' [BP/1/386]).

Calcaneum—The calcaneum is unremarkable for basal Sauropodomorpha, being subtriangular in ventral view with a tapered medial margin. The lateral surface is twice as long as it is tall. Mild pitting in the form of two shallow fossae can be seen on the lateral surface; however, it is difficult to substantiate the degree of taphonomic exaggeration present in this feature.

Pes—An almost complete and articulated right foot is preserved (Fig. 11). However, although each digit can be readily distinguished, it is clear that some of the bones have experienced the same distorting process evident in other parts of the skeleton of *E. entaxonis*, resulting in the 'withered' appearance of pedal digits III and IV.

Metatarsal I (mt I) is a relatively short element. Its widest proximal breadth (measured obliquely from the ventromedial to the dorsolateral corner of the proximal articular surface) is 0.61–0.62 times its total proximodistal length. Although this is an unexpectedly low ratio (e.g., Yates, 2008) for a basal sauropodomorph, it is nonetheless appreciably more gracile than the first metatarsals of the comparably derived lower Elliot taxa *Blikanasaurus* and *Antetonitrus*, which display an mt I proximal-width/length ratio of 0.89 and 0.77, respectively. Other non-sauropodan sauropodomorphs (in particular the Massospondylidae) tend to display considerably more gracile dimensions (e.g., *Massospondylus*: 0.38 [BP/1/5241]; *Lufengosaurus*: 0.39 [Young, 1941]; *Mussaurus*: 0.41 [Otero and Pol, 2013]; *Plateosaurus*: 0.46 [SMNS 13200, GPIT1]).

Interestingly, *Riojasaurus* (PVL 3526) possesses a relatively elongate mt I with a proximal-breadth/length ratio of approximately 0.45, and Yates (2008) records the equivalent metric in *Melanorosaurus* (NM QR1551) as 0.58, comparable in length to *E. entaxonis*. However, the referred, fully articulated skeleton of *Melanorosaurus* (MN QR 3314; Yates, 2007b) presents a first metatarsal proximal-breadth/length ratio of approximately 0.80 (B.W.M., pers. observ.) (character conflict in the *Melanorosaurus* hypodigm is discussed in greater detail in Discussion).

As in most non-sauropodan sauropodomorphs, the subovoid proximal articular surface of mt I in *E. entaxonis* is twisted dorsolaterally with respect to the transverse axis of the distal condyles, resulting in acute dorsal and ventral margins when approximating a 'living' orientation. The proximal surface is also orthogonal to the main axis of the shaft, differing from more derived, graviportal forms (e.g., *Antetonitrus* + Sauropoda) that tend to exhibit an anteriorly sloping proximal surface of the first metatarsal that is obliquely oriented with respect to the proximodistal axis of the bone. As in most basal sauropodomorphs, the proximal end of the first metatarsal is volumetrically smaller than the proximal surfaces of metatarsals II and III.

The shaft is markedly elliptical in cross-section and narrows mediolaterally as it extends distally. The minimum transverse width of the shaft is 0.40 times the total length of the bone. This metric is intermediate for non-sauropodan taxa, being similar to the dimensions displayed by the Early Jurassic sauropodiforms *Jingshanosaurus* (0.46) and *Aardonyx* (0.45), but broader than many other basal sauropodomorphs (e.g., *Pantydraco* [Yates, 2003b]; *Anchisaurus* [Galton, 1976]; *Lufengosaurus* [LV 003]; *Massospondylus* [BP/1/4377]; *Plateosaurus* [Huene, 1926]), which tend to display a minimum midshaft width of between 0.21

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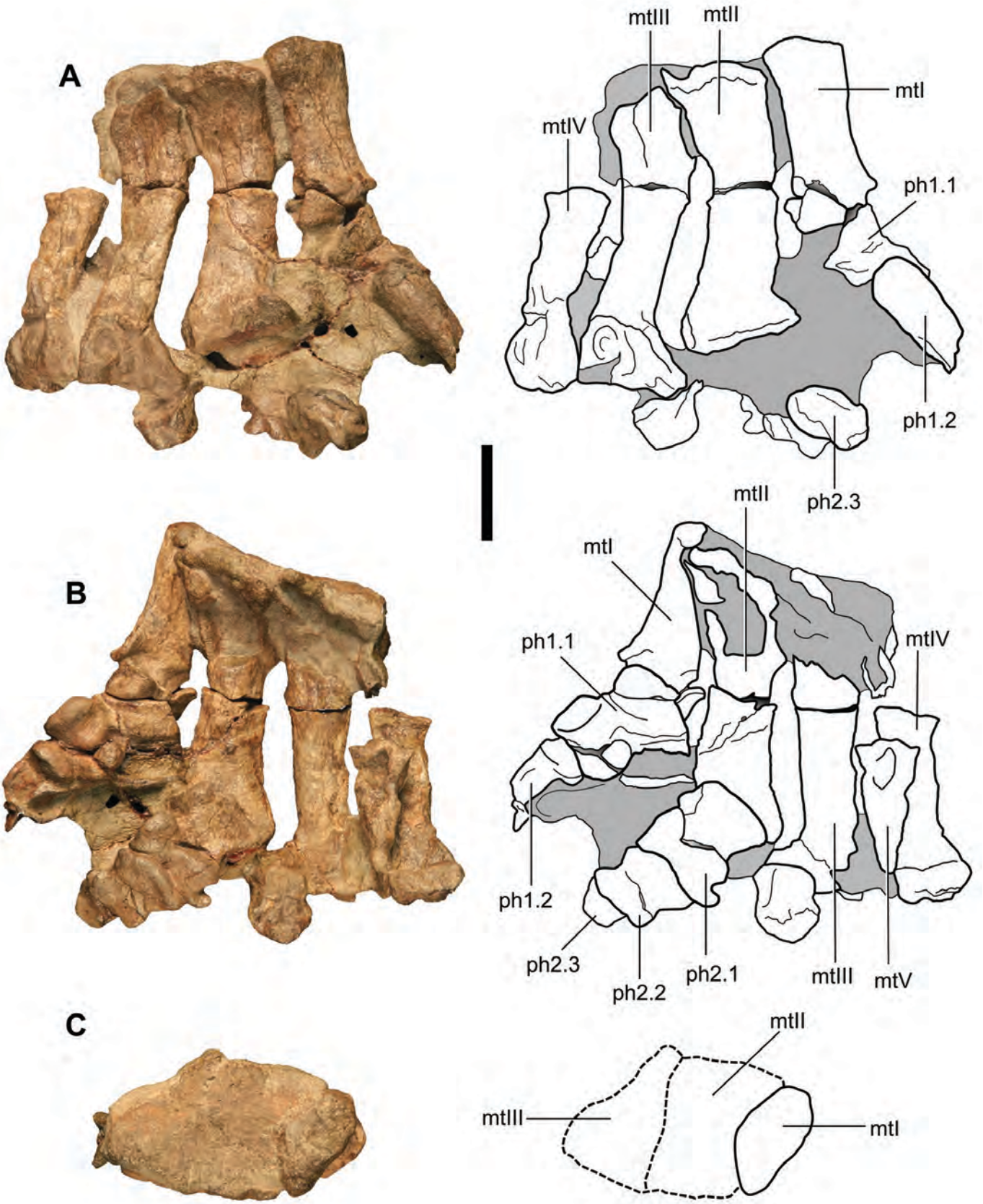


FIGURE 11. Right pes of *Eucnemesaurus entaxonis* (BP/1/6234) in **A**, dorsal view and **B**, ventral view. **C**, hypothesized relationships of the proximal metatarsus. **Abbreviations: mtI**, metatarsal I; **mtII**, metatarsal II; **mtIII**, metatarsal III; **mtIV**, metatarsal IV; **mtV**, metatarsal V; **ph1.1**, first phalanx of pedal digit I; **ph1.2**, second phalanx of pedal digit I; **ph2.1**, first phalanx of pedal digit II; **ph2.2**, second phalanx of pedal digit II; **ph2.3**, third phalanx of pedal digit II. Scale bar equals 5 cm.

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and 0.31 total length. In contrast, the 'near-sauropods' *Blikanasaurus* and *Antetonitrus* display an even stouter ratio of approximately 0.50–0.53.

Poor preservation and adherent matrix obscures an accurate examination of the differential morphology of the distal condyles. However, it is clear that the more proximally located medial condyle was considerably reduced compared with the lateral condyle, as is typical for basal Sauropodomorpha. A subtle extensor depression can be seen in the middle of the anterior face of the distal end.

The proximal articular surface of metatarsal II is dorsoventrally elongate. Based on its articulation with the first metatarsal, it is obvious that the medial margin of the proximal articular surface is deeply concave. Unfortunately, the lateral margin cannot be as easily discerned, making it difficult to substantiate whether or not the proximal surface of metatarsal II in *E. entaxonis* conformed to the biconcave (hourglass) morphology generally found in basal Sauropodomorpha. It appears, however, that the lateral margin was distinctly less concave than the medial, as is generally observed in most basal sauropodomorphs (Fig. 11). The ventral margin of the proximal end is less symmetrical than the dorsal margin, possessing a large flange of bone that extends medially and thus cradles the ventral margin of metatarsal I. A similar medially directed flange can be seen in the proximal second metatarsals of a number of non-massospondylid sauropodomorphs (e.g., *Leonerasaurus*; *Melanorosaurus* [NM QR1551]; *Aardonyx* [BP/1/6253]; *Antetonitrus*; *Tazoudasaurus* [contra Allain and Aquesbi, 2008]; cf. Smith and Pol, 2007; Pol et al., 2011). In contrast, the taxa grouped together within the Massospondylidae (e.g., *Massospondylus*; *Lufengosaurus*; *Coloradisaurus*; *Glacialisaurus*) are united in having a ventrolateral flange that is significantly more developed than the ventromedial process (Smith and Pol, 2007). Other sauropodomorphs (e.g., *Plateosaurus*; *Riojasaurus; Blikanasaurus*) display a ventral margin of the proximal metatarsal II that is subequal in its development at the medial and lateral corners.

The shaft of metatarsal II is subcircular in cross-section, similar to the condition in *Melanorosaurus* but different from a number of other sauropodomorph taxa that display a quadrangular shaft in cross-section (e.g., *Massospondylus*; *Coloradisaurus*; *Blikanasaurus*; *Antetonitrus*). The minimum transverse width of the shaft is approximately 0.25 times the maximum length of the bone, similar in basic proportions to the majority of other Elliot taxa (e.g., *Plateosauravus*; *Melanorosaurus*; *Aardonyx*; *Antetonitrus*) with the exception of *Massospondylus* (0.17). Taxa such as *Riojasaurus* and *Plateosaurus* also have comparably gracile second metatarsals with a minimum shaft width/total length ratio of approximately 0.18.

The distal condyles display a strong medial cant, as is seen—to greater and lesser degrees—in the distal condyles of metatarsals II–IV of all sauropodomorph dinosaurs. Neither condyle is markedly differentiated from the other, although the medial condyle appears to have been more dorsoventrally extensive than the lateral. No collateral ligament pit can be observed on either condyle, although the lateral extent of the lateral condyle (where the deepest pit is generally located) is possibly abraded.

The proximal surface of metatarsal III—the longest bone in the pes—is partially obscured in a manner similar to that of metatarsal II. Nonetheless, it appears that the outline of the proximal surface of metatarsal III in *E. entaxonis* was roughly an isosceles triangle with a short dorsal margin and extensive medial and ventrolateral margins that meet ventrally to form an acute angle. This same morphology is seen in a number of non-sauropodan sauropodomorph taxa (e.g., *Massospondylus* [e.g., BP/1/4377]; *Antetonitrus*; *Plateosauravus*), whereas a number of massospondylid genera display a subtrapezoidal proximal metatarsal III with an obtuse ventral margin (see Smith and Pol, 2007). The 'near-sauropod' *Blikanasaurus* also displays an obtuse ventral margin of proximal metatarsal III, although this may represent a corollary of the convex lateral margin, which is divided into two discrete facets that articulate firmly with the bifacial medial surface of metatarsal IV—a possible autapomorphy of that genus. Because *Herrerasaurus* displays a trapezoid-shaped metatarsal III with a wide ventral margin (Novas, 1994), it is possible that the acute, triangular morphology observed in some sauropodomorphs represents a derived feature of those taxa.

The length of metatarsal I relative to metatarsal III remains conservative throughout basal Sauropodomorpha, and the ratio of 0.56 observed in *E. entaxonis* is roughly consistent with a great many closely related genera (e.g., *Plateosaurus*; *Riojasaurus*; *Massospondylus* [BP/1/4377]; *Aardonyx; Antetonitrus*). Outside of Eusauropoda, only *Blikanasaurus* displays a heightened mt I/mt III ratio, with a value of 0.63.

The shaft of metatarsal III in *E. entaxonis*, although having experienced a degree of taphonomic deflation, is subtriangular in cross-section with a flat, broad dorsal surface and a rounded ventral surface. As in *Glacialisaurus*, the medial side is slightly broader than the lateral. The minimum midshaft width is approximately 0.19 times the proximodistal width of the bone (although this metric is tentative considering the aforementioned deflation). This is similar to the same measurement in *Plateosauravus* (0.18), being greater than that observed for *Massospondylus* (0.15; BP/1/4377, BP/1/5241) and less than the comparatively robust *Antetonitrus* (0.21) and *Blikanasaurus* (0.25).

The distal end is badly deformed, although the medial condyle appears to have been more transversely extensive than the lateral condyle.

Metatarsal IV is poorly preserved, with the morphology of the proximal end obscured due to its adherence to the underside of the fibula and the distal end being badly eroded. As in most basal sauropodomorphs, the fourth metatarsal is only negligibly shorter than the third.

The funnel-shaped fifth metatarsal is preserved adhered to the underside of the distal end of metatarsal IV. As with all non-sauropodan sauropodomorphs (and most basal dinosaurs), metatarsal V is considerably shorter than the rest of the metatarsus (although, it bears repeating, in no genera is it ever appreciably shorter than the first metatarsal). The transverse width of the proximal surface of the fifth metatarsal in *E. entaxonis* is 0.5 times its total proximodistal length. This is consistent with most basal forms (e.g., Massospondylus: 0.53; BP/1/5241). Derived forms such as *Blikanasaurus* and *Vulcanodon* (and most likely *Antetonitrus*, although the distal end of metatarsal V is not preserved in that taxon) have a comparatively wider fifth metatarsal, with a width/length ratio of approximately 0.75–0.77. The medial and lateral margins of metatarsal V in *E. entaxonis* taper smoothly from the proximal to the distal ends. This differs from a number of genera (e.g., *Blikanasaurus*; *Antetonitrus*) where the proximal half expands at a larger angle (from the proximodistal axis) than that observed in the distal half of the bone (Yates, 2003b). Unlike *Massospondylus*, metatarsal V of *E. entaxonis* appears to have lacked the faint oblique ridge that runs distomedially from the ventrolateral corner of the proximal end towards midshaft, whereupon a pronounced ventrally oriented swelling of the attenuated distal half is generally observed. Instead, a deeply concave pit can be observed within the proximal half of the ventral surface of *E. entaxonis*, but this may be a preservational artefact.

Digits I and II preserve their full allotment of non-terminal phalanges (one in the former, two in the latter) as well as their respective unguals, although the preservation of the latter in digit II is poor. Also present is an isolated first pedal phalanx from digit I of the left foot that is preserved in articulation with its associated ungual, which in turn is missing the distal portion.

In keeping with the rest of the pedal morphology, the non-terminal phalanges of *E. entaxonis* are relatively squat, approaching

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proportions more typical of the derived sauropodiform condition (e.g., *Aardonyx*; *Melanorosaurus*; *Antetonitrus*) than that of the comparatively gracile Massospondylidae (e.g., *Massospondylus*; *Coloradisaurus*). The maximum transverse width of the proximal end of the first phalanx of digit II (the best preserved non-terminal phalanx of the articulated pes) is subequal to its proximodistal length. This contrasts with the same ratio in both *Massospondylus* (0.65; BP/1/5241) and *Plateosaurus* (0.68; GPIT1), as well as many other basal sauropodomorphs (e.g., *Pantydraco*; *Riojasaurus*; *Adeopapposaurus*; *Seitaad*; *Leyesaurus; Mussaurus*) that tend to display pedal phalanges that are proximodistally longer than transversely broad (Apaldetti et al., 2013). The dorsal surface of the first phalanx of digit I is appreciably narrower than the ventral surface and coplanar with respect to the dorsal margins of the distal condyles. The difference in mediolateral width between the dorsal and ventral surfaces may be less in other phalanges; however, the level of preservation makes this difficult to confirm. In all observable elements, the ventral incursion of the distal condyles exceeds that of the dorsal.

The better-preserved, isolated first pedal phalanx from the left foot exhibits deep collateral ligament fossa on both distal condyles. In the articulated right pes, preservation of this element is only sufficient to observe ligament fossa on the medial condyles of the first phalanges of the first and second digits.

The first pedal ungual (I-2) of *E. entaxonis* is preserved in both the articulated right pes and the isolated left digit, although in both it is missing the distal apex. Although incomplete, this element would have undoubtedly been shorter than the first metatarsal, a symplesiomorphy of all sauropodomorphs basal to *Melanorosaurus* (McPhee et al., 2014). The proximal surface of ungual I-2 is laterally compressed and triangular in outline with a narrow dorsal margin and comparatively broad ventral surface. This differs from more derived forms (e.g., *Melanorosaurus*; *Antetonitrus*) that display a more circular-shaped proximal end of the first pedal ungual. The proximodorsal process is pointed and well developed, in contrast to the practically absent flexor tubercle—a morphology consistent with most basal Sauropodomorpha. The beginnings of a distinct vascular groove can be seen on the lateral and medial surfaces of the better-preserved left element, just proximal to the break.

The proximal portion of pedal ungual II is preserved in articulation with the non-terminal phalanx; however, its poor preservational condition precludes any useful comment on its morphology.

PHYLOGENETIC RESULTS

The phylogenetic analysis returned eight most parsimonious trees (MPTs) of length 1244, consistency index (CI) = 0.34, and rescaled consistency index (RCI) = 0.7 (Fig. 12). Overall, the topologies of these trees do not differ greatly from previous cladistic analyses of basal sauropodomorphs (e.g., Yates, 2007a, 2007b; Yates et al., 2010; Otero and Pol, 2013; McPhee et al., 2014). The genus *Eucnemesaurus* is monophyletic, with the sister-taxon relationship between *E. entaxonis* and *E. fortis* supported by a single unambiguous synapomorphy: length of first caudal centrum less than its height (char. 184.1; but see below). The family Riojasauridae are also recovered as a monophyletic group, diagnosed by essentially the same femoral features listed in Yates (2007a) (i.e., longitudinal axis of the femur offset less than ten degrees [char. 280.1; novel to this analysis]; hemispherical femoral head [char. 283.1]; posterior 'tubercle' on femoral head [char. 284.0; but see below]; lesser trochanter at least as high as its basal width [char. 289.1]; rounded profile of the fourth trochanter [char. 295.0]).

Interestingly, novel positions are hypothesized in this topology for *Plateosauravus, Ruehlia, Anchisaurus*, and *Leonerasaurus*. *Plateosauravus* and *Ruehlia* are located within the monophyletic Plateosauridae in the current topology, not basal to it as in previous analyses (e.g., Yates, 2007a, 2007b; Otero and Pol, 2013). *Anchisaurus*, used as the specifier taxon for the group Anchisauria in most recent taxonomic treatments (e.g., Yates, 2007a, 2007b, 2010; Otero and Pol, 2013), is resolved in a novel position basal to the Massospondylidae. *Leonerasaurus* is recovered in a highly derived position near the base of Sauropoda, a somewhat more derived position than in previous analyses (Pol et al., 2011; Otero and Pol, 2013) (see below for further discussion). It should also be noted that, congruent with the results of Martínez et al. (2012), the problematic basal saurischian *Eoraptor* was resolved as one of the basal-most sauropodomorphs currently known (Fig. 12A).

Our exploratory analyses yielded the following results: analysis of the data matrix with the Riojasauridae constrained to be non-monophyletic results in 65 MPTs with a best score only a single step longer than in the initial analysis (1245). The majority of the fundamental MPTs in that analysis place *Eucnemesaurus* in a position at the base of Sauropodiformes, a position consistent with the relatively derived condition of several characters within *E. entaxonis* (Fig. 12B) (see below for further discussion). It should also be noted that in the constrained analysis the monophyly of *Eucnemesaurus* is not supported in a number of fundamental MPTs, with *E. fortis* considerably more basal with respect to *E. entaxonis* in these instances. Accordingly, the strict consensus tree places both taxa in a sizeable polytomy along with most non-sauropodan massopods. Similar to a subset of the constrained analysis, the monophyly of *Eucnemesaurus* is also not supported in the implied weighting analyses, with *E. entaxonis* considerably more derived than *E. fortis* in all tested scenarios (K = 1−10). This result is not altogether surprising, however, given the apomorphies shared between *E. entaxonis* and *Melanorosaurus* (see also below).

Analysis of the data matrix with the removal of *Riojasaurus* (see Discussion) leads to a dramatic increase in the number of MPTs (from 8 to 123) and a much more poorly resolved consensus tree, again with *Eucnemesaurus* spp. placed in a considerably more derived position amongst the core grouping of non-sauropodan sauropodiforms. Constraining against the monophyly of the Riojasauridae results in the 'traditional' positioning of *Anchisaurus* within Sauropodiformes, whereas its position remains unchanged in the reduced majority consensus tree in which *Riojasaurus* is absent.

DISCUSSION

E. entaxonis and the 'Riojasauridae'

The features supporting *Eucnemesaurus* monophyly, much as those diagnosing the genus itself, pertain predominantly to the femur (see Results above). These same features, with the exception of the obliquely directed long axis of the fourth trochanter (not included in the current data matrix), are also the primary diagnostic features of the Riojasauridae. Given the continued paucity of information pertaining to the non-hindquarter regions of *Eucnemesaurus* spp., it is therefore likely that many of the unknown features of *Eucnemesaurus* are being polarized in phylogenetic analysis by the substantially more complete *Riojasaurus*—probably influencing the phylogenetic position of *Eucnemesaurus* considerably. For example, the sole unambiguous synapomorphy uniting *E. fortis* and *E. entaxonis* within the Riojasauridae pertains to the first caudal centrum being higher than it is long. However, this is the typical condition for most non-massospondylid sauropodomorphs and is rendered autapomorphic here simply because of the opposite state apparently being present in *Riojasaurus*. Because there are no caudal vertebrae figured in Bonaparte (1971), it is difficult to substantiate the scoring of this character (originally scored from the mounted display skeleton within the museum of the Instituto Miguel Lillo,

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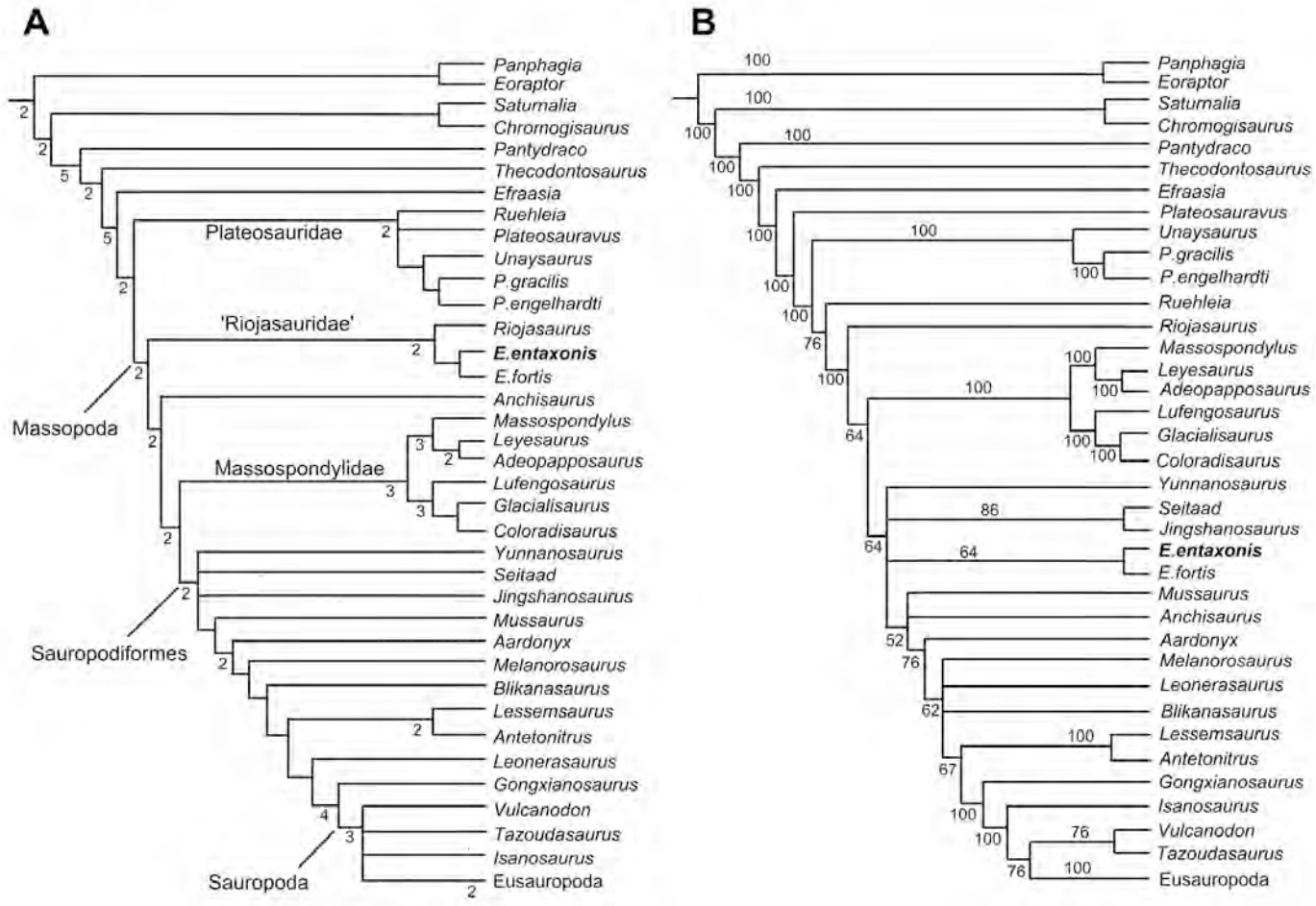


FIGURE 12. Results of cladistic analyses. **A**, abbreviated strict consensus tree of 8 MPTs with a best score of 1244 steps. Numbers below nodes represent Bremer support values higher than 1. Tree begins at basal-most nodes within Sauropodomorpha; **B**, 50% majority consensus when the monophyly of the 'Riojasauridae' has been constrained against (65 MPTs with best score of 1245 steps).

Tucumán [PVL])—a concern that applies to a number of elements amongst the vast array of material referred to *Riojasaurus*.

This uncertainty is emblematic of the myriad issues surrounding the *Riojasaurus* hypodigm, and the validity of phylogenetic inferences dependent upon its inclusion. *Riojasaurus* was first introduced in a preliminary fashion as a component of a larger study of the tetrapod fauna of the Los Colorados Formation of the Ischigualasto-Villa Unión Basin (Bonaparte, 1971). Since then, only one additional study has explicitly dealt with *Riojasaurus*, when Bonaparte and Pumares (1995) referred a fairly complete skull (PURL 56; found in association with an almost complete subadult skeleton) to the genus. Although easily differentiated from the contemporaneous Los Colorados taxa *Coloradisaurus* and *Lessemsaurus* with respect to the relatively gracile bauplan of the former, and the comparatively derived morphology in the latter, *Riojasaurus* remains too poorly represented within the current literature to confirm the monospecificity of the large amount of material referred to it (see Bonaparte, 1971). This uncertainty was recently underscored by author A. M. Yates, who has expressed doubt regarding the systematic equivalence of the femoral element(s) used to score *Riojasaurus* (using non-type material within the collections of the Paleontología de Vertebrados, Instituto San de Miguel de Tucumán, based on assumed synonymy with PVL 3808) within the current matrix.

The above considerations have particular bearing on the presumed phylogenetic significance of the 'posterior tubercle'—the obtuse bulge on the posterior side of the femoral head that Yates (2007a) suggested as a synapomorphic reversal to the non-dinosaurian condition supporting a monophyletic Riojasauridae. Although certain non-dinosaurian dinosauromorphs (e.g., *Lagerpeton*) have a distinct notch on the posterior surface of the femoral head (= the medial tuberosity: Sereno and Arcucci, 1994), most early dinosaurs—including basal sauropodomorphs—have at most a subtle protuberance on the posterior surface of the femoral head (although the homology of the latter to the former is uncertain). Although it appears that in several specimens of sauropodomorph this protuberance is moderately more pronounced, its expression can be highly variable both within and between taxa (e.g., the assemblage BP/1/386 [see Otero et al., 2015] preserves three femoral heads, two without the feature and one with it, while the femur of Rheulia [MB.R.4753] also preserves a pronounced posterior tubercle). The possibility that family- or genus-defining status has been afforded a feature that may have only become exaggerated in individual specimens is therefore a valid concern. Although this character remains as a synapomorphy of the Riojasauridae for now, further investigation is into its homology and distribution within basal sauropodomorph taxa is warranted.

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The a priori removal of *Riojasaurus* from the current data matrix, although dramatically affecting the overall resolution of the analysis, ultimately favors a position for *Eucnemesaurus* close to the base of Sauropodiformes—and closer to other Elliot taxa such as *Aardonyx* and *Melanorosaurus*. The fact that this same result occurs with the addition of a single step when constraining for the non-monophyly of the Riojasauridae emphasizes the degree to which *Riojasaurus* (as currently understood and coded) has significant bearing on our understanding of character polarity and sister-taxon relationships within non-sauropodan Sauropodomorpha. Clearly, a detailed, monographic treatment (ideally one that codes PURL 56 and PVL 3808 as separate operational taxonomic units [OTUs] in order to assess their character-based affinities) of all the material associated with *Riojasaurus* is required in order to corroborate the taxonomic validity of *Riojasurus*, as well as strengthening phylogenetic hypotheses that center upon this taxon.

Novel Positions of Previously Existing Taxa—Several of our phylogenetic results present novel positions for key taxa, and these warrant further discussion. The strict consensus tree places *Plateosauravus* and *Ruehlia* within the monophyletic Plateosauridae, differing from all previous analyses (e.g., Yates, 2007a, 2007b, 2010; Otero and Pol, 2013; McPhee et al., 2014) that place these taxa basal to this group. Although only weakly supported by two synapomorphies (laterally expanded tables at the midlength of the dorsal surface of the neural spines in both cervical and pectoral vertebrae [char. 149.2; known only for *Ruehlia* and convergently acquired in Massospondylidae]; posteriorly projecting heel on the distal end of the iliac ischial peduncle [253.1; present also in *Riojasaurus* and some massospondylids]), this result nonetheless suggests an expanded, global distribution of plateosaurids that also encompasses southern Africa—a result geographically congruent with the phylogenetic hypotheses of Novas et al. (2011) (although see below for a discussion on problems pertaining to *Plateosauravus*).

Anchisaurus is resolved in a non-'anchisaurid' (sensu Yates, 2007a, 2007b, 2010) position basal to the Massospondylidae. The derived position of the Massospondylidae relative to *Anchisaurus* is supported by several unambiguous synapomorphies (raised postorbital rim of the orbit [char. 55.1]; absence of a deep septum spanning the interbasipterygoid space [char. 85.0; process present in *Anchisaurus, Riojasaurus, Plateosaurus*, and *Efraasia*]; length of the humerus 55–65% the length of the femur [char. 205.1]; proximal width of the first metacarpal 80–100% of its length [227.2]; size of the ungual of pedal digit III less than 85% of the ungual of pedal digit II in all linear dimensions [359.1]). Two of these characters, however, are highly homoplastic throughout Sauropodomorpha (205, 359), whereas a small grade consisting of Massospondylidae, *Yunnanosaurus*, and *Jingshanosaurus* all display the derived condition for characters 55 and 205 (including *Mussaurus* in the case of the latter), despite this condition being reversed in all more apical Sauropodomorpha. The condition in *Anchisaurus* in these trees is therefore interpreted as being plesiomorphic within Sauropodomorpha, rather than being secondarily reversed. Unsurprisingly, only a single additional step is required to place *Anchisaurus* at the base of Sauropodiformes, whereas the results of the implied weighting analysis places *Anchisaurus* amongst Sauropodiformes when K is larger than 2 (data not shown). Clearly, a more detailed exploration of the effect of homoplasy on current sauropodomorph matrices is warranted, especially with respect to the confounding mosaic of characters evident in *Anchisaurus*. The uncertainty surrounding the morphological relationships of *Anchisaurus*, as well as its newly labile position, count among the reasons why McPhee et al. (2014) opted instead for the use of Sauropodiformes (the most inclusive clade containing *Saltasaurus* but not *Massospondylus*) as a stem-based alternative to 'Anchisauria.'

Leonerasaurus is retrieved in a relatively derived position near the base of Sauropoda in our analysis, a surprising result given the removal of the similarly gracile *Anchisaurus* from the pectinate, large-bodied grouping of Sauropodiformes. This result is potentially explicable via the large amounts of missing information within this OTU, but a confluence of characters approaching the 'sauropodan' condition (e.g., procumbent dentary teeth; four sacral vertebrae; non-sinuous deltopectoral crest; preacetabular process of the ilium exceeding the anterior margin of the pubic peduncle; proximal surface of the first metatarsal subequal in size to the second; straight lateral margin of the proximal surface of the second metatarsal) nonetheless support a more derived position. Although the possibility remains that the gracile morphology of *Leonerasurus* is exaggerated by its subadult age (see Pol et al., 2011), the basal sauropod *Vulcanodon* also bears an elongate pes (Cooper, 1984), an observation consistent with our hypothesized taxonomic position for *Leonerasaurus* (see also Otero and Pol, 2013).

The relatively small number of coding alterations and new characters added in this study has resulted in some modest yet interesting changes to previous hypotheses of basal sauropodomorph phylogenetics. Further taxonomic work refining taxon hypodigms and systemic work defining new cladistic characters is necessary to test the stability of these phylogenetic results.

E. entaxonis and the Interrelationships of South African Basal Sauropodomorpha

Sauropodomorph diversity within the Elliot Formation of South Africa is strongly partitioned between the lower and upper sections of the formation. Although the upper Elliot (Early Jurassic) is showing signs of containing more taxonomic diversity than just the abundant and well-known *Massospondylus* spp. (Yates et al., 2010, 2011), the majority of sauropodomorph taxonomic variation is exclusive to the lower Elliot (Late Triassic). However, the understanding and taxonomic organization of this variation has proven persistently elusive (e.g., Van Heerden, 1979). Besides *Eucnemesaurus*, we regard two other lower Elliot sauropodomorph taxa as being of near-certain validity: *Blikanasaurus cromptoni*, based on its distinctive 'dwarfed' morphology (Galton and Van Heerden, 1998), and *Antetonitrus ingenipes*, based on its clearly unique collection of relatively derived apomorphies (Yates and Kitching, 2003; McPhee et al., 2014). However, serious questions remain regarding the validity of the two remaining lower Elliot taxa: *Melanorosaurus readi* and *Plateosauravus cullingworthi*. The new information presented by *E. entaxonis* thus has bearing on the stratigraphic, taxonomic, and adaptive significance of both of the above genera—especially in light of the outwardly progressive shift from primitive to relatively derived forms observed with the LEF.

Plateosauravus cullingworthi—ostensibly the most basal of all the Elliot taxa (see e.g., Yates, 2007a, 2007b, 2010)—has experienced a taxonomic past almost as confused as that of *Eucnemesaurus* (see Haughton, 1924; Huene, 1932; Van Heerden, 1979; Yates, 2003a). Known primarily from a large assemblage of bones recovered in 1918 near Hershel, Eastern Cape, the 'type' series (SAM-PK-3341–3356, 3602–3603, 3607–3609) is composed of three or more moderately sized individuals as well as a considerably more massive animal represented by a few dorsal/sacral vertebrae and an almost complete pair of ischia. This latter, larger material (SAM-PK-3607-3609) was originally selected as the type material for *Euskelosaurus africanus* by Haughton (1924), and doubt remains as to the conspecifity of this material to the rest of the *Plateosauravus* type material. Furthermore, although clearly plesiomorphic for Sauropodomorpha in a number of respects (see below), *Plateosauravus* nonetheless displays the contradictory attributes of humeri that are elongate relative

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to other bones in the assemblage and comparatively high posterior dorsal neural spines—both derived features within Sauropodomorpha. For the time being, it is difficult to say whether this is explicable via homoplastic convergence or evidence of a multitaxic assemblage.

E. entaxonis shares with *Plateosauravus* (to the exclusion of other lower Elliot taxa) a number of characters consistent with the non-sauropodan condition. These include (1) dorsal vertebrae with subcircular neural canals; (2) an anteriorly positioned lesser trochanter; (3) a fourth trochanter located mainly in the proximal half of the shaft; and (4) a rectangular distal end of the tibia with an acute anteromedial corner. Although most of these features clearly distinguish *Plateosauravus* from the comparatively derived morphology of *Melanorosaurus* (with the exception of the elongate humeri and high posterior dorsal neural arches), the exclusive autapomorphies distinguishing the former from both *Eucnemesaurus* and *Melanorosaurus* are subtle: a 'square'-shaped postacetabular process and the excavated embayment of the lateral surface of the tibial posterior descending process (Yates, 2003a, 2007a). Unfortunately, the forelimb in *Eucnemesaurus* remains unknown and the significance that such information could bring to bear on the putatively elongate forelimb of *Plateosauravus* remains enigmatic.

Melanorosaurus is currently interpreted as occupying a relatively close phylogenetic position to Sauropoda (e.g., Yates, 2007a, 2007b; Pol et al., 2011). Although known from a large collection of syntypic and referred material (Haughton, 1924; Galton et al., 2005; Yates, 2007b; Bonnan and Yates, 2007), thus far only the skull of a referred complete skeleton (NM QR3314; Yates, 2007b) has received a formal description and diagnosis with reference to both autapomorphies and unique character constellations. Further uncertainties relate to the cohesiveness of the syntype material itself, which includes bones collected from at least two distinct—albeit neighboring—localities as well as other disassociated material, possibly cataloged under SAM-PK-3449 subsequent to initial collection (Haughton, 1924; Galton et al., 2005; B.W.M., pers. observ.). Consequently, the distinguishing characters of the postcrania of *Melanorosaurus* are limited to a vaguely communicated unique suite of derived features (i.e., dorsal neural spines that are approximately 1.5 times as tall as they are long; four to five sacral vertebrae; sagittal furrow on the ventral surface of the anterior caudal centra; distal migration of the major femoral trochanters; femoral shaft elliptical in cross-section with a reduced sigmoidal curvature; proximal breadth of mtI roughly 0.6 times its proximodistal length), of which at least two (anteroposterior constriction of the femoral shaft; proportions of the first metatarsal) now appear present in *E. entaxonis* (see Yates [2003a, 2007b, 2008] for a further commentary on the distinguishing postcranial features of this taxon).

Yates (2007b) suggested the presence of a pitted excavation (= 'non-articulating gap') within the first primordial sacral rib as a possible postcranial autapomorphy of *Melanorosaurus* (based primarily on the morphology of the two major sets of referred material: NM QR1551 and 3314). This observation is interesting insofar as it means that the two sacral vertebrae anterior to the pit-possessing element in NM QR1551 are in effect both dorsosacrals, contra Galton et al. (2005) who identified them as the dorsosacral and first-primordial sacral vertebrae. This observation, along with the possibility that *Melanorosaurus* may have also been in possession of a caudosacral (i.e., at least five sacral vertebrae in total), suggests either the autapomorphic acquisition of upwards of two additional sacral vertebrae in *Melanorosaurus*, or character continuity shared exclusively with Eusauropoda (Upchurch et al., 2004). However, a caudosacral is unambiguously observable only in NM QR3314, whereas this same individual appears to lack the additional dorsosacral described for NM QR1551 (pers. observ. B.W.M.), rendering the homology of the non-articulating gap of Yates (2007b) contentious. Nonetheless, although character conflict within the *Melanorosaurus* hypodigm is not restricted to the sacral elements alone (the proportions of the first metatarsals of NM QR1551 and 3314 are wildly divergent; see above), and future care should be taken when regarding referred material of *Melanorosaurus* as a single operational taxonomic unit, the presence of a similar excavated pit in the first primordial sacral of *E. entaxonis* appears to corroborate Yates' diagnosis of the same element in *Melanorosaurus* (NM QR1551). The presence of this feature in both *Eucnemesaurus* and referred specimens of *Melanorosaurus* suggests either a wider distribution of this character than previously appreciated or a closer taxic relationship between these two taxa than implied by the current consensus tree.

These caveats aside, it is evident from the morphologies outlined above that *Eucnemesaurus entaxonis* appears to represent something of an intermediate form between the relatively plesiomorphic *Plateosauravus* and the relatively derived *Melanorosaurus*. However, although these morphologies could be taken as evidence of either an anagenetic series, local adaptation, or population-level variation (or a combination thereof), testing these various scenarios is hampered by the continued lack of resolution in regards to the temporal duration of the lower Elliot (and of the Elliot Formation generally), as well as the poorly recorded stratigraphic provenance of the majority of the sauropodomorph specimens collected over the past century. Although Yates (2008) has suggested that the lower Elliot forms a homogeneous sedimentary unit in which the same large-bodied forms (i.e., *Blikanasaurus*) are found throughout strata representing a short depositional sequence—in which case the hypothesis of anagenesis would be convincingly falsified—the evidence cited for this is slight (see Yates, 2008). Because *E. entaxonis* was discovered just above the Molteno-Elliot contact, and as new, preliminary data tentatively suggest that most of the more derived, sauropodiform taxa are found higher up in the sequence, it remains a plausible possibility that *E. entaxonis* represents an ancestral population of basal sauropodomorphs to more derived forms such as *Melanorosaurus*. Nonetheless, the biostratigraphic and temporal delineation of the Elliot Formation remains in its early stages, with much more work (and fossil material) required yet if we are to begin elucidating the true population dynamics of lower Elliot Sauropodomorpha.

Functional Morphology of *E. entaxonis*

The most striking anatomical features observable within *E. entaxonis* are the surprisingly robust foot architecture and the presence of a deep brevis fossa on the ventral surface of iliac postacetabular process. The stout metatarsus evinces the relatively early occurrence (at least phylogenetically) of a robust, subentaxonic pes amongst Late Triassic basal sauropodomorphs and suggests an early experiment in a slower, subgraviportal form of locomotion. Given the incipient adoption of a form of pedal architecture later emblematic of the obligatorily quadrupedal sauropods, it is interesting that the brevis fossa should be as deeply developed as it is in *E. entaxonis*. Although *Saturnalia, Thecodontosaurus*, and *Efraasia* retain relatively deep brevis fossae (Benton et al., 2000; Yates, 2003b, 2003c), the tendency early within Sauropodomorpha—especially in the large-bodied forms—is to significantly reduce the extent of the brevis fossa, with most taxa displaying at most a shallow embayment on the ventral or ventrolateral surface of the postacetabular process (e.g., *Adeopapposaurus* [PVSJ569]; *Mussaurus* [Otero and Pol, 2013]; *Plateosauravus* [SAM-PK-3609]). A brevis fossa as deeply excavated as that exhibited by *E. entaxonis* is therefore unknown in a sauropodomorph of its relatively derived position (with the possible exception of *Riojasaurus* [PVL 3808]) and may be indicative of a specialized locomotor strategy unique to *E. entaxonis* amongst the lower Elliot sauropodomorph assemblage.

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Recently, McPhee et al. (2014; see also Mallison, 2010a, 2010b) have suggested that a hypertrophied M. caudofemoralis brevis complex may be related to the adducting forces required to steady the feet beneath the body of a large, wide-gaited biped. In this context, the brevis fossa of *E. entaxonis* may relate to a specialized form of obligate/habitual bipedality within an early radiation of broad-footed, massopodan sauropodomorphs. This interpretation, if corroborated, would provide compelling evidence of divergent locomotor strategies between *E. entaxonis* and the putatively quadrupedal *Melanorosaurus* (Yates, 2007b; Rauhut et al., 2011). However, it should be noted that the distinctly oblique passage of the fourth trochanter towards the medial margin of the femur in *Eucnemesaurus* is possibly representative of the 'transitional' condition whereby the fourth trochanter becomes located entirely on the medial margin of the femoral shaft in sauropodomorphs from *Melanorosaurus* onwards. Unfortunately, because the forelimb of *Eucnemesaurus* remains unknown, the complete skeletal anatomy and function of the locomotor apparatus of the genus can only be guessed at. Clearly, a great deal more well-preserved, associated fossil material is required in order to more fully elucidate the functional, evolutionary, and taxonomic constraints at work within the sauropodomorphs both within the lower Elliot and beyond.

Biogeographic Implications of *E. entaxonis*

Although it is axiomatic that southern Pangean landmasses as closely allied as Argentina and South Africa should have experienced a large degree of faunal interexchange in the Late Triassic, that this relationship should be embodied in at least two sister-taxon relationships (*Lessemsaurus* + *Antetonitrus* and the 'Riojasauridae') appears to provide strong support for a pan-Gondwanan fauna that, at least in terms of its observable range, extended from the Free State-Lesotho border through roughly 2700 km to the La Rioja/San Juan provinces of Argentina. This relationship is all the more remarkable given that region-specific monophyly is rare even in areas that preserve a rich localized sauropodomorph assemblage (e.g., China, South Africa). However, although support for the *Lessemsaurus* + *Antetonitrus* clade appears fairly robust (e.g., McPhee et al., 2014; current analysis), it is possible that the Riojasauridae may yet prove chimerical (see above). Therefore, any additional information regarding the *Riojasaurus* hypodigm will be of considerable biogeographical value in allowing us to test further whether this assemblage is represented by multiple taxa that expand this cosmopolitan, basal-massopodan fauna, or dissolve it entirely.

The faunal closeness of South America and southern Africa is also hinted at within the Massospondylidae, which contains both the Los Colorados genus *Coloradisaurus* and the upper Elliot genus *Massospondylus*. The Late Triassic age generally ascribed to *Coloradisaurus* (along with all Los Colorados fauna e.g., Bonaparte, 1971, 1973; Arcucci et al., 2004; Apaldetti et al., 2013), in association with the unexpectedly robust pes of *E. entaxonis*, highlights a previously overlooked and intriguing inconsistency: although the complete metatarsus of *Plateosauravus* remains unknown, there has as yet been no material recovered from within the lower sections of the Elliot Formation that is of comparable gracility to the wealth of foot remains known for the Early Jurassic taxon *Massospondylus*. This suggests that the elongate pes morphology of *Massospondylus* was either inherited from a known lower Elliot taxon that subsequently adopted a more gracile bauplan following the end-Triassic extinction event, or—more likely—was retained from an ancestor that was not present during deposition of the lower Elliot Formation. Although the possibility remains that the massospondylid 'proto-population' exists undiscovered within the lower Elliot, over a century's worth of fossil-prospecting has yet to recover a convincing candidate. If this discrepancy is therefore not explicable due to sampling bias, an external origin becomes the most likely explanation.

Although the Massospondylidae achieved a cosmopolitan distribution during the Early Jurassic—with forms known from China (*Lufengosaurus*; Barrett et al., 2005), Antarctica (*Glacialisaurus*; Smith and Pol, 2007), Argentina (*Adeopapposaurus* and *Leyesaurus*; Martínez, 2009; Apaldetti et al., 2011), South Africa (*Massospondylus*; Kitching and Raath, 1984), and possibly India (*Pradhania*; Novas et al., 2011) and North America (*Sarahsaurus* cf. Row et al., 2010)—only *Coloradisaurus brevis* hails from rocks confidently datable to the Late Triassic. In further treatments on the subject of massospondylid origins, it may therefore prove useful to look to South America—in the capacity of a null hypothesis—as the area of origin of the Massospondylidae. Unfortunately, the paucity of similarly aged Late Triassic rocks throughout the rest of Gondwana will undoubtedly render such hypotheses difficult to substantiate.

CONCLUSION

The above work has further established *Eucnemesaurus* as a valid genus that, although still mysterious with regard to substantial areas of its anatomy, can now be shown to be represented by two species—*E. fortis* and *E. entaxonis*. Additionally, although the new anatomical data provided by this new specimen currently support the idea of a monophyletic radiation of 'riojasaurids' at the base of Massopoda, the possibility remains that future phylogenetic analyses might resolve other relationships, with the *Riojasaurus* hypodigm certainly warranting closer scrutiny.

Serious questions also remain regarding the validity and interrelationships of other LEF taxa, uncertainties further complicated by the intriguing mosaic of primitive and derived features present in *E. entaxonis*. Nonetheless, the question of whether the derived characters within this suite are better explained as synapomorphies supporting a closer relationship to Sauropodiformes, or homoplasies exclusive to *E. entaxonis*, remains clouded by our continued poor understanding of the complete anatomy of *Eucnemesaurus* spp., as well as the contradictory assemblage of characters within the prevailing *Melanorosaurus* hypodigm.

Clearly, a more robust understanding of the character complexes of LEF Sauropodomorpha, set against a framework of improved stratigraphic and temporal control, is required in order to more fully elucidate the durations and variability of lineages during this important period of sauropodomorph evolution.

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SCIENTIFIC REPORTS

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A new basal sauropod from the pre-Toarcian Jurassic of South Africa: evidence of niche-partitioning at the sauropodomorph–sauropod boundary?

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The early evolution of sauropod dinosaurs remains poorly understood, with a paucity of unequivocal sauropod taxa known from the first twenty million years of the Jurassic. Recently, the Early Jurassic of South Africa has yielded an assemblage of dental and post-cranial remains displaying a more apomorphic character suite than any other similarly aged sauropodomorph. These remains are interpreted as a new species of basal sauropod and recovered cladistically as the sister taxon to *Vulcanodon* +more derived Sauropoda, underscoring its importance for our understanding of this pivotal period of sauropod evolution. Key changes in the dentition, axial skeleton and forelimb of this new species suggest a genuine functional distinction occurring at the sauropodiform-sauropod boundary. With reference to these changes, we propose a scenario in which interdependent refinements of the locomotory and feeding apparatus occurred in tandem with, or were effected by, restrictions in the amount of vertical forage initially available to the earliest sauropods. The hypothesized instance of niche-partitioning between basal sauropodan taxa and higher-browsing non-sauropodan sauropodomorphs may partially explain the rarity of true sauropods in the basal rocks of the Jurassic, while having the added corollary of couching the origins of Sauropoda in terms of an ecologically delimited 'event'.

Sauropod dinosaurs are justly famous for their redoubtable size, long geological reign, and unique physiology. However, prior to the early Middle Jurassic, relatively little is known of the early period of sauropod evolution. Although a number of non-sauropodan sauropodomorph taxa are known from the first twenty million years of the Jurassic[1–7], only a handful of similarly aged taxa have been described as basal sauropods - an assignation that remains equivocal for most, if not all. *Chinshakiangosaurus* from the

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Fengjiahe Formation of China is based on a single dentary that displays an ambiguous mixture of primitive and derived characters[8], while other Lower Jurassic Chinese basal 'sauropods' await either formal description ('*Kunmingosaurus*'), or are too fragmentary to diagnose ('*Zizhongosaurus*')[9,10]. *Lamplughsaura* from the Upper Dharmaram Formation of India is of uncertain phylogenetic affinity, being recovered as either a stem taxon close to the base of Sauropodomorpha, or as a basal sauropod close to '*Kotasaurus*' and *Vulcanodon* within the one cladistical assessment of its relationships[11]. The latter taxon, long considered the earliest-known exemplar of the basal sauropod condition[12], has been temporally reallocated to a sedimentary lens contained within the early Toarcian Drakensburg Group basalts[13,14], while the putative Early Jurassic age of the Indian Kota Formation (which, along with '*Kotasaurus*', also contains the basal sauropod *Barapasaurus*) is poorly supported, with both the dinosaurian and mammalian faunal assemblage suggestive of a late Early Jurassic age at the oldest[15]. Furthermore, Triassic sauropods such as *Antetonitrus* and *Isanosaurus* have been recently found to either be poor analogs for the basal sauropod condition[16], or incorrectly dated[17].

Here we describe material belonging to a new medium-sized sauropodiform dinosaur possessing a more apomorphic character suite than anything previously collected from within the Early Jurassic upper Elliot Formation of South Africa. This material contributes not only to our understanding of the timing of the genesis and subsequent radiation of Sauropoda, but also helps elucidate macroevolutionary and palaeoecological trends pertaining to the guild-structuring and functional diversity of Sauropodomorpha within the earliest Jurassic.

Institutional abbreviations: BP: Evolutionary Studies Institute (previously Bernard Price Institute), University of the Witwatersrand, South Africa.

Results

SYSTEMATIC PALAEONTOLOGY

Saurischia Seeley 1888
Sauropodomorpha von Huene 1932
Sauropodiformes Sereno 2007 (sensu[16])
Sauropoda Marsh 1878
Pulanesaura eocollum gen. et sp. nov.

Holotype. The neural arch of an anterior dorsal vertebra (BP/1/6882) that is missing the dorsal apex of the neural spine.

Type locality and horizon. The *Pulanesaura* material was obtained from a small (3 m × 3.5 m) quarry on the farm Spion Kop 932 in the Senekal District of the Free State, South Africa (Fig. 1). The quarry is located just over a kilometer East-North East of the holotype locality of *Aardonyx celestae*, in a higher stratigraphic position than that taxon within the early Jurassic upper Elliot Formation. The much smaller *Arcusaurus pereirabalorum* was recovered from the edge of the same quarry, and a detailed schematic of the excavation is figured in[18] (see also Supplementary Information Fig. S1). The upper Elliot Formation on Spion Kop consists of a series of stacked channel sandstone bodies with little intervening overbank siltstones, the quarry itself being situated in a poorly bedded, coarse to sandy siltstone lens. The two-dimensional geometry and internal facies relationships of this lens suggests that it represents the fill of a low-energy, cut-off channel. Most age estimates suggest that the upper Elliot Formation is no younger than the Pliensbachian (183–191mya), with a consensus range of late Hettangian to Sinemurian (i.e., ~200mya or younger[19,20]).

Referred material. The Spion Kop assemblage is composed of the partial remains of at least two subadult-to-adult individuals. The referred material is considered conspecific with the holotype with respect to the following: a) the bones were found in close association in a fine matrix with no evidence of high velocity transport; b) the different bones give a consistent phylogenetic signal that argues against a random aggregation of taxa having been brought together from a wide area in a flowing fluvial regime; and c) duplicated elements show no evidence of character conflict or other factors that may suggest the presence of more than one species of large-bodied, derived sauropododiform dinosaur. The referred material consists of: 2 teeth; mid-cervical vertebra; five dorsal neural arches; a single right dorsal rib; three caudal vertebra; left clavicle; distal right humerus; left ulna; ?right fourth metacarpal; three ischia; left and right tibiae; two first pedal unguals (see Supplementary Information for catalogue details). The humerus was recovered from a lens within the main quarry but approximately 1m below the rest of the material. While this element is provisionally referred to *Pulanesaura* with reference to the above criteria, its relative disassociation from the rest of the material means it is excluded from the diagnosis.

Etymology. "*Pulane*", Sesotho, meaning "rain-maker/bringer", in reference to the rain-soaked conditions under which the dinosaur was excavated, plus "-saura", Latin, feminine, meaning "lizard"; "eo", Greek, meaning "dawn", plus "collum", Latin, meaning "neck", in reference to the hypothesized function of the neck presaging the sauropod condition in the new taxon.

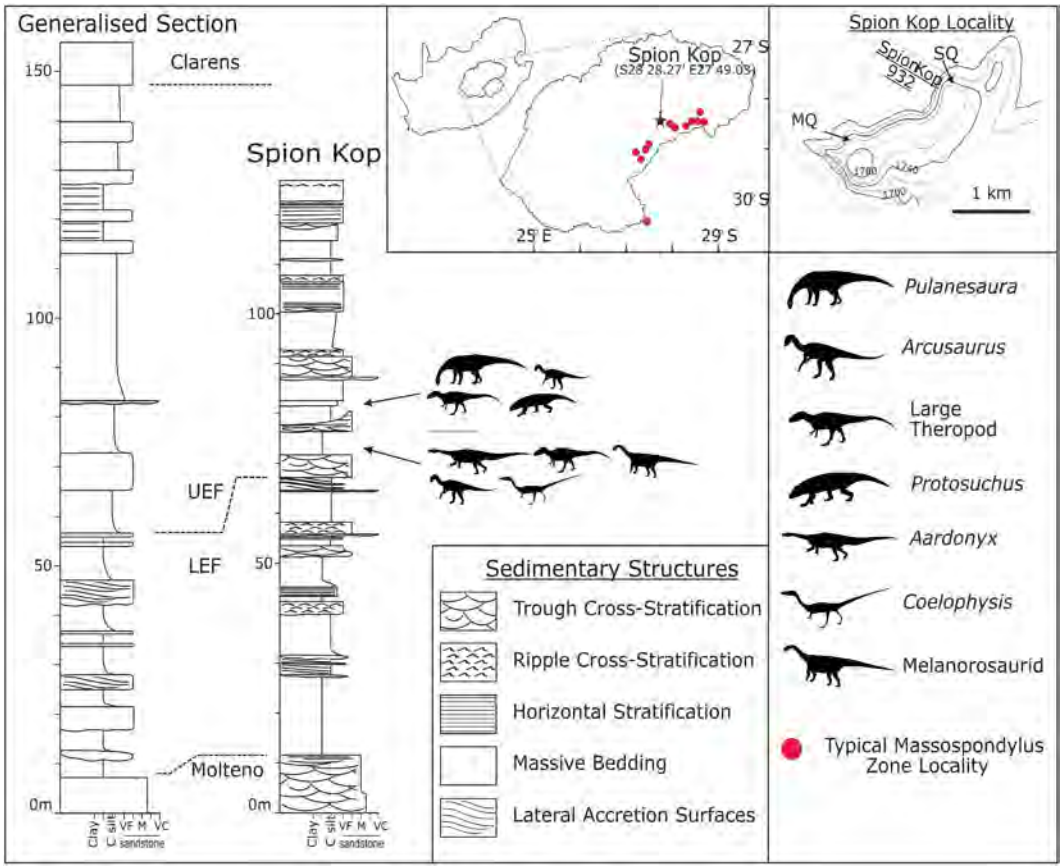


Figure 1. Stratigraphic succession of Spion Kop Farm, illustrating the faunal assemblages recovered from the upper Elliot Formation as preserved on the farm. SQ, 'Sauropod [*Pulanesaura*] Quarry'; MQ, 'Marc's [*Aardonyx*] Quarry'. All cartographic information was recorded by JN and reproduced using Inkscape (vers. 0.91). All dinosaur silhouettes were drawn by the authors except for the one next to *Arcusaurus*, which is licensed under the CC-BY-SA GNU Free Documentation License and is attributed to Arthur Weasley. The original image and use policy for the image is available here: http://en.wikipedia.org/wiki/File:Thecodontosaurus.jpg.

Diagnosis. A medium-sized transitional sauropodiform dinosaur, the holotype (BP/1/6882) of which is diagnosed with respect to a unique set of characters (autapomorphies marked with an asterisk): Neural spine high and anteriorly inclined; prezygapophyses mediolaterally extensive and sheet-like*; and anterior infradiapophyseal fossae showing an externally constricted, medially-tapering, 'pinched' morphology*.

The referred material is diagnosed thusly: Teeth with apicobasal grooves on both the labial and lingual surfaces, denticles restricted to the apical third of the crown, and crowns with extensive enamel wrinkling easily discernible with the naked eye; anterior-to-middle cervical vertebrae with anteroposteriorly short and dorsoventrally high neural spines and dorsally-raised, obliquely-set postzygapophyseal articular facets; dorsoventrally tall neural spines in the anterior dorsal vertebrae, being approximately three times taller than anteroposteriorly long; middle-to-posterior dorsal neural arches with neural spines over 1.6 times as high as long; anterior caudal vertebra with incipient prezygadiapophyseal laminae; anterior caudal transverse processes laterally restricted, triangular in shape and located on both the neural arch and centrum, the latter being almost twice as high dorsoventrally as anteroposteriorly long and lacking a ventral sulcus; hyposphene on anterior caudal vertebra; mediolaterally expansive radial fossa on the proximal ulna; tibia with a proximal surface over twice as long anteroposteriorly than transversely wide with similarly transversely restricted shaft; transversely compressed first pedal ungual with a convexly rounded proximoventral margin.

Description. The crowns of two isolated teeth, both of which are broken at the root-crown juncture, are known for *Pulanesaura*. Their semi-spatulate shape is similar to that of many non-sauropodan sauropodomorphs and most basal sauropods (e.g., *Tazoudasaurus*[21], *Barapasaurus*[22], and *Shunosaurus*[23]) (Fig. 2). Both teeth are 'D'-shaped in cross-section with a strongly convex labial surface, while the larger of the two (BP/1/6204) is slightly lingually recurved. Denticles are present on the apical third of

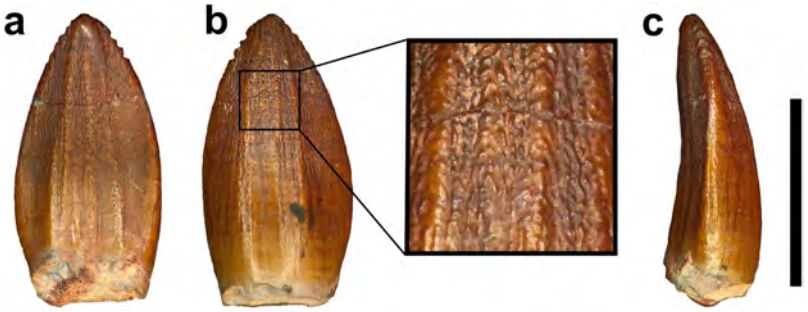


Figure 2. Tooth of *Pulanesaura eocollum* (BP/1/6204) in (**a**) lingual view; (**b**) labial view with expanded detail of tooth surface; (**c**) ?mesial view. Scale bar equals 1cm. Photographs by BWM.

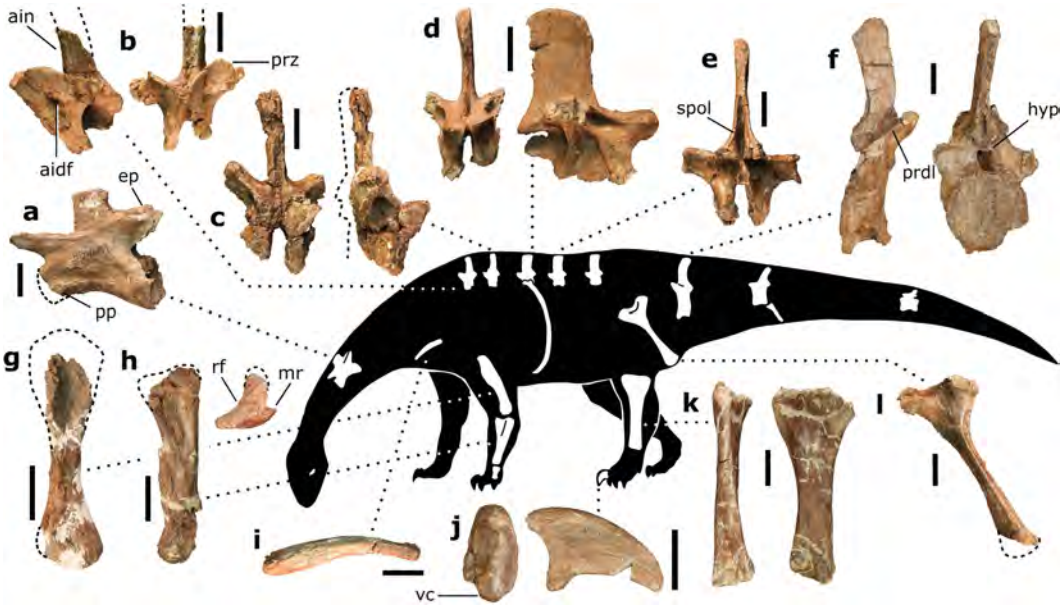


Figure 3. Representative bones of *Pulanesaura eocollum*. (**a**) anterior-to-middle cervical vertebrae (BP/1/6199) in left lateral view; (**b**) holotypic anterior-most dorsal neural arch (BP/1/6882) in left lateral and anterior views; (**c**) anterior dorsal neural arch (BP/1/6984) in anterior and right lateral views; (**d**) anterior mid-dorsal neural arch (BP/1/6183) in anterior and right lateral views; (**e**) middle dorsal neural arch (BP/1/6770) in posterior view; (**f**) anterior caudal vertebra (BP/1/6646) in right lateral and posterior views; (**g**) right humerus (BP/1/6193) in anterior view; (**h**) left ulna (BP/1/6210) in lateral and proximal views; (**i**) ?left clavicle (BP/1/6752) in dorsal view; (**j**) left pedal ungual I (BP/1/6186) in proximal and medial views; (**k**) left tibia (BP/1/6200) in anterior and lateral views; (**l**) right ischium (reversed) (BP/1/7366) in lateral view. Abbreviations: aidf, anterior infradiapophyseal fossa; ain, anterior incline of the neural spine; ep, epipophysis; hyp, hyposphene; mr, medial ridge; pp, parapophysis; prdl, prezygodiapophyseal lamina; prz, prezygapophyses; rf, radial fossa; spol, spinopostzygapophyseal lamina; vc, ventral convexity. Scale bars equal 5 cm in a-f and i, j; 10 cm in g, h, k, l. Silhouette drawn by BWM Photographs by BWM.

the crown but are only minimally expressed. Despite being both phylogenetically and serially plastic, denticles restricted to the apical third are present in most basal sauropods (e.g., *Spinopohorosaurus*[24], *Barapasaurus*[22,25]). The teeth display strong apicobasal fluting on both the labial and lingual surfaces, with this being especially pronounced on the latter surface in which a series of grooves radiate symmetrically from either side of the mesiodistal midline. These grooves are interpreted as incipient lingual sculpting, which is present in all eusauropods[26]. Prominent enamel wrinkling is present in the apical half of the tooth crown, as in sauropods[25].

The single preserved cervical vertebra is probably from the anterior to middle part of the neck and is missing the anterior end of the centrum, precluding determination of whether the bone was opisthocoelous as in more derived sauropods or amphicoelous as in all known non-sauropodan sauropodomorphs[2] (Fig. 3a). The centrum is acamerate as in non-sauropodan sauropodomorphs, but is lower than the neural

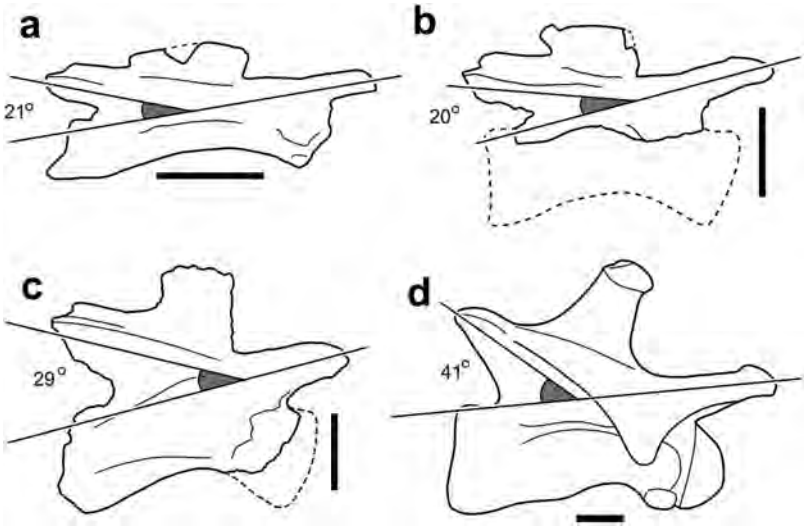


Figure 4. Changes in morphology of the anterior-to-middle cervical vertebrae throughout Sauropodomorpha. (**A**) *Massospondylus* (BP/1/5241); (**B**) *Aardonyx* (BP/1/6662); (**C**) *Pulanesaura*, (BP/1/6199); (**D**) *Patagosaurus* (from[29]). Scale bars equal 5cm.

arch in the dorsoventral height of the posterior face, a derived feature shared with all sauropods (sensu[27]). The diapophyses are preserved as low tubercles, consistent with the interpretation of the vertebra as from the anterior half of the cervical series, while the absence of pronounced diapophyseal laminae retains the plesiomorphic condition for Sauropodomorpha (although see[4]). However, the postzygapophyses are elevated with respect to the prezygapophyses, with the former dorsally offset from the sagittal plane by about 30°, a morphology consistently observed in basal sauropods (e.g., '*Kotasaurus*'[28], *Tazoudasaurus*[21], *Patagosaurus*[29], Fig. 4). The neural spine is comparatively tall for an anterior/middle cervical, with its maximum dorsoventral height roughly equivalent to its anteroposterior length.

There are five dorsal neural arches preserved, representing each region of the dorsal axial column (Fig. 3b–e). With the exception of the features of the holotypic dorsal vertebra mentioned in the diagnosis (see also Fig. S2), the most remarkable aspect of the dorsal vertebrae of *Pulanesaura* is the great relative height of the neural spines of the anterior dorsal vertebrae, which are approximately three times as high as anteroposteriorly long (Fig. 3c). In progressively posterior dorsal vertebrae the neural spines increase in length along the sagittal axis, changing from a distinctly anteroposteriorly compressed morphology in the anterior-most elements to more mediolaterally narrow, anteroposteriorly elongate neural spines from the mid-dorsals onwards (Fig. 3d). The neural spines of the middle-to-posterior dorsals nonetheless remain relatively high for basal Sauropodomorpha, with their dorsoventral height being over 1.6 times the length of their respective bases. Spinal laminae are restricted to the sheet-like spinopostzygapophyseal laminae (especially prevalent in the mid-dorsals onwards) that form large, buttressing structures between the postzygapophyses and the posterior margins of the neural spine (Fig. 3e). These structures are finer, and the post-spinal recess that they frame deeper, than the same processes in *Antetonitrus* (BP/1/4952).

Pneumatic sculpting is possibly present within the posterior infradiapophyseal fossa of one of the posterior dorsal neural arches, a morphology described in detail in Yates *et al.*[30].

The centrum of the anterior caudal vertebra is biconcave, with its posterior facet almost twice as high as the anteroposterior length of the ventral surface, lending a considerably anteroposteriorly compressed morphology to the bone (Fig. 3f). This morphology is only known in *Tazoudasaurus*[21] outside of Eusauropoda. There is a pronounced offset between the anterior and posterior articular facets, with the ventral margin of the posterior articular facet located at a level ventral to that of the anterior facet. No sulcus is present on the ventral surface of the centrum. The neural spine is three times higher than anteroposterior length of the base, proportionally taller than in any other taxon known from the Elliot Formation. Although the dorsal margins of both transverse processes/diapophyses are not preserved, the well-preserved struts of bone that extend ventrolaterally from the prezygapophyses strongly suggest the presence of low yet well-defined prezygadiapophyseal laminae, possibly representing the incipient development of the laminar configuration seen in the anterior caudals of more derived sauropod taxa (e.g., *Tazoudasaurus; Mamenchisaurus*[31]). The anteroposteriorly short transverse processes are preserved as laterally abbreviated, wedge-shaped protuberances than span the neurocentral juncture, showcasing the derived condition within Sauropodomorpha. Ventral to the postzygapophyses a small yet well-developed hyposphene is present.

The single ?left clavicle is spatula-shaped, with a tapered medial end and an expanded lateral end (Fig. 3i). The element is broadly triangular in cross-section, with the apex of the triangle directed dorsally,

similar to clavicles of *Massospondylus* (BP/1/5241). The ventral surface of the expanded lateral end is heavily striated, suggesting strong ligamentous attachments with the acromial region of the scapula. The clavicle is moderately bow-shaped in dorsal view, with the dorsoventrally flattened lateral end directed posteriorly with respect to the medial end. This contrasts with the comparatively straight clavicles of more derived sauropod dinosaurs (e.g., *Spinophorosaurus*[24], *Omeisaurus*[32]; *Jobaria*[33]).

Although the proximal end of the humerus is very poorly preserved, the general morphology is reminiscent of that of *Vulcanodon.* This is most evident with respect to the long, anteroposteriorly narrow humeral shaft that extends proximally to over half the preserved length of the humerus, the minimal transverse expansion of the distal condyles, and the absence of a clearly defined cuboid fossa[12] (Fig. 3g).

The ulna is missing the proximal articular surface (Fig. 3h). Nonetheless, a deep, mediolaterally extensive radial fossa is readily observable[34]. The medial process of the proximal ulna of *Pulanesaura* is distinct in being a well-defined strut of bone that rises from about the mid-height of the shaft, appearing to become increasingly anteroposteriorly narrow towards its apex. This differs from the condition observed in *Antetonitrus* in which the medial process is an obtusely delineated ridge of bone that is thicker anteroposteriorly than laterally (BP/1/4952). However, it is possible that this feature is due to deformation.

The manus is currently represented by a single metacarpal IV, which is triangular in proximal view and stout in general proportions, consistent with the semi-stout, possibly load-resisting morphology of the manus of derived sauropodiforms.

The ischium retains the plesiomorphic sauropodomorph condition of a long, cross-sectionally triangular ischial shaft with a dorsoventrally expanded distal end (Fig. 3l).

The tibia showcases the 'vulcanodontid' condition of having a proximal articular surface is over twice as long anteroposteriorly than transversely wide (Fig. 3k). As in *Antetonitrus* and more derived sauropodiforms, this surface is relatively flat with respect to the horizontal plane, lacking the anterodorsal incline of the proximal end seen in more basal forms. Nonetheless, the cnemial crest of *Pulanesaura* retains the basal condition for Sauropodomorpha insofar as the anterior-most projection of the crest also represents the highest proximal point of the tibia. In the basal sauropods *Vulcanodon*[12], *Tazoudasaurus*[21] and *Spinopohorosaurus*[24] the anterior-most projection of the cnemial crest is located approximately at the proximodistal midpoint of the process. The shaft of the tibia is mediolaterally compressed in a similar, if slightly less pronounced, manner to that of *Tazoudasaurus* and *Vulcanodon*. In contrast, non-sauropodan sauropodomorphs tend to display tibial shafts that are subcircular in cross-section.

Similar to the condition in basal sauropods, pedal ungual I is a tall, mediolaterally compressed bone with a ventrally convex proximal surface (Fig. 3j). In contrast, the first pedal ungual of derived non-sauropodan sauropodiform taxa (e.g., *Antetonitrus*; *Blikanasaurus*) tends towards a dorsoventrally squat morphology in which the proximal surface is ventrally flat[16].

A cladistic analysis of the relationships of *Pulanesaura* was conducted using a modified version of the data matrix of McPhee *et al.*[35], resulting in 69 MPTs with a shortest length of 1264 (see Supplementary Information). The strict consensus tree of these MPT's resolves *Pulanesaura* as the sister-taxon to *Vulcanodon* + more derived sauropods (Fig. 5). This position is supported by the following unambiguous synapomorphies: pneumatic sculpting within the posterior infradiapophyseal fossa of the dorsal vertebrae (ch. 162); height of mid-dorsal neural spines greater than 1.5 times the length of the base (due to a possible reversal to the plesiomorphic state in *Gongxianosaurus*) (ch. 167); well-developed, sheet-like spinopostzygapophyseal laminae in the dorsal vertebrae (ch. 171); anterior caudal transverse process extending from the neural arch to the centrum (ch. 188); and a dorsoventrally tall, transversely flattened first pedal ungual (ch. 367). The derived position of *Pulanesaura* is also supported by a number of characters that are either rendered ambiguous due to a lack of information at nodes immediately basal or apical to it, or present a slightly more inclusive distribution (see Supplementary Information). These include: coarsely wrinkled tooth enamel (ch. 117); longitudinal grooves on the labio-lingual surfaces of the teeth (ch. 119); mid-cervical neural arches higher than the posterior face of the centrum (ch. 133); hyposphenal ridge on the anterior caudal vertebra (ch. 186); prezygadiapophyseal laminae on the anterior caudal vertebra (ch. 187); absence of a well-defined flexor fossa on the anterior surface of the distal humerus (ch. 213); proximal surface of the tibia over twice as long anteroposteriorly than transversely wide (ch. 310); and the anteromedial corner of the distal tibia forming a non-acute, right angle (ch. 315).

Because of differing taxonomic opinions on the node-or-stem-based definition for Sauropoda, our phylogenetic hypothesis of *Pulanesaura* places it as either a basal sauropod (*sensu*[27,36], or as the sister taxon to Sauropoda (*sensu*[16,37,38]). Regardless of taxonomic definition, *Pulanesaura* is the most derived sauropodiform known from the Elliot Formation or securely aged contemporaneous deposits worldwide for which its phylogenetic relationships can be stated with relative confidence.

Discussion

Pulanesaura is part of an increasingly taxonomically diverse group of sauropodomorph dinosaurs from the upper Elliot Formation. Although the exact age of these deposits is still under investigation[39], it is clear from multitaxon deposits at localities like Spion Kop[4,18] that at least some Elliot sauropodomorphs lived contemporaneously (Fig. 1), suggesting the presence of guild-level divisions amongst sympatrically associated taxa. Although niche partitioning via differential feeding strategies and neck mechanics of contemporaneous Eusauropoda (i.e., 'low-browsing' diplodocoids vs. 'high-browsing' titanosauriforms) has been discussed at length in the literature (e.g.,[40–43]), it has never been proposed as an explanatory

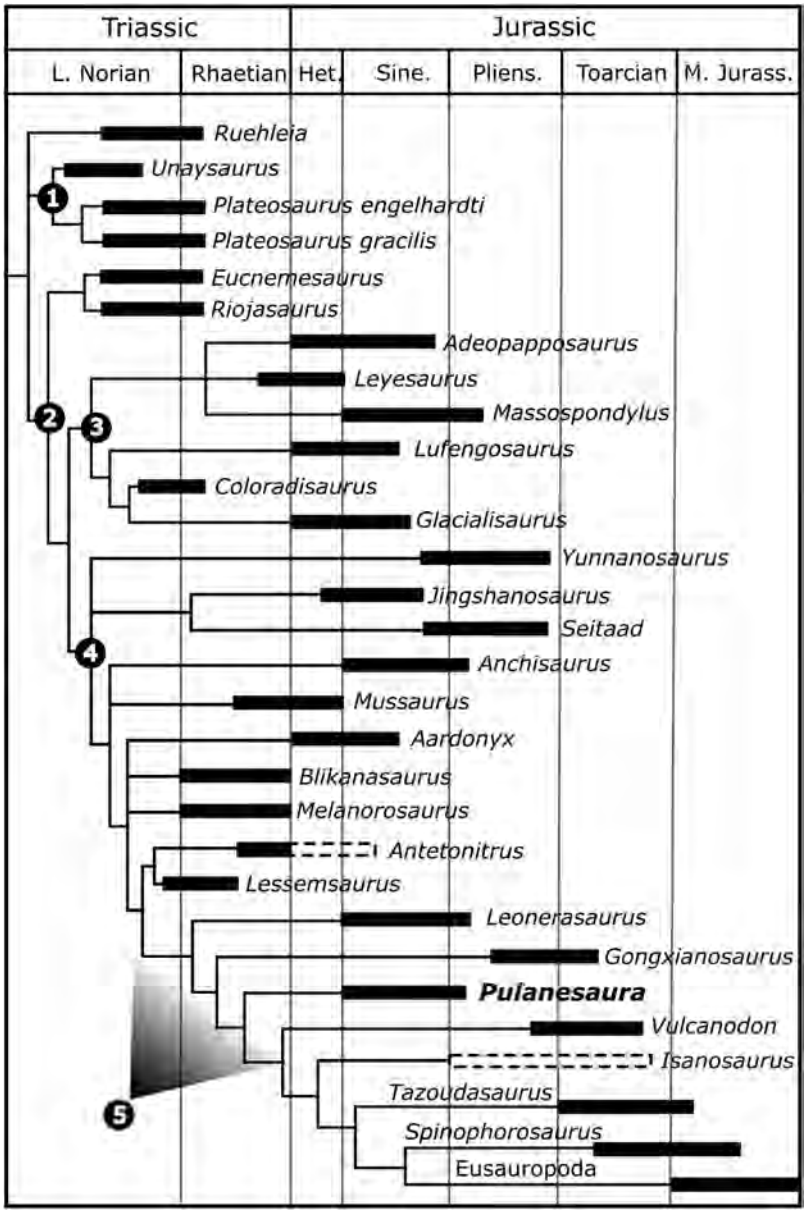


Figure 5. Abbreviated strict consensus tree showing relationships and hypothesised stratigraphic ranges of plateosaurian dinosaurs (*sensu*[27]). Dashed lines represent uncertainty in temporal duration. 1, Plateosauridae; 2, Massopoda; 3, Massospondylidae; 4, Sauropodiformes; 5, Sauropoda (node left undesignated in order to reflect current disagreements regarding the taxonomic definition of Sauropoda [see text]).

model for the diversity of basal sauropodomorph taxa in Late Triassic/Early Jurassic deposits like the Elliot Formation. Although the exploitation of increasingly larger vertical foraging ranges is often cited as a key ecological driver in the origins of the sauropodan bauplan (e.g.,[44–46]), this fails to explain the continuing numerical superiority of non-sauropodan sauropodomorphs for most of the Early Jurassic, many of which were of comparable size to the earliest sauropods (e.g., *Jingshanosaurus*; *Aardonyx*).

The derived suite of features present in *Pulanesaura* place it as sister to Sauropoda (or as a basal member of this taxon depending on phylogenetic definition) and strongly differentiates it from other known Elliot sauropodomorphs. These features relate primarily to changes in the feeding apparatus (wrinkled enamel in the dentition), axial morphology (non-planar cervical zygapophyseal facets; high neural spines in both cervical and anterior dorsal vertebrae) and forelimb (lack of flexor-pit on the distal humerus; deep radial fossa on the proximal ulna). These features, and their departure from the plesiomorphic sauropodomorph condition, indicate a genuine functional distinction occurring at the very base of Sauropoda with implications for our understanding of both the basal foraging strategy, and evolutionary context, of the sauropodan condition.

Most sauropodomorph taxa known from the latest Triassic through the earliest Jurassic, including those thought to be antecedent to the sauropodan bauplan (e.g., *Melanorosaurus; Lessemsaurus*; *Antetonitrus*) retain the semi-abducted, flexed forelimb posture plesiomorphic to Sauropodomorpha[47]. In some taxa, e.g., *Antetonitrus*, osteological markers suggest the presence of hypertrophied caudofemoralis brevis musculature that would have assisted with occasional bipedal locomotion[16]. The combination of a mobile grasping hand, flexed forelimb, and at least some degree of facultative bipedality probably represents an early solution to a catholic feeding regime in the first bulk-browsing dinosaurian herbivores. While rearing, and with the neck extended and raised at an oblique angle to the substrate, some of the larger non-sauropodan sauropodiform taxa could have fed at heights of ~5 meters. With the majority of the available forage thought to have occurred between ground level and 6 meters[44], this would have enabled exploitation of the great majority of the browsing gallery.

However, while a dexterous hand and flexed/abducted forelimb would have been of appreciable utility in either grasping at foliage and/or supporting the body while leaning sub-vertically against the trunks of large trees, these same features may have compromised sauropodomorph fitness at some point along the size continuum[48,49]. For example, in modern eutherian mammals, all taxa with masses exceeding 300 kg have erect, non-crouched forelimbs to best mediate the increased compressive stresses on the bones[50]. Nonetheless, although the fossil trackway record suggests that facultative-habitual quadrupedality appears early in sauropodomorph evolution (e.g.,[51]) (potentially as a response to the increasingly high intake of low-quality vegetable matter and the large gut-capacities required to process it), the majority of evidence suggests a substantial delay between this novel locomotor strategy and meaningful alterations in the biomechanical efficiency of the forelimb[16]. In this respect, the uniquely massive scapular blade of non-sauropodan sauropodiform taxa such as *Yunnanosaurus*, *Lessemsaurus*, and *Antetonitrus* (and possibly *Gongxianosaurus*)[5,16,52] possibly represents a trade-off between the additional anchorage required to counteract the increased shear stresses experienced by a large-bodied quadruped with a less than erect forelimb on the one hand, and the necessary mobility of the forelimb for bipedal high-browsing on the other. Likewise, the autapomorphically long cervical vertebrae of the smaller, possibly habitually bipedal Massospondylidae can also be viewed in the context of a trade-off between overall body-size and the need to feed across as wide a range of the trophic sphere as possible[53].

In contrast to the above, the appendicular and axial morphology showcased by *Pulanesaura* potentially relates to a concerted change in the postural and behavioural locomotor complex towards an energetically conservative form of specialised low-to-mid browsing at the base of Sauropoda. In basal non-sauropodan taxa (e.g., *Plateosaurus*; *Massospondylus*; *Aardonyx*) the line of articulation across the zygopophyses of all non-posterior cervical vertebrae is only minimally offset from the sagittal. In *Pulanesaura* and other basal sauropods (e.g., ?*Lamplughsaura; Tazoudasaurus*; *Shunosaurus*; *Patagosaurus*), this relationship alters dramatically, with the postzygapophyses being offset from the prezygapophyses by as much as 40° (Fig. 4). It is possible that this change reflects alterations in the kinematic potential of the sauropodomorph neck, especially with respect to degrees of flexion along the dorsoventral axis. Similarly, the apomorphically tall anterior dorsal neural spines of *Pulanesaura* (and other basal sauropods) may instance the reorganisation and/or hypertrophy of the posterior epaxial neck musculature as a means of counteracting tensile stresses while the neck is held at a low-to-horizontal angle, while also affording additional purchase for the large dorsal neck ligaments responsible for storing the elastic energy instrumental in recovery from a ventrally flexed position[54]. The expansive, sheet-like prezygapophyses of the anterior-most dorsal vertebra also bear mention as potential bracing mechanisms at the base of the neck.

These changes, when considered alongside aspects of the *Pulanesaura* forelimb that indicate a more erect, columnar stance (reduction in flexor anatomy, anteriorly braced proximal radius), suggest the development of simultaneous and possibly interdependent innovations towards a non-grasping, fully parasagittal forelimb in concert with a neck with more anterior flexibility via a posteriorization of its muscle architecture[55]. While the coarse enamel wrinkling characteristic of sauropod teeth is of unknown functional significance, the possibility that it is related to differing functional requirements for processing flora commonly encountered at the low-to-mid browsing ranges (possibly juvenile and/or small members of the 'seed-fern' and pinophytan groups[56]) warrants future investigation. Taken in aggregate, this suite of features is strongly suggestive of a feeding strategy concentrated upon the lower ranges of the total available forage, differentiating *Pulanesaura* from contemporaneous sauropodomorphs that engaged in high-browsing, at least occasionally. Furthermore, the presence of similar (if less developed) character suites in other 'near-sauropod' forms such as *Leonerasuarus*[57] and *Lamplughsaura*[11] is suggestive of a foraging strategy that potentially optimizes as an ancestral condition for Sauropoda itself.

Recently, Sander[58] and Sander *et al.*[45], have modelled a series of evolutionary cascades, each dependent on a constellation of both primitive and novel influences, which led to the unique gigantism of sauropod dinosaurs. Many of these influences pivot upon physiological traits that are either plesiomorphic (e.g., lack of tooth-on-tooth occlusion [i.e., mastication], long neck, small head) or derived (e.g., invasive post-cranial pneumaticity) for Sauropodomorpha. While the exaptive potential of these traits in facilitating the high body masses of sauropod dinosaurs has been convincingly demonstrated in recent years[45], the timing and coalescence of these traits in terms of the diversification and global dispersal of Sauropoda is still poorly known[25,59].

The additional information provided by *Pulanesaura* places alterations of the neck and forelimb at the base of a potentially novel cascade feature in which the temporary abandonment of the higher reaches

of the browsing gallery led to the breaking of locomotory constraints inhibiting true gigantism. Sander[58] places "upright stance" at the base of the cascade "metabolism", citing the obvious energetic advantages of a limb that is oriented in the manner of an inverted pendulum, while the long neck of sauropod dinosaurs is interpreted as being ecologically and adaptively advantageous at a number of cascade levels. However, while 'upright stance' is mentioned only with reference to the hindlimb within the expanded model[58], both Remes[47] and Sander *et al.*[45], draw attention to the shift from an adductor-driven to an abductor-driven locomotory system in the forelimb paralleling the move towards gigantism in the early evolution of Sauropoda. Unfortunately, at our current anatomical resolution, changes in axial structure appear at the same time as changes in forelimb structure[29], so it is unclear whether modifications of the neck drove postural changes or vice versa. Furthermore, the lack of preservation of pivotal anatomical structures in *Pulanesaura* (e.g., scapula, complete manus/pes), as well as the persistent incompleteness of the early sauropod record, continues to obscure a clear reading of whether the shift to a fully erect forelimb occurred in a stepwise fashion from near-sauropod grade animals such as *Antetonitrus*, or represents a genuine breakaway bioecological strategy of Sauropoda *sensu stricto*.

Nonetheless, we emphasize that the adoption of a less laterally oriented forelimb, as facilitated by the anteroventral rotation of the glenoid (thus bringing the forelimb more directly in line with the vector of the ground reaction forces) and a deepening of the radial fossa of the ulna, in tandem with specific changes in the architecture of the anterior axial column, represent perhaps the most important, non-pneumatic contributions to the cascade of traits ultimately leading to sauropod gigantism[34,47]. Contextually, these changes convey an instance of niche partitioning amongst contemporaneous sauropodomorph taxa within the earliest Jurassic Elliot Formation of South Africa, one in which the loss of a regularly assumed bipedal posture placed increasing selective and mechanical pressure upon the neck to become the critical food-gathering organ, requiring in turn a stable, erect base with which to support this organ. Although obligate quadrupedality has been inferred as early as the Late Triassic with respect to the relatively derived *Isanosaurus*[60], the temporal provenance of this taxon should be treated with caution in light of recent doubts regarding the temporal relationships of the Nam Phong Formation[17].

While the scenario outlined above is hypothesised to have played an important role in taking basal sauropods out of direct competition with sympatric non-sauropodan sauropodomorph dinosaurs capable of efficient rearing, it nonetheless would have limited the amount of vegetable matter accessible to them to within only a few meters from the ground[46], potentially explaining the rarity of sauropod dinosaurs within the earliest Jurassic ecosystems. As previously noted by McPhee *et al.*[16], the major burst of sauropod diversification seems to have only occurred towards the end of the Early Jurassic, suggesting an initial lag between the suite of locomotory and biomechanical novelties already present in basal taxa like *Pulanesaura,* and the inferred spike in sauropodan fitness ultimately conferred by these novelties (see also[21]).

The unique suite of characters unequivocally shared between *Pulanesaura* and taxa immediately apical to it further supports a divergence time for Sauropoda *sensu stricto* close to the Triassic-Jurassic boundary. While rare constituents of the sauropodomorph faunal assemblage, the discovery of *Pulanesaura* demonstrates that early sauropods were nonetheless active upon the desiccated floodplain of the upper Elliot Formation, buoying the prospects for other mid-to-low-latitude early Jurassic formations to also yield basal sauropod remains. Additional finds and increased anatomical and taxonomic resolution is required in order to better test the model presented here, and to further disentangle the ecological dynamics at play in the diversification and respective specialization of different groups of sauropodomorph dinosaurs. Isotopic analysis of dental remains as a means of assessing the reality of differential trophic-level interactions between various browsing strategists would assist in the exploration of this latter question. However, biomechanical and calorific considerations are likely to prove the crucial factors in future investigations of the energetic advantages and disadvantageous inherent in the diverse modes of locomotion and food acquisition that the sauropodomorph-sauropod transition is only just now beginning to reveal.

Methods and Materials. Excavation and preparation: Exposed *in-situ* bone was consolidated using a dilute solution of Paraloid B-72 in acetone solvent. Once consolidated, the specimens were excavated with the use of both a rock saw and hand tools including rock hammers, chisels, and shovels. They were removed from the ground in plaster jackets composed of layers of burlap and plaster of Paris. During this process they were protected by a layer of newspaper dampened in water. Rock matrix was removed from the specimen in the lab primarily with handheld pneumatic airscribes. Fossilized bone was consolidated using an approximately 10% solution of Paraloid B-72 solid grade thermoplastic acrylic resin in 100% acetone solvent. Individual pieces of bone were glued together using either cyanoacrylate (various brands) or a highly concentrated (~30%) solution of Paraloid B-72 in 100% acetone solvent.

The phylogenetic analysis of *Pulanesaura* was drawn from the data matrix originally introduced by Yates[27] and subsequently employed (with various alterations) by a number of other sauropodomorph workers (e.g.,[1,16,35,36]). The data matrix (see supplementary material), comprising 55 taxa and 365 characters, was analysed using TNT 1.1[61] using a heuristic search of 1000 replicates of Wagner trees followed by TBR branch swapping with 10 trees saved per replication. Characters were equally weighted. The following 40 multistate characters were treated as ordered: 8, 13, 19, 23, 40, 57, 69, 92, 102, 117, 121,

131, 144, 147, 149, 150, 157, 162, 167, 170, 177, 205, 207, 225, 230, 237, 245, 254, 257, 270, 283, 304, 310, 318, 338, 351, 354, 356, 361, 365.

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Author Contributions

Wrote the article: B.W.M., J.N.C., M.F.B. and A.M.Y. Excavated and initially diagnosed the material: A.M.Y. and M.F.B. Stratigraphic analysis: J.N. Prepared the figures: B.M.W., J.N.C. and J.N. Conducted the phylogenetic analysis: B.W.M. and J.N.C.

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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.

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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

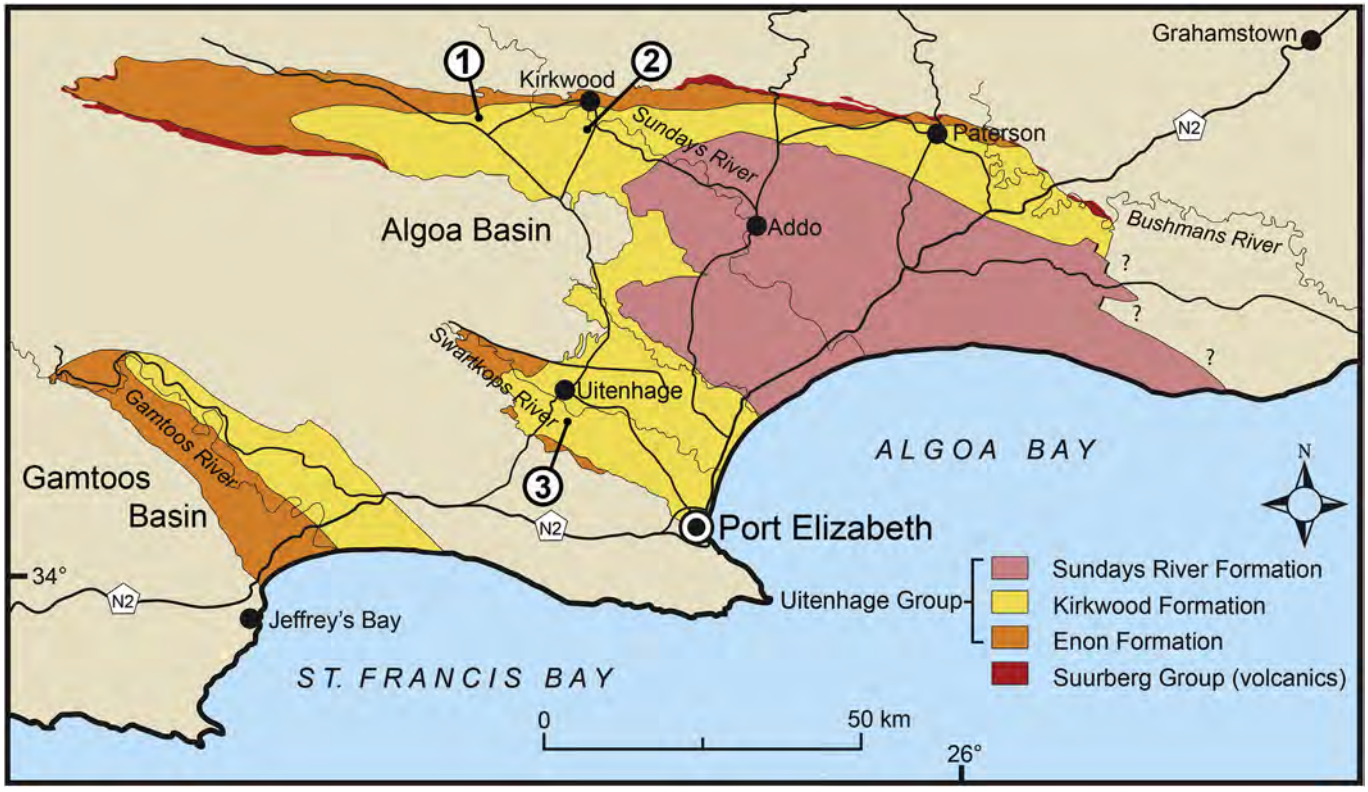


Fig. 1. Geology of the Uitenhage Group, Algoa Basin, Eastern Cape, South Africa. Numbers indicate localities of the specimens described herein. 1, Umlilo Game Park (AM 6125, AM 6128, AM 6130); 2, Kirkwood Cliffs (AM 6000, AM 6004); 3, KwaNobuhle Township (AM 4755).
Figure modified from Muir et al. (2015).

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 (~139–131 Ma; 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 Schwarz, 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 to the 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, 1932; Romer, 1956; Jacobs et al., 1996; Canudo et al., 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 (Table 1).

The nomenclature for vertebral laminae employed in this study is taken from Wilson (1999), along with the modifications suggested by Carballido and Sander (2014). 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

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 neural 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

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 (Figs. 2, 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 opisthocoelous, 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 parapophysis – 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 hypothesized 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

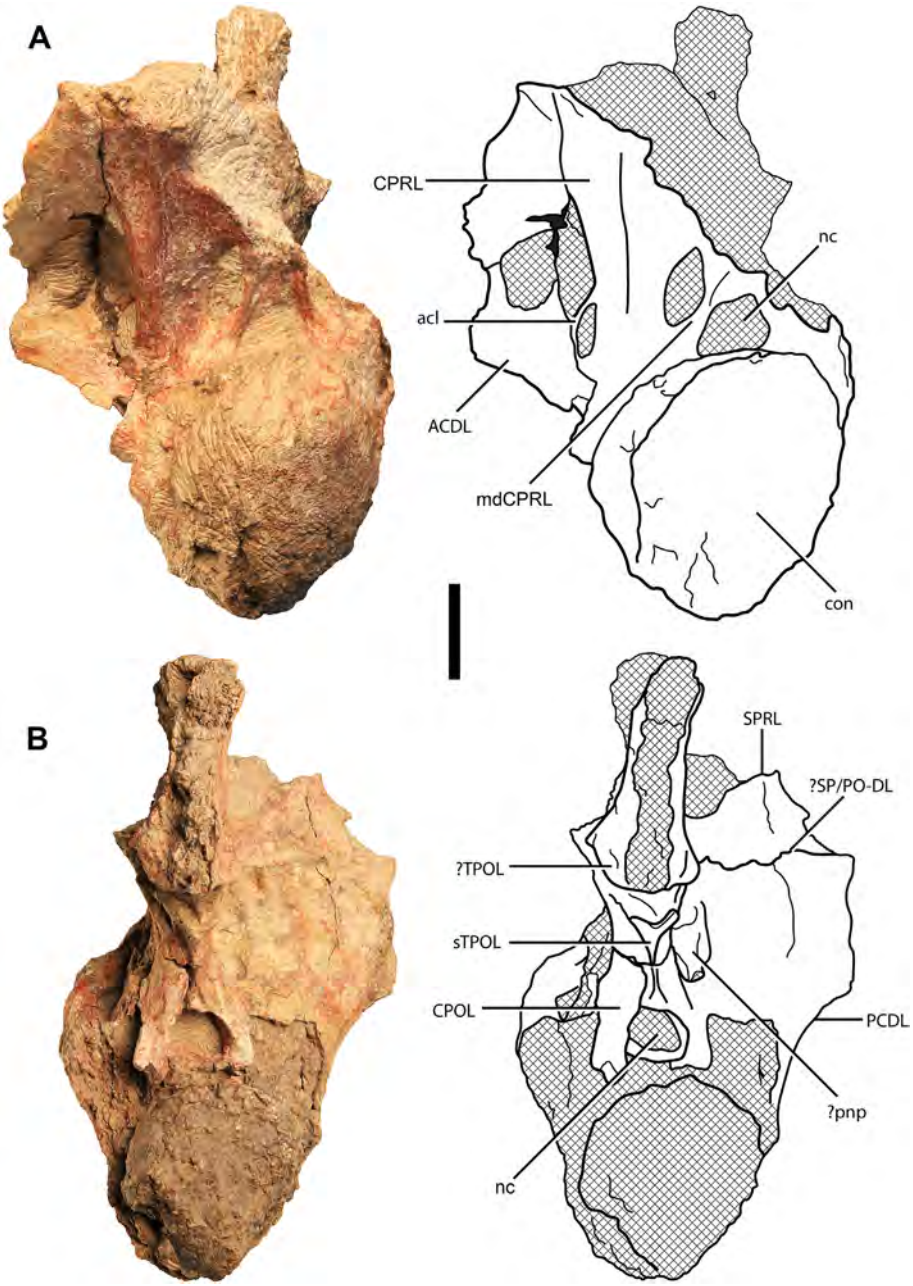


Fig. 2. AM 6125 in **A**, anterior and **B**, posterior views. See text for abbreviations. Scale bar equals 5 cm.

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° (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 2 cm 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

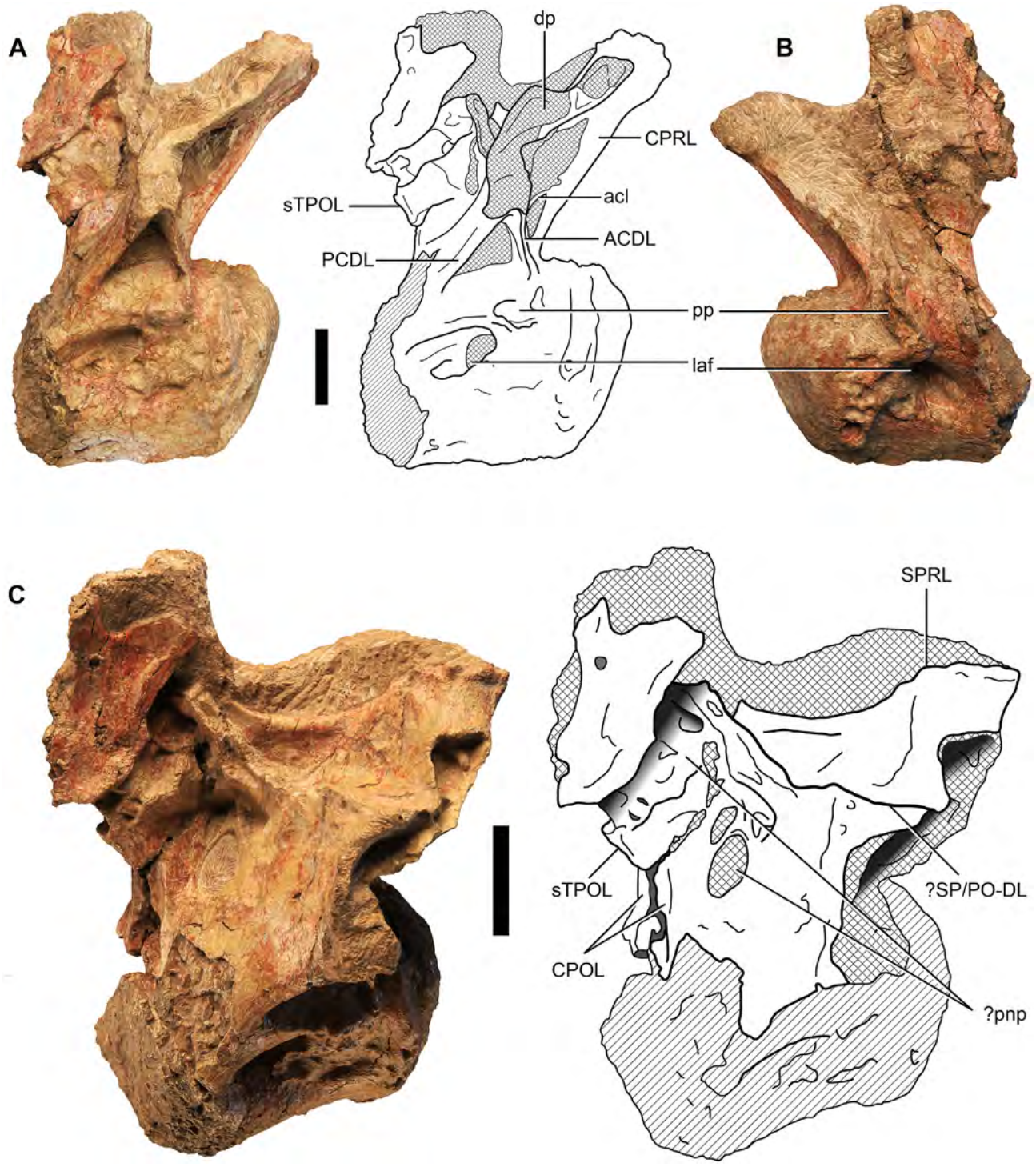


Fig. 3. AM 6125 in **A**, right lateral; **B**, left lateral; and **C**, dorsolateral views. See text for abbreviations. Scale bars equal 5 cm.

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., *Apatasaurus* (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 recognized 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 AM 6128 is therefore more similar to that observed in *Giraffatitan* (Taylor, 2009). The anterior surface of the neural spine is dominated by the paired SPRLs, processes which are likely homologous to the 'stranded' spinal laminae of Wilson (2012). These laminae are

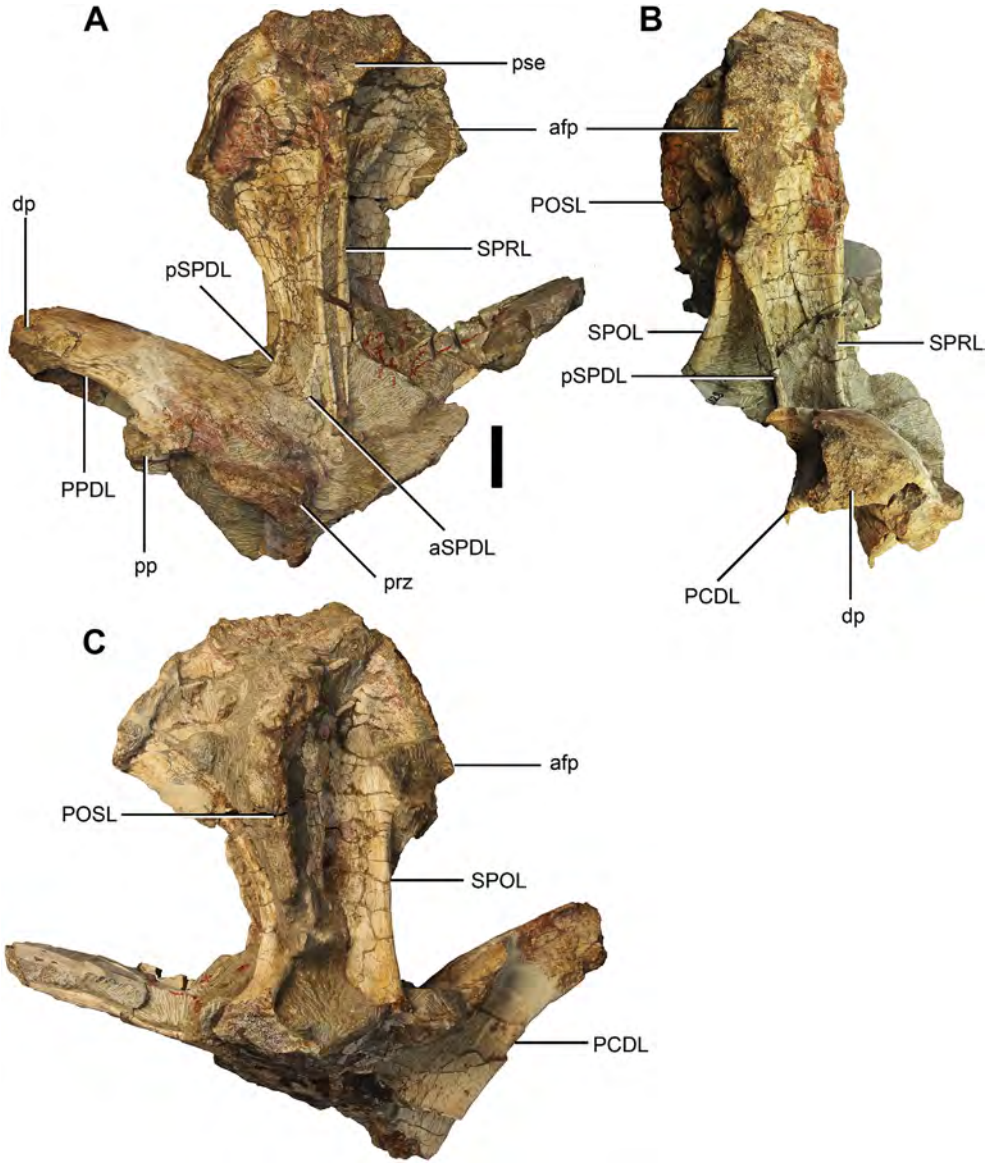


Fig. 4. AM 6128 in **A**, anterior; **B**, right lateral; and **C**, posterior views. See text for abbreviations. Scale bar equals 5 cm.

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; although see Wilson, 2012)). 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 prezygoparapophyseal 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 characterizes *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),

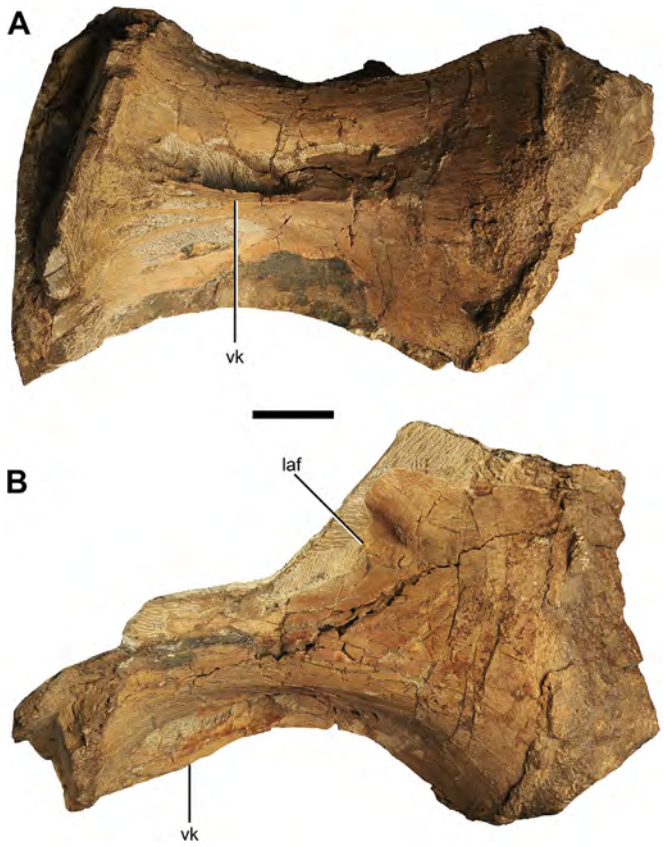


Fig. 5. AM 6130 in **A**, ventral and **B**, right lateral views. See text for abbreviations. Scale bar equals 5 cm.

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

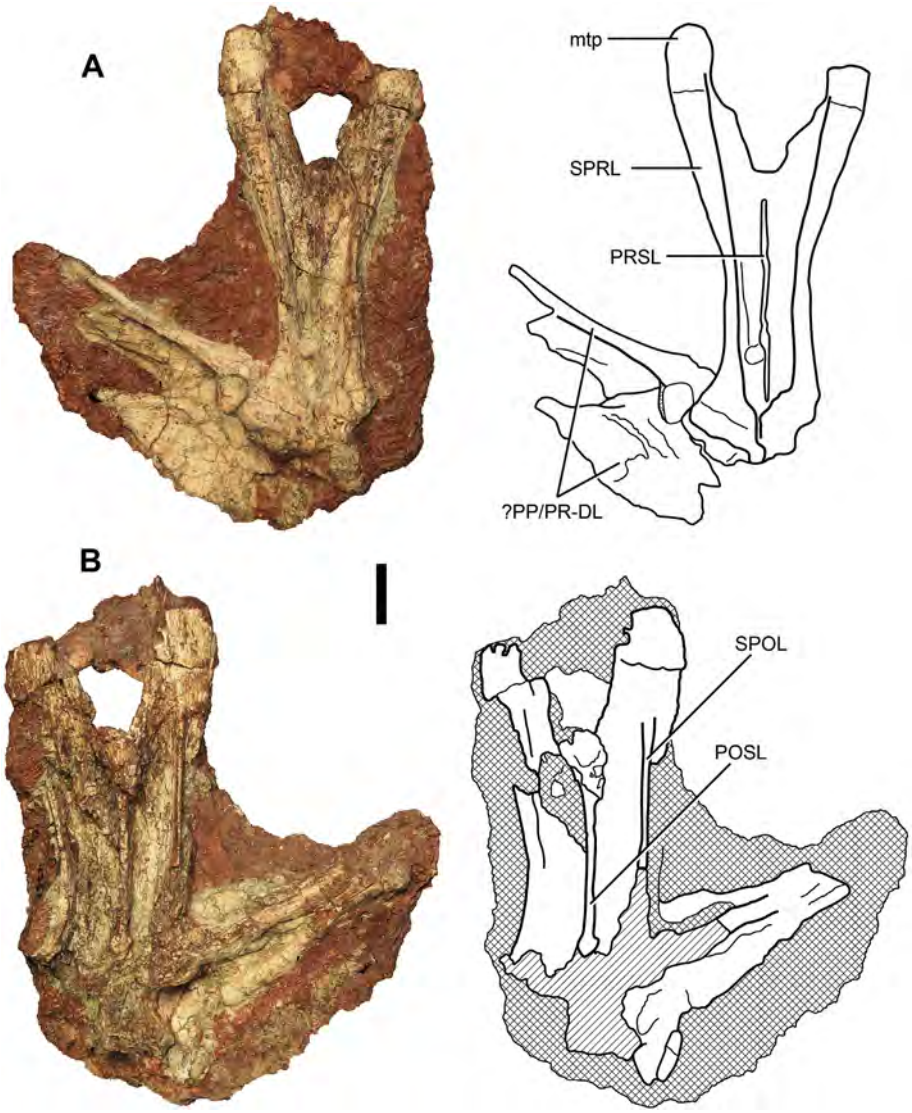


Fig. 6. AM 4755 in **A**, anterior and **B**, posterior views. See text for abbreviations. Scale bar equals 5 cm.

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

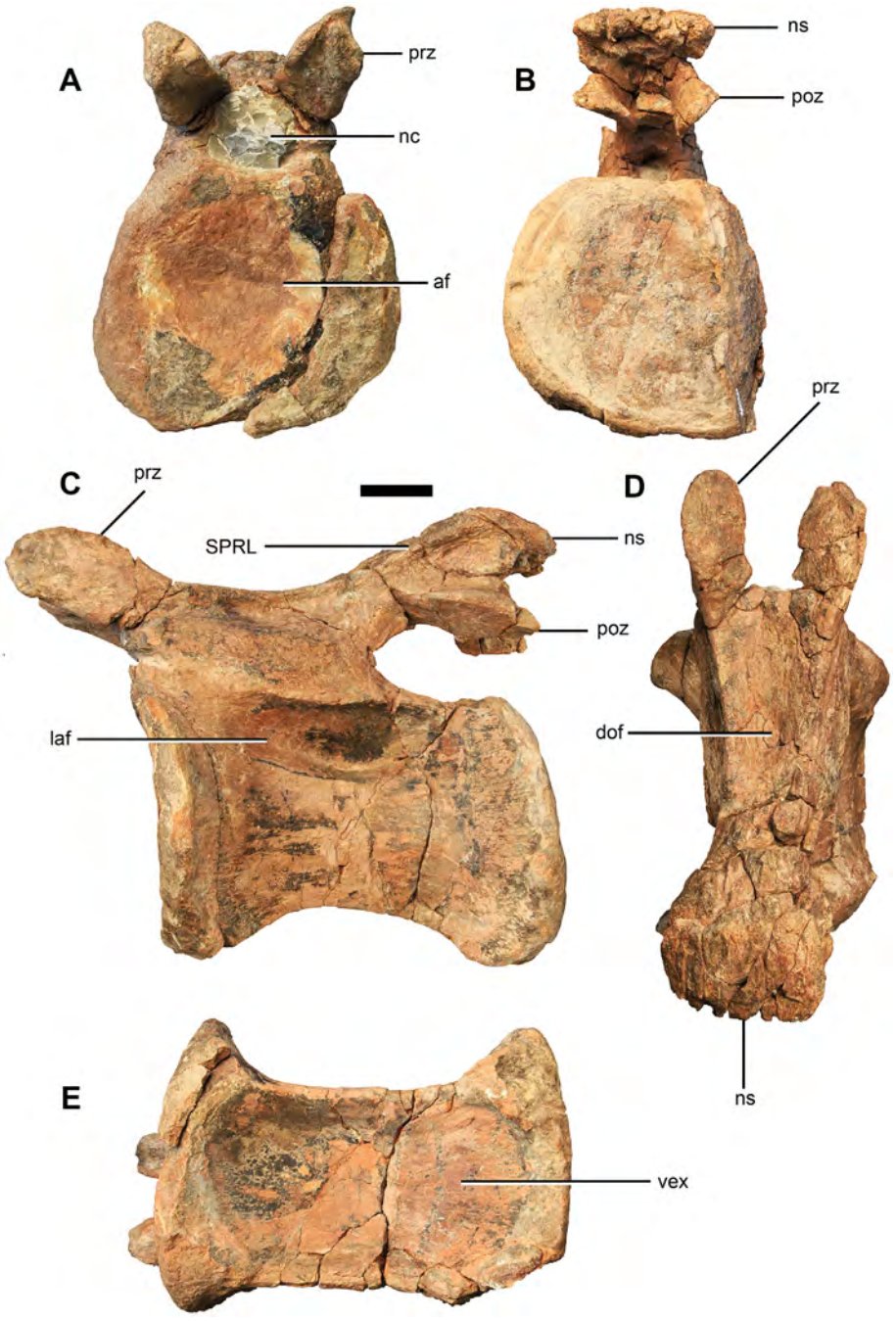


Fig. 7. AM 6000 in **A**, anterior; **B**, posterior; **C**, left lateral; **D**, dorsal; and **E**, ventral views. See text for abbreviations. Scale bar equals 5 cm.

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. 3–4 cm). 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 Upper 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° 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 as well. 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.

Description. 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

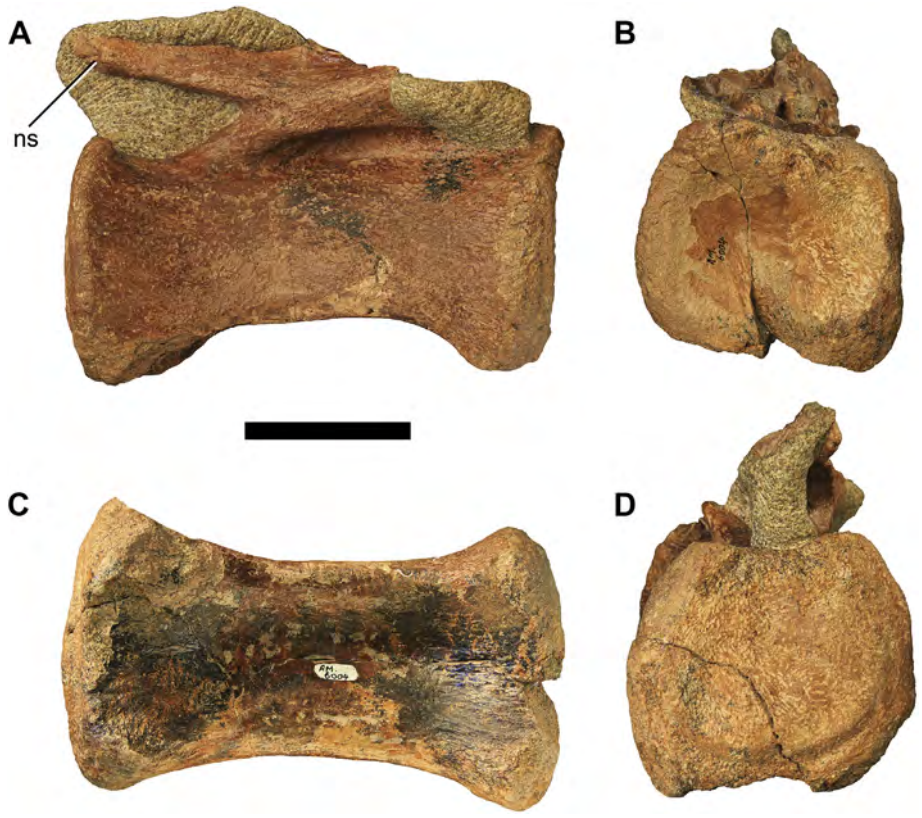


Fig. 8. AM 6004 in **A**, right lateral; **B**, anterior; **C**, ventral; and **D**, posterior views. See text for abbreviations. Scale bar equals 5 cm.

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 regionalization 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.

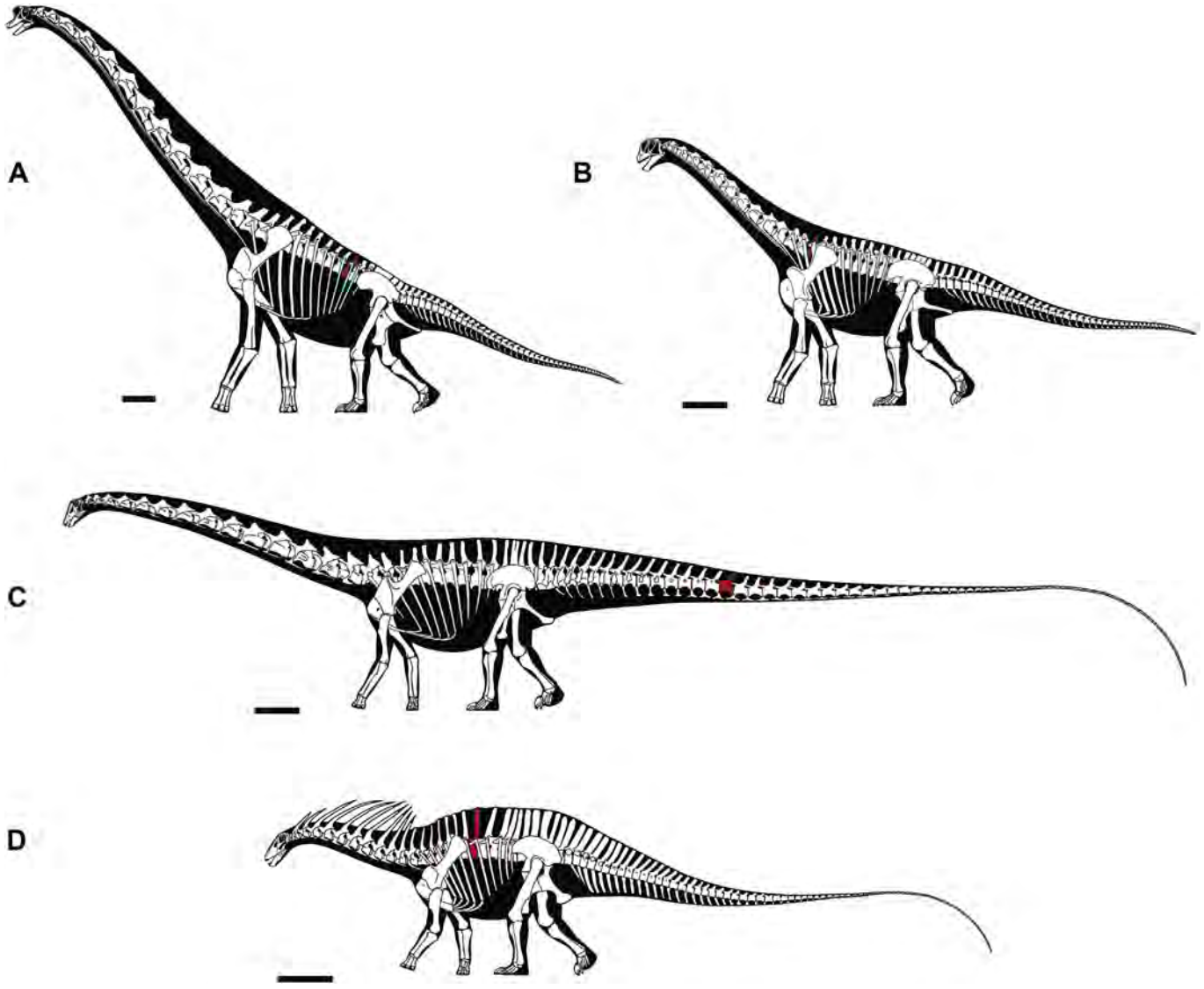


Fig. 9. Sauropod diversity present within the Kirkwood Formation. **A**, AM 6128 (after *Giraffatitan*); **B**, AM 6125 (after *Camarasaurus*); **C**, AM 6000 (after *Diplodocus*); and **D**, AM 4755 (after *Amargasaurus*). Scale bars equal 1 m.
Images courtesy of Scott Hartman.

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 hypothesized 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 recognized 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 et al., 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, 2014). 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; Mateus et al., 2014; Mocho 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 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, 2011), 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, 2014). 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

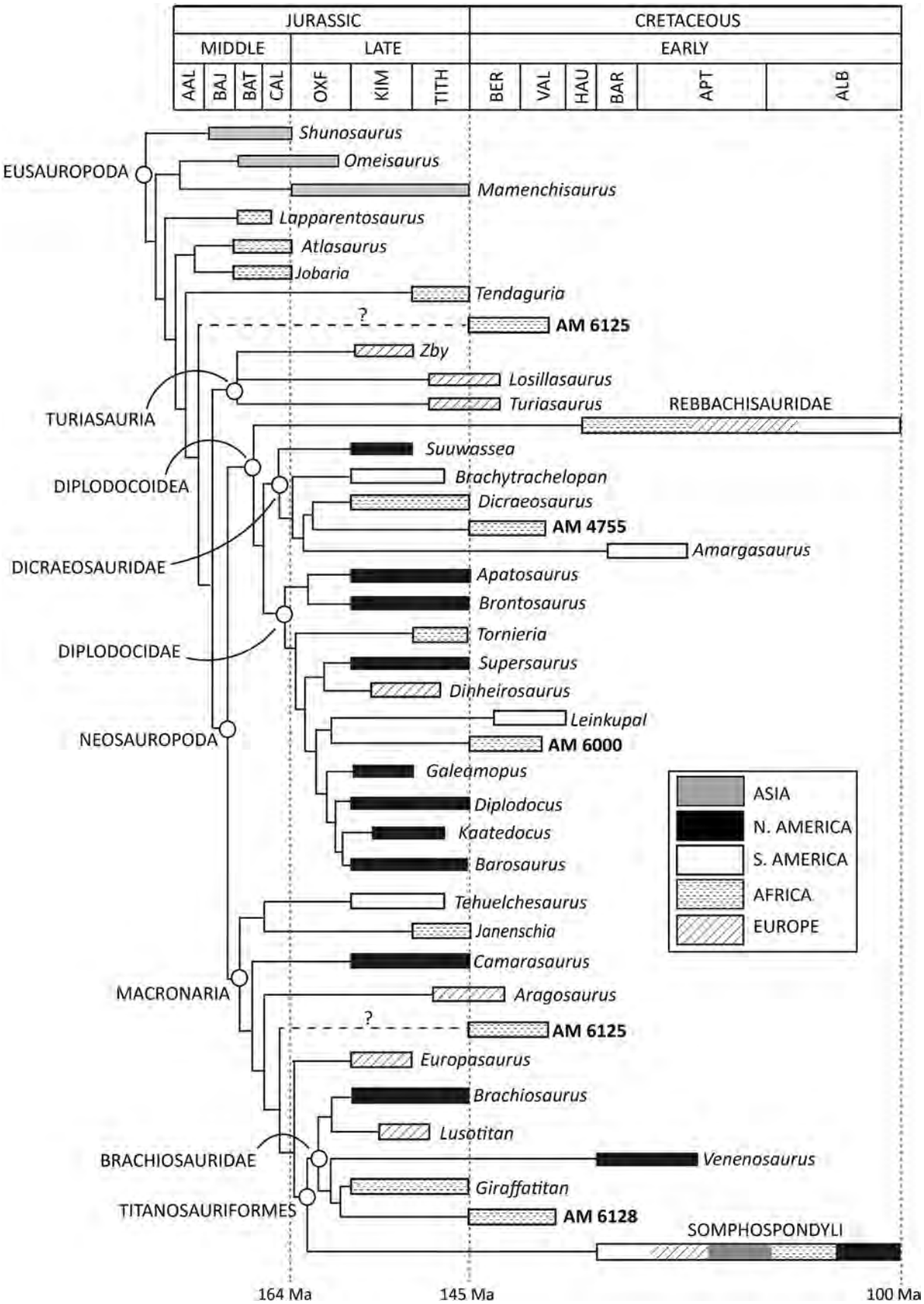


Fig. 10. Composite cladogram illustrating sauropod diversity across the Jurassic–Cretaceous boundary, with hypothetical positions of Albany Museum specimens. Phylogenetic reconstruction based on the analyses of Whitlock (2011), Mannion et al. (2013), Carballido and Sander (2014), Royo-Torres et al. (2014),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

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; see also Pereda-Suberbiola et al., 2013). 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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A hyper-robust sauropodomorph dinosaur ilium from the Upper Triassic–Lower Jurassic Elliot Formation of South Africa: Implications for the functional diversity of basal Sauropodomorpha

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ABSTRACT

It has generally been held that the locomotory habits of sauropodomorph dinosaurs moved in a relatively linear evolutionary progression from bipedal through “semi-bipedal” to the fully quadrupedal gait of Sauropoda. However, there is now a growing appreciation of the range of locomotory strategies practiced amongst contemporaneous taxa of the latest Triassic and earliest Jurassic. Here we present on the anatomy of a hyper-robust basal sauropodomorph ilium from the Late Triassic–Early Jurassic Elliot Formation of South Africa. This element, in addition to highlighting the unexpected range of *bauplan* diversity throughout basal Sauropodomorpha, also has implications for our understanding of the relevance of “robusticity” to sauropodomorph evolution beyond generalized limb scaling relationships. Possibly representing a unique form of hindlimb stabilization during phases of bipedal locomotion, the autapomorphic morphology this newly rediscovered ilium provides additional insight into the myriad ways in which basal Sauropodomorpha managed the inherited behavioural and biomechanical challenges of increasing body-size, hyper-herbivory, and a forelimb primarily adapted for use in a bipedal context.

1. INTRODUCTION

With a temporal range of potentially 15 – 20 million years, the ?late Norian to ?Pliensbachian Elliot Formation of South Africa is one of the few global terrestrial deposits to preserve the Triassic–Jurassic transition (Duncan et al., 1997; Bordy et al., 2005). Palaeontologically, the majority of recent work has focused on the formation's unparalleled sauropodomorph dinosaur record, with a growing number of valid taxa now recognised across its lower and upper subunits (e.g., Bordy et al., 2004; Yates et al., 2010; McPhee et al., 2015a, b; Otero et al., 2015). These discoveries have dramatically altered previous assessments of the morphological and taxonomic diversity present within the Elliot Formation.

Although recent discoveries in the upper Elliot Formation (Early Jurassic) evidence a more morphologically and functionally disparate range of sauropodomorphs than the otherwise ubiquitous *Massospondylus* (e.g., Yates et al., 2010; McPhee et al., 2015b), establishing the extent of taxonomic diversity of the lower Elliot Formation (Late Triassic) has proven much more challenging (McPhee et al., 2015a). Whereas this unit is clearly represented by more than the single "waste-basket" taxon '*Euskelosaurus*' (van Heerden, 1979; Kitching and Raath, 1984), the range of *bauplan* diversity for most lower Elliot taxa (i.e., *Eucnemesaurus*; *Plateosauravus*; *Sefapanosaurus*; '*Melanorosaurus*') remains relatively conservative, with this assemblage distinguished mainly by post-cranial character suites of varying subtlety and reliability (see McPhee et al., 2015a for further discussion). Compounding this problem is the recent concern that both *Antetonitrus* (currently the most derived taxon known within the "lower Elliot

Formation") and at least one specimen associated with the '*Melanorosaurus*' hypodigm (NMQR 3314 [Yates, 2007]) derive from the upper Elliot Formation. However, pending a full revision of the biostratigraphic relationships of Elliot Formation Sauropodomorpha (McPhee, Choiniere, and colleagues, under preparation), this issue is currently beyond the scope of the present contribution. Known only by a single holotypic epipodium of unparalleled robustness, *Blikanasaurus* therefore represents one of the few remaining departures from the conservative LEF bauplan (Galton and van Heerden, 1985, 1998). Unfortunately, the incompleteness of this enigmatic taxon precludes further assessment of its skeletal anatomy.

During our recent work in the collections of the National Museum, Bloemfontein, South Africa, we rediscovered a historically collected sauropodomorph ilium. This element is unprecedented in its robusticity and clearly differs from all other sauropodomorph ilia known to palaeontological science. Here we describe this ilium, which we hypothesize to be from the lower Elliot Formation. We then discuss its implications for the morphological and functional variation exhibited by the basal sauropodomorphs of the Late Triassic and Early Jurassic.

Institutional abbreviations: BMNH, British Museum of Natural History, London, United Kingdom; BP, Evolutionary Studies institute, Johannesburg, South Africa (formerly Bernard Price Institute); MB.R., Museum für Naturkunde–Leibniz-Institut für Evolutions und Biodiversitätsforschung an der Humboldt-Universität zu Berlin; NMQR, National Museum, Bloemfontein, South Africa; PVL, Paleontología de Vertebrados, Instituto 'Miguel Lillo,' San Miguel de Tucumán, Argentina; SAM-PK, Iziko-South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum fur Naturkunde Stuttgart, Stuttgart, Germany.

2. METHODS and MATERIALS

2.1 Material: NMQR 4125, a large right ilium. NMQR 4125 is readily distinguished as a dinosaur with respect to its large, entirely perforate acetabulum (Langer et al., 2010a; Nesbitt, 2011). Furthermore, it can be distinguished from both Sauropoda and Theropoda with respect to the pointed, dorsoventrally low preacetabular process that nonetheless falls considerably short of the elongate preacetabular condition of Ornithischia. It is also appreciably larger in general size than known, basal representatives of either of the latter two taxa (e.g., *Lesothosaurus* [Luca, 1984; Butler, 2005]; *Tawa* [Nesbitt et al., 2009]). NMQR 4125 is therefore confidently assigned to basal Sauropodomorpha.

2.2 Locality and Horizon: The specimen was found in a collection of material whose provenance and association is unknown. This material was collected sometime between the opening of the National Museum in 1877 and the beginning of B. S. Rubidge's tenure as director in 1980, and is potentially associated with the collection efforts of his predecessors J. van Heerden or A. W. Crompton (Rubidge pers. comm., 2016). Arbitrary numbers have been assigned to this material with hopes of assessing its relationships. The original number of the specimen (visible on the specimen) was UNS 162.

Although lacking in provenance information, it is clear that NMQR 4125 is a Stormberg Group (the last depositional series of the Karoo Supergroup) fossil. This is argued upon the following: a) the National Museum did not conduct research in southern African fossil-bearing deposits outside of the RSA (i.e., Zimbabwe, Zambia) and b) the morphology of the ilium is highly

suggestive of a non-sauropodan sauropodomorph. In contrast, the only other dinosaur-bearing unit in South Africa – the Early Cretaceous Kirkwood Formation – preserves a relatively derived assemblage of diplodocoid and basal macronarian sauropods , taxa that generally present ilia with markedly different morphologies to that observed in NMQR 4125 (see McPhee et al., 2016).

Within the Stormberg, it is unlikely that NMQR 4125 comes from the lowermost Molteno Formation given the near-total absence of vertebrate fossils known from the unit (Raath et al., 1990). Furthermore, the uppermost sedimentary unit of the Stormberg – the Clarens Formation – is characterised primarily by yellow-white aeolian sandstones, sediment that is a poor match for the matrix still adhered to the element (see below). It is therefore highly likely that NMQR 4125 derives from the middle Stormberg unit – the Elliot Formation. Additionally, we tentatively suggest that the element was collected from the Late Triassic lower Elliot Formation (LEF) with respect to the following two lines of reasoning: Firstly, in the majority of cases bone recovered from the upper Elliot Formation (UEF) is distinctly reddish in hue and often shows signs of extensive sun-baking/cracking (and/or explosive deformation). This is consistent with current assessments of the UEF as a seasonally desiccated floodplain within an ephemeral fluvial system (Bordy et al., 2004a, b). In contrast, NMQR 4125 is a mottled yellow-brown in general colouring, lacks any significant evidence of prolonged subaerial exposure, and is also free of the ironized hematite that often encases the surface of bones discovered within the UEF (*contra* Kitching and Raath, 1984). Secondly, the sizeable siltstone mass adhered to the medial surface of the ilium showcases the distinctive olive-grey and purple colouring typical of the much wetter (a meandering, perennial fluvial system) LEF (E. Bordy pers. comm, 2016). In

contrast, the UEF is generally typified by sediment that is brick-red in general colouring. Nonetheless, in the absence of genuine provenance data, the above suggestion remains somewhat speculative.

3. DESCRIPTION

NMQR 4125 is a large element, measuring 56 cm from the anterior tip of the preacetabular process to the posterior tip of the postacetabular process. The most distinguishable feature of the ilium is the low height of the dorsal iliac blade relative to the expansive transverse width of the acetabulum. Although the dorsal margin of the iliac blade immediately above the acetabulum is not fully preserved, it is clear from the unbroken dorsal margins of both the pre- and postacetabular processes that, when complete, the dorsal iliac blade would not have been much higher than currently preserved. When reconstructed (Fig. 1), the height of the iliac blade (as measured from the dorsal-most point of the acetabulum to the dorsal margin of the iliac blade) is approximately 0.23 times the anteroposterior length of the ilium (measured from the anterior tip of the preacetabular process to the posterior tip of the postacetabular process). This differs markedly from the great majority of other basal sauropodomorphs, which tend to display values between 0.30 (e.g., *Plateosauravus* [SAM-PK 3609]; *Melanorosaurus* [NM QR1551]) and 0.35 (e.g., *Massospondylus* [BP/1/4693]; *Riojasaurus* [PVL 3808]). It also differs from the dorsoventrally tall iliac blades of later sauropods (Upchurch et al., 2004). With respect to the general morphology of the of the lateral profile of NMQR 4125, a similarly low iliac blade is also observed in an ilium (BMNH R1539) currently referred to *Thecodontosaurus* from the

Rhaetian of England (although it is difficult to tell if it is complete as preserved). However, it should be noted that this element appears to differ dramatically in morphology to other iliac material referred to this taxon (see Benton et al., 2000: fig. 15). The ilium of *Yunnanosaurus* is notable for its low, anteroposteriorly biased lateral profile (Young, 1942: fig. 11), whereas a similarly low iliac blade may have been present in an isolated ilium from the Late Triassic Caturrita Formation of Brazil (Bittencourt et al., 2012), but it is too poorly preserved to say for certain.

The preacetabular process, although dorsoventrally narrow (i.e., non-lobe-shaped) and anteriorly tapering as in most non-sauropodan sauropodomorphs, is nonetheless distinguished from the 'typical' condition with respect to its anteroposterior length and general multi-dimensional breadth. In the majority of basal sauropodomorphs the preacetabular process is subtriangular in general outline, with the sharply-tapered anterior point terminating well short of the anterior margin of the pubic peduncle (Fig. 2). In contrast, the preacetabular process of NMQR 4125 is anteroposteriorly elongate so as to appear more subrectangular in lateral view than subtriangular. The broadly-rounded, non-acute anterior margin of the process terminates level with the anterior margin of the pubic peduncle. Although certain basal taxa (i.e., *Anchisaurus*; *Leonerasaurus*) are noteworthy in having preacetabular processes that extend beyond the anterior margin of the pubic peduncle (and hence are proportionally more anteroposteriorly elongate than in NMQR 4125), they are nonetheless distinguishable from NMQR 4125 on account of being more prominently anteriorly tapering as well as displaying generally more gracile dimensions. The very basal *Saturnalia* also preserves a preacetabular process that extends to the anterior margin of the pubic peduncle, although the ventral

convexity of the preacetabular process in that taxon differs from the concave morphology evident in NMQR 4125 (Langer, 2003; Bittencourt et al., 2012).

The dorsoventral depth of the preacetabular process of most sauropodomorph taxa generally exceeds the mediolateral width by a substantial margin (although note that the preacetabular process is at times oriented obliquely so that the ventral margin is more laterally positioned than the dorsal margin, which in effect reverses this relationship). However, whereas the preacetabular process in NMQR 4125 is atypical in being mediolaterally broader than dorsoventrally deep, it is not markedly so, and hence lacks the planar (i.e., attenuated along at least one axis) morphology observed in the SAM-PKe process of a number of basal sauropodomorphs (e.g., *Massospondylus* [BP/1/4693]; *Antetonitrus* [NMQR 1545]). Again, the preacetabular condition in NMQR 4125 is chiefly reminiscent of the morphology of the Durdham Down ilium (BMNH R1539; Benton et al., 2000).

As in the majority of basal sauropodomorphs, the postacetabular process is dorsoventrally low and anteroposteriorly elongate. However, similar to the condition observed in e.g., *Mussaurus* (Otero and Pol, 2013), *Yunnanosaurus* (Young, 1942), *Efraasia* (SMNS 17928), and some specimens of *Plateosaurus*, the anteroposterior length of the postacetabular process of NMQR 4125 is augmented by the absence of a strong ventral ridge (= brevis crest) joining the postroventral corner of the postacetabular process to the posterior end of the ischial peduncle (although this may be exaggerated due to breakage). The postacetabular process is raised at a slight angle relative to the horizontal, although this is not as marked as in BMNH R1539 (= ?*Thecodontosaurus*). The postacetabular process is rounded in lateral profile, with the posteroventral corner appearing to have been more acute than the posterodorsal corner,

similar to e.g., *Riojasurus, Ruehlia,* and *Plateosaurus* (Yates, 2003a). This contrasts with the more square-shaped postacetabular processes of e.g., *Efraasia* and *Plateosauravus*. Nonetheless, it is suggested here that the dual vagaries of taphonomic deformation and intra-generic variation exert more influence over the observed profile of the basal sauropodomorph postacetabular process than is generally appreciated (*contra* Yates, 2003a).

Neither of the major postacetabular muscle-origin sites are in strong evidence. A number of basal sauropodomorph specimens (e.g., SAM-PK 382 '*Euskelosaurus*'; *Anteonitrus* [NM QR1545]) preserve a pronounced tubercle on the laterodorsal side of the postacetabular process, probably related to the origin of one of the major knee flexors (e.g., M. iliofibularis or M. flexor tibialis externus [Carrano, 2000; Carrano and Hutchinson, 2002]). However, the lateral surface of the postacetabulum of NMQR 4125 is unremarkable save for a slight fringe of rugose texturing that extends along the dorsal margin (probably related to the M. iliotibialis). The second major postacetabular attachment, the M. caudofemoralis brevis, originates on the ventral surface and is often accompanied by a pronounced fossa and/or shelf: the brevis fossa/shelf. Although this latter feature is potentially synapomorphic for Dinosauria (Novas, 1996), it appears to have swiftly become reduced within Sauropodomorpha, with only some forms retaining a clear fossa and/or laterally expanded shelf on the ventral surface of the postacetabulum (e.g., *Eucnemesaurus* [McPhee et al., 2015a]; *Riojasaurus* [PVL 3808]). Although the medial surface of the postacetabular process of NMQR 4125 has sustained some damage and hence it is difficult to discern the full extent of the ventral surface, it does not appear to have housed an unambiguous brevis fossa.

In lateral view, both iliac peduncles exhibit the typical basal sauropodomorph condition of a well-developed ischial peduncle and a larger, anteroventrally curving pubic peduncle. Nonetheless, the latter process is proportionally shorter dorsoventrally when compared to most other basal sauropodomorph taxa (Fig. 2). The ventral surface of the pubic peduncle is semi-circular in general outline with a flat-to-concave posterior margin. In keeping with the generally robust proportions of the ilium, the ventral surface of the pubic peduncle is about 1.35 times wider transversely than anteroposteriorly long. The ventral surface of the ischial peduncle is subrectangular in general outline (also being widest transversely), while the posteroventral corner lacks the pronounced 'heel' seen in some basal sauropodomorph taxa (e.g., *Plateosauravus* [SAM-PK 3609]).

The supracetabular crest rises from the posterolateral edge of the pubic peduncle just proximal to the dorsoventral midpoint. The crest is strongly developed and laterally flaring, with its widest point at the nexus of the preacetabular process and the pubic peduncle. Although the supracetabular crest makes no meaningful incursion onto the ischial peduncle, it remains a well-delineated ridge for most of its length, terminating at a point proximal to, and roughly equivalent with, the level of the anteriormost portion of the ischial peduncle. The crest projects laterally throughout its length, and hence lacks the ventral deflection seen in primitive saurischian taxa such as e.g., *Saturnalia* (Langer, 2003). The acetabulum itself is broadly concave and mediolaterally wider relative to its length than in any other saurischian taxon (including Sauropoda, see e.g., Hatcher [1901: fig 10, 1903: pl. 5]), a feature that appears to be unique to the taxon represented by NMQR 4125. The maximum transverse width of the acetabulum is 0.7 times the total anteroposterior length of the acetabulum (measured from the

posteroventral margin of the pubic peduncle to the anteroventral margin of the ischial peduncle). It is difficult to calculate this metric from the images and measurements published in most sauropodomorph literature, but in the basal sauropodomorph taxa *Massospondylus* (BP/1/4693), *Plateosauravus* (SAM-PK 3609), and '*Melanorosaurus*' (NMQR 1551) (all taxa which display 'typical' basal sauropodomorph iliac proportions) these ratios are 0.4, ~0.55, and 0.5, respectively, well below that of NMQR 4125 (Fig. 2). The phylogenetic and palaeobiological implications of the peculiar proportions observed in NMQR 4125 are discussed in depth below.

4. DISCUSSION

4.1. *Taxonomic affinities of NMQR 4125*

Taxonomic assignment NMQR 4125 beyond indet. Sauropodomorpha is particularly difficult due to its combination of an unusual morphology, lack of additional anatomical information beyond a single element, and the near-absence of provenance data. Moreover, there is currently insufficient phylogenetic information on iliac variation within basal sauropodomorphs to allow an assignment of the specimen to a higher taxonomic grouping within the clade. Nonetheless, the highly robust proportions of NMQR 4125 would appear to limit its affinities to taxa of comparable robustness – in the case of the Elliot Formation this is primarily restricted to *Antetonitrus* and *Blikanasaurus* (and to a lesser extent *Aardonyx*). There are abundant and obvious morphological differences between NMQR 4125 and the ilium (NMQR 1545) tentatively assigned to *Antetonitrus* by McPhee et al. (2014: fig. 15). These relate mainly to the

high iliac blade and narrower transverse breath of the acetabulum of the latter. Therefore, a stronger taxonomic link might be postulated between NMQR 4125 and *Blikanasaurus*, a LEF taxon of equally unprecedented robusticity. Unfortunately, *Blikanasaurus* is currently only known from a single epipodium (SAM-PK 403: Fig. 3), so assessing the degree of morphological similarity between NMQR 4125 and the former is not possible.

Of some interest are the observed similarities between NMQR 4125 and the considerably smaller ilium associated with the *Thecodontosaurus* holotypic assemblage (BMNH R1539; see above). The basal position generally hypothesised for *Thecodontosaurus* (or a subset of elements referred to the genus) is potentially suggestive of a similarly basal position for NMQR 4125 (Benton, 2000; Yates, 2003b). However, other very basal sauropodomorphs (e.g., *Saturnalia:* Langer [2003]), as well as sauropodomorph outgroups (e.g., *Herrerasaurus* [Novas, 1994]; *Guaibasaurus* [Langer et al., 2010b), display markedly dissimilar ilia. The similarities between NMQR 4125 and BMNH R1539 are therefore unlikely to be explained via symplesiomorphy alone. Although the extremely small size of all the elements from the Durdham Down assemblage is inconsistent with the appreciably larger absolute proportions of NMQR 4125, that the latter and BMNH R1539 potentially represent a mutual, early divergence from the typical sauropodomorph *bauplan* is nonetheless an intriguing possibility. Although the incompleteness of the early sauropodomorph record precludes further exploration this issue, the otherwise uniquely robust dimensions of both specimens raises questions as to the underlying functional causes driving the development of this morphology.

4.2. *Functional implications of the morphology observed in NMQR 4125*

The scaling relationships between body mass and skeletal robusticity have been explored extensively over the past several decades (see Carrano [1999] and references therein). Generally speaking, as animals increase in size (in any non-mass related size metric, e.g., height) the functional stresses acting on the skeleton can be expected to increase accordingly. For large animals (those generally exceeding 300kg in size [Biewener, 1989]) this problem is mitigated with respect to two key appendicular alterations: 1) the adoption of a more erect limb posture and hence an increase in effective mechanical advantage (Bienwener, 2005) and 2) an increase in the cross-sectional diameter/circumference of the long-bones relative to their length (Campione and Evans, 2012). Work within non-avian Dinosauria has demonstrated that, consistent with observations pertaining to mammals and birds (Bienwener, 2005), limb robustness scales roughly within an isometric continuum (= geometric similarity) with respect to size (Carrano, 1999, 2001). Due to the much larger sizes generally attainable by quadrupeds, dinosaurian robusticity is therefore disproportionally distributed among large-bodied quadrupedal taxa (e.g., Sauropoda, Ceratopsidae, Eurypoda).

It is hence not surprising that most non-sauropodan sauropodomorphs scale relatively consistently with respect to limb and locomotor dynamics (e.g., the intermediate grade of "large-bodied semi-bipeds" of Carrano [1999, 2001]). However, while the general length of NMQR 4125 is consistent with ilia of similarly sized animals (e.g., *Antetonitrus* [NMQR 1545]; *Jingshanosaurus* [Zhang and Yang, 1994: fig 33]), the massive transverse dimensions of the acetabulum suggest an animal of appreciably larger mass. Whereas this could simply be taken as evidence of a shift towards a more obligate form of quadrupedal locomotion, the general

proportions of the element (i.e., width of the acetabulum verses height of the iliac blade) are incongruent with the relative proportions exhibited by other large-bodied saurischian quadrupeds (i.e., Sauropoda), none of which display a similar dramatic expansion of the acetabular region. This raises questions pertaining to both the nature of the mediolateral stresses that were being accommodated, as well as the presumed primacy of size related scaling effects versus those imparted by historical and biomechanical constraints.

Within Archosauria (primarily Dinosauromorpha), the development of a deeply concave (often perforate) acetabulum is part of a derived locomotory suite coincident with the shift towards a fully erect hindlimb characterized primarily by protraction-retraction in the parasagittal plane. This represents a departure from the semi-sprawled, rotary gait primitive to Archosauromorpha whereby movement of the hindlimb occurred via abduction-adduction in the dorsoventral plane (Hutchinson and Gatesy, 2000; Caranno, 2000, Bates and Schachner, 2012). The well-developed acetabulum of derived archosaurs thus provided additional mediolateral support (primarily by limiting abduction of the femur) in a parasagittal biped for which the hindlimb was carried directly beneath the body. Furthermore, Hutchinson and Gatesy (2000: 746) have noted that the lateral expansion of the supracetabular crest within Dinosauromorpha would have resulted in a concomitant increase in the moment arm of the M. iliofemoralis muscle group. This group, in changing functionality from a swing-phase (in quadrupedal, semi-sprawling archosaurs) to a stance-phase abductor, was instrumental to the adoption of parasagittal locomotion by providing a dedicated counter-force to the natural adduction moments exerted on the hindlimb when the foot is positioned medial to the hip-joint (Hutchinson and Gatesy, 2000; Bates and Schachner, 2012).

The hyper-developed supracetabular crest of NMQR 4125 could thus be interpreted in light of a marked increase in the abduction properties of the M. iliofemoralis. However, this muscle group (or the enlargement thereof) is intimately connected with bipedality insofar as heightened stance-phase abduction is unlikely to be warranted in a quadrupedal context: the presence of contralateral forelimb obviating any additional adduction moments the hindlimb may experience. With respect to NMQR 4125, this can be interpreted in one of two ways: 1) either the taxon represented by this ilium developed a unique, functionally-divergent means of maintaining bipedality at increased, if not gigantic, size (and thus providing a rare example of the manner in which historical and/or biomechanical constraints can affect skeletal robusticity independent of simple scaling trends) or, 2) the retention of a plesiomorphic anatomy, coupled with marked size increase, led to an "inflation" of certain features that are nonetheless uninformative with respect to specific mechanically-mediated locomotory strategies. Given that the latter is not necessarily incompatible with the former, as well as the strong functional link repeatedly observed between phenotype and behavior (Szalay, 2000), the first possibility is tentatively favoured here.

Recently, McPhee et al. (2014) argued that the hypertrophied M. caudofemoralis brevis observed in *Antetonitrus* related to an increase in its adductor properties as a means of supporting the hindlimb under the body during phases of bipedal locomotion. Hence, this interpretation needs to be reconciled with the scenario outlined above. In contrast to NMQR 4125, the typical condition in Sauropodomorpha is for the relative dorsoventral height of the iliac to blade to increase while the transverse width of the acetabulum remains comparatively static. This occurs in tandem with the expansion of the ilium anterior and posterior to the

acetabulum (the pre- and postacetabular processes), facilitating enlargement of the major hindlimb protractors (e.g., the knee extensor M. iliotibialis) and retractors (e.g., the knee flexor M. iliofibularis). As demonstrated by Carrano (2000), an enlarged iliac blade would have increased surface-area purchase for M. iliofemoralis, heightening its properties as a stance-phase hindlimb stabiliser, whereas its slight anterior migration in concert with the marked expansion of the preacetabular process potentially imparted a degree of protraction-based action during swing (within Sauropoda these modifications reached their apparent zenith in the massive, lobate preacetabular process of *Brachiosaurus* [Riggs, 1903; Carrano, 2005: fig. 8.9]). It is therefore possible that M. caudofemoralis brevis was active primarily during swing-phase and developed in wider-gaited taxa as a means of countering the increased size of the M. iliofemoralis, particularly for sauropodomorphs in which the iliac blade is proportionally higher than that observed in NMQR 4125. If the latter muscle group was also developing towards swing-phase activation as a possible femoral protractor (Carrano, 2000), additional adduction forces may have been required in order to reinforce medial motions of the hindlimb at the end of the swing-phase. This scenario may also potentially explain the increased (mainly anteroposterior) dimensions of the preacetabular process in MNQR 4125: a comparatively low iliac blade led to an increase in the mechanical burden of the major knee extensors in the absence of supplementary protraction moments of the M. iliofemoralis.

Further analysis of this issue is unfortunately hampered by the lack of additional hindlimb material associated with NMQR 4125, as well as the tentative association of the referred ilium NMQR 1545 to the *Antetonitrus* holotypic assemblage (BP/1/4952). Nonetheless, it is clear with respect to the above that future caution should be exercised in attributing to the marked

robusticity of other basal sauropodomorph specimens a form – incipient or otherwise – of sauropod-like obligate quadrupedality.

4.3. *NMQR 4125:* Blikanasaurus *as potential taxonomic homologue?*

The distinctive morphology of NMQR 4125 is without obvious parallel with respect to the known sauropodomorph fauna of the Elliot Formation. As stated above, the robustness of the element would appear to restrict it to a small handful of taxonomic candidates, of which *Blikanasaurus* was deemed the most probable match. Known only from a stocky epipodium in which all the distal elements have undergone marked proximodistal reduction, *Blikanasaurus* has been hypothesized to represent an early saurischian experiment in graviportal quadrupedality (Galton and van Heerden, 1985, 1998), or even a true basal sauropod (Galton and Upchurch, 2004; Yates, 2004, 2007). Whatever its precise phylogenetic affinities, the question remains as to why distal limb robusticity (accomplished by dramatic shortening of the pedal elements) was carried to such an extreme in this particular taxon?

As has been recently argued by McPhee et al. (2015b), it is probable that the retention of specific plesiomorphic structures in a number of non-sauropodan sauropodomorphs relates to a catholic feeding ecology predicated upon exploitation of the full vertical range of accessible forage, i.e., while standing bipedally. Presuming that this hypothesis is at least partially accurate, it is unlikely that this strategy presents a uniform signal throughout basal Sauropodomorpha, with varying degrees and modes of facultative–habitual bipedality occurring basal to Sauropoda. If, with respect to the above, NMQR 4125 belongs to a taxon that falls

within the loose parameters of this scenario, then the question obtains as to the potential morphological correlates that this marked increase in mass would have exercised over the rest of the hindlimb. One potential outcome is a *Blikanasaurus*-like reduction in the proximodistal relationships of the distal hindlimb in order to support this additional weight. The potential (functional and taxonomic) link between *Blikanasaurus* and NMQR 4125 is also supported by the possible stratigraphic equivalence between the two specimens, with the holotype of *Blikanasaurus* recovered from near the base of the lower Elliot Formation (Yates, 2008; BWM and JNC personal observation). However, until iliac material of comparable robustness to NMQR 4125 is confirmed by new discoveries, its proposed stratigraphic and taxonomic relationships can only be stated tentatively for the time being.

5. CONCLUSIONS

The new material described herein, although unfortunately lacking in provenance information, is nonetheless highly autapomorphic for Sauropodomorpha. This implies either the presence of a previously unknown taxon within the Elliot Formation, or that the iliac morphology of an already (yet poorly) known taxon was more unique than general sauropodomorph variation would suggest. For the latter reason, we refrain from naming this diagnosable material, and suggest that *Blikanasaurus*, or a *Blikanasaurus*-like animal might be the most likely candidate to possess a similar ilium. Future discoveries will undoubtedly help clarify the taxonomic affinities of NMQR 4125. Regardless of the precise relationships of NMQR 4125, what is clear is that at least one form of highly robust basal sauropodomorph developed a unique, functionally-

divergent form of stance-phase hip stability, likely in response to the intersected mechanical challenges of increased mass, a widened gait, and a possibly bipedal locomotory habit. This further underscores the appreciable variation in bulk-browsing strategies, and the attendant range of *bauplans* that evolved to facilitate these strategies, distributed throughout basal Sauropodomorpha.

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FIGURE CAPTIONS

Figure 1. NMQR 4125 in A, lateral; B, medial; C, dorsal; D, ventral; E, anterior; and F, posterior views. Abbreviations: ibl, iliac blade; isp, ischial peduncle; poap, postacetabular process; prap, preacetabular process; pup, pubic peduncle; sac, supracetabular crest; sed, adhered sediment. Scale bar equals 5 cm.

Figure 2. Iliac variation throughout basal Sauropodomorpha. A, NMQR 4125 in lateral and ventral views; B, '*Melanorosaurus*' (NMQR 1551) in lateral and ventral views; referred *Massospondylus* (BP/1/4693) in lateral and ventral views (reversed for comparison); ?*Thecodontosaurus* (BMNH R1539) in anterolateral view; *Plateosauravus* (SAM-PK 3609) in

lateral view (reversed for comparison); *Ruehleia* (MB.R.4718.101) in lateral view (reversed for comparison). Scale bars equal 5 cm.

Figure 3. Line drawing of left pes of *Blikanasaurus* (SAM-PK 403) in dorsal view. Scale bar equals 5 cm.

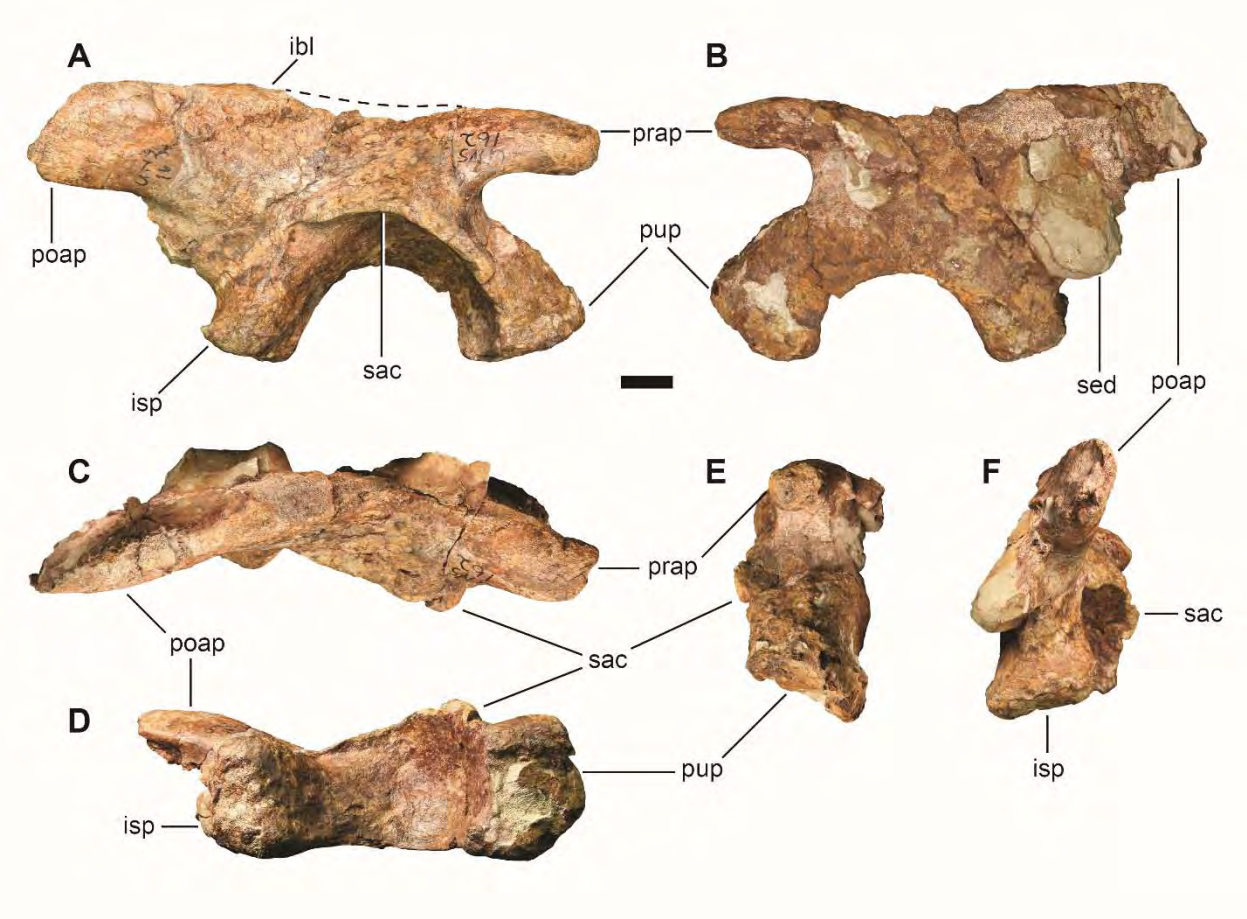


Figure 1.

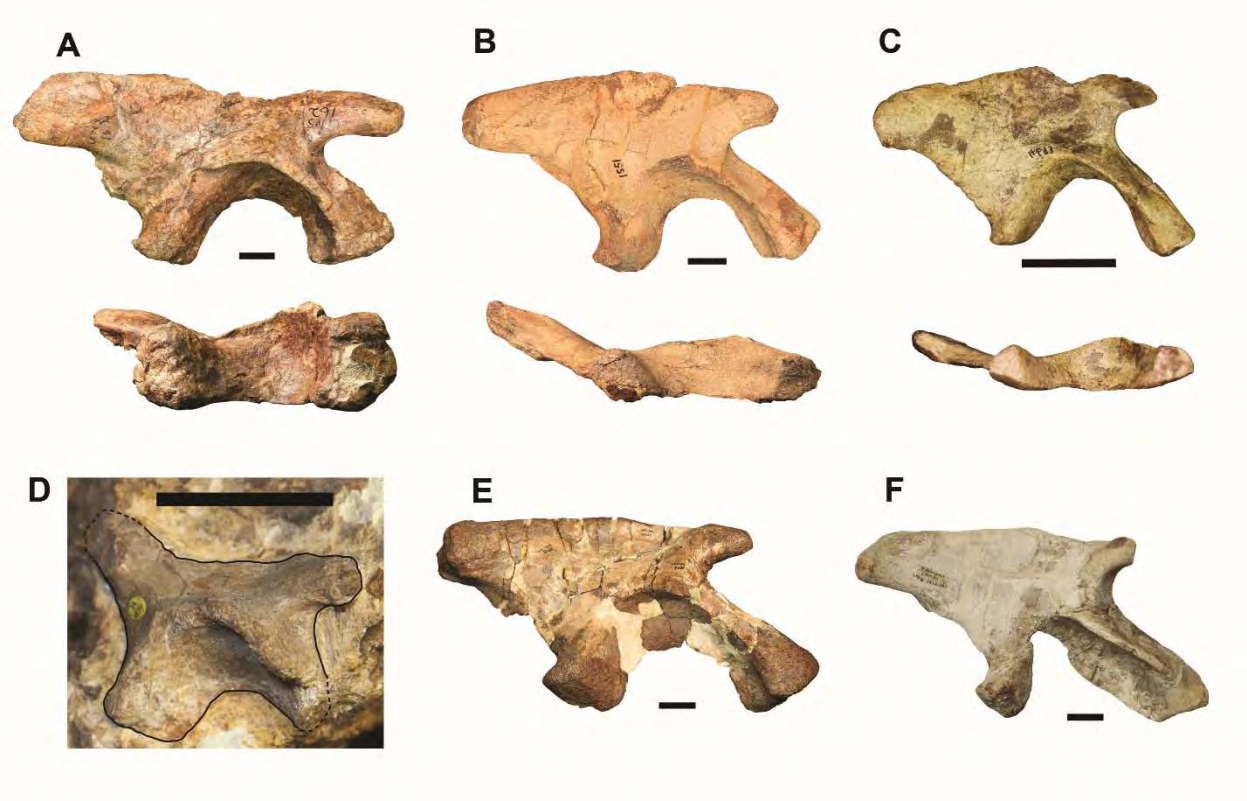


Figure. 2

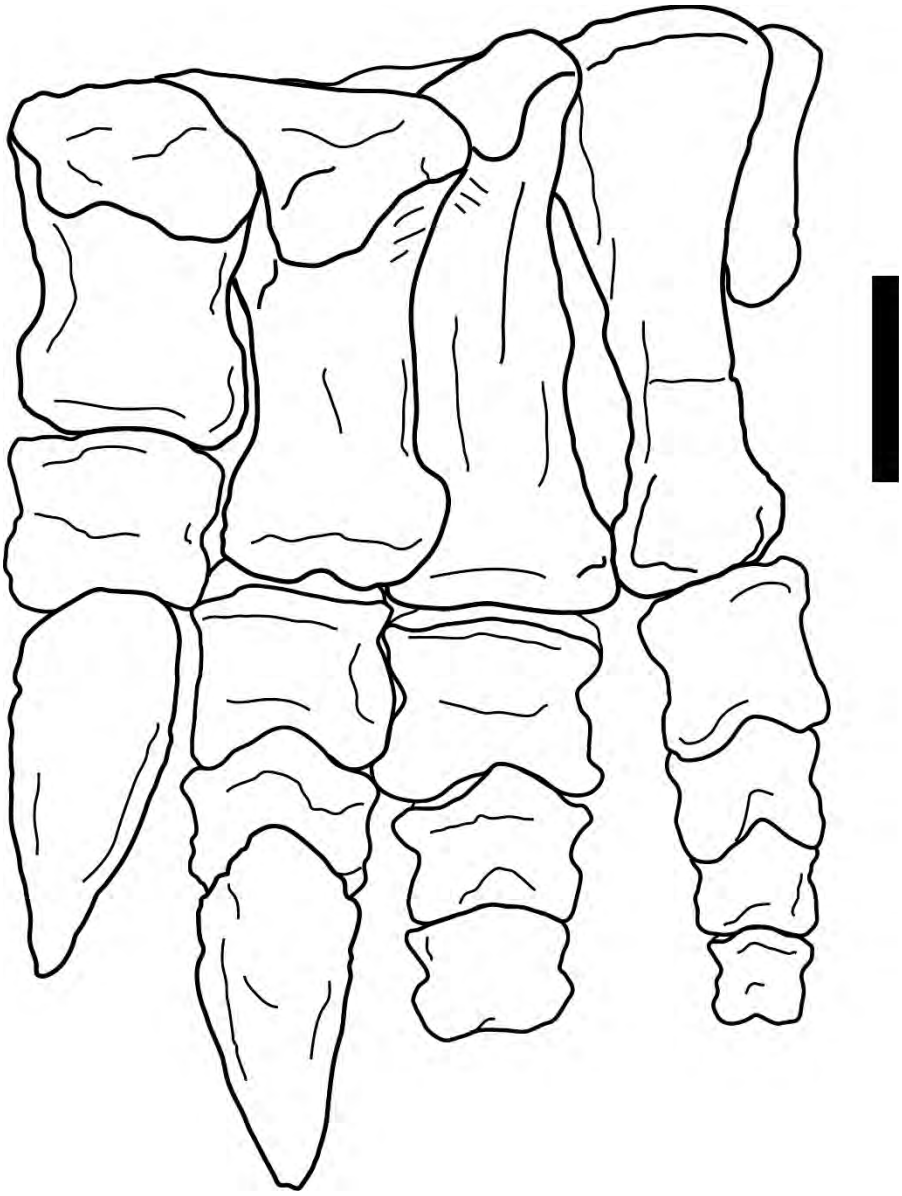


Figure 3.

6. KEY FINDINGS and FUTURE WORK

The series of analyses presented herein have further underscored the significance of the palaeontological record of the South African Mesozoic to our understanding of key stages within the evolution of sauropodomorph dinosaurs.

Each analysis represents a contribution to several current sauropodomorph research agendas, relating primarily to questions of phylogeny, taxonomy, palaeoecology, and palaeobiogeography. The key findings of each study are highlighted below. This will be accompanied by a brief discussion of the additional questions that arose while undertaking each respective study, as well as future lines of investigation that are likely to help resolve these issues.

6.1. *EUCNEMESAURUS*

The primary aim of this study was to provide new information on this poorly understood genus, which was previously known only by disassociated, fragmentary material collected from throughout the formation (Yates 2007b). Given the noted dearth of articulated specimens recovered from the lower Elliot Formation (LEF), even an individual as incomplete as BP/1/6234 is of appreciable utility in recognizing and delimiting character-state polarities between *Eucnemesaurus* and other equally poorly known LEF taxa (e.g., *Plateosauravus*). Specifically, it was found that the genus *Eucnemesaurus* appears valid, and is potentially represented by more than a single species. However, the validity of other LEF sauropodomorphs is less certain, particularly for taxa that have not been the subject of

recent revisions, e.g., *Platerosauravus*. Although due, in part, to the abovementioned incompleteness of most specimens, the interrelationships of LEF Sauropodomorpha remains complicated by the relatively conservative morphology exhibited by most specimens. This has led to the confounding instances of character overlap and/or conflict exhibited within and between hypodigms recognized within this study (McPhee et al., 2015a), with most distinctions based not on unambiguous differences in *bauplan*, but on the possession of either unique character suites and/or autapomorphic attributes of varying subtlety and reliability.

This uncertainty is perhaps best exemplified by the two major assemblages referred to *Melanorosaurus* (NMQR 3314 and 1551), which in the course of this research were shown to be morphologically (as well as potentially stratigraphically) inconsistent. This taxon is important for basal sauropodomorph studies for several reasons, not least amongst them the fact it was named almost one century ago and is thus incorporated into most systematic studies as an OTU, as well as forming an anchor taxon in a current stem-based definition of Sauropoda. A thorough revision of this important taxon is therefore long overdue. A similar concern also obtains for the validity of the South American genus *Riojasaurus*, which in turn has serious implications for the hypothesized monophyly of the Riojasauridae (*Riojasaurus* + *Eucnemesaurus*). However, given the myriad issues surrounding the *Riojasaurus* hypodigm (not least determining the provenance and interrelationships of the wealth of material referred to it), this is likely to represent a much more labour-intensive undertaking than correcting the issues specific to *Melanorosaurus*.

Additional fossil sampling notwithstanding, a more in-depth exploration of the biostratigraphic relationships of many iconic LEF taxa (e.g., *Antetonitrus*; *Melanorosaurus*) is

likely to yield a more immediate clarification of some of the issues stated above. The implementation of a refined, high-resolution biostratigraphic framework, in addition to bounding the appearance of each exemplar within a vertical continuum, will have the added corollary of providing a quantitative temporal constraint with respect to hypotheses predicated upon tracking phenotypic change throughout the formation. This latter goal will be of particular efficacy to determining if the 'core' (i.e., typical) LEF sauropodomorph assemblage simply represents an assortment of discrete species-taxa evolving/diversifying in a mosaic manner (the null assumption), or a more dynamic, reticulate complex of populations in which one is only minimally differentiated with respect to the other in the context of a relatively short temporal span.

6.2. *PULANESAURA*

This study was of particular importance to our understanding of the early evolution of sauropod dinosaurs. As explained within the introduction, both the taxonomy and diagnostic relationships of Sauropoda are currently in a state of flux, with little by way of consensus as to what precisely constitutes a "true" sauropod. This confusion is primarily explicable with respect to three main factors: 1) the paucity of well-preserved/diagnosable basal sauropod material from the earliest Jurassic; 2) the scientific discourse over what designates a "sauropod" is based on the mutable positions of unstable nodes on the tree (Langer et al., 2010) and 3) the tendency for many workers to regard any large-bodied, putatively quadrupedal sauropodomorph as a sauropod (e.g., Ezcurra and Apaldetti, 2012; Otero and Pol, 2013). Therefore, the *Pulanesaura* assemblage, in preserving a number of relatively apomorphic post-cranial elements from major sections of both the axial and

appendicular skeleton, allows for direct comparison between other taxa that have recently been hypothesized as representing basal members of Sauropoda (e.g., *Antetonitrus*: Yates and Kitching, 2003). Furthermore, the phylogenetic analysis, in confidently assigning to *Pulanesaura* a position effectively straddling the basal sauropodomorph–sauropod transition, also provides empirical insight into both the morphological and/or functional criteria that may be employed when distinguishing between the two groups.

With respect to this latter point, a specific hypothetical scenario was advanced, whereby the initial radiation of Sauropoda can potentially be viewed as a departure from the primitive sauropodomorph foraging strategy in which bipedality still played a key role – primarily in facilitating browsing at the upper reaches of the available vertical forage. In contrast, the energetically conservative form of neck-dependent low-to-mid browsing inferred for *Pulanesaura*, in addition to removing basal Sauropoda from direct competition with higher browsing 'prosauropods', may have had the crucial corollary of breaking a number of behavioural, locomotory, and anatomical constraints that were previously impeding the acquisition of true gigantism. This strategy, in addition to adding an explicit ecological dimension to sauropod origins, is without observed parallel within the sauropodomorph record of the upper Elliot Formation. Therefore, the information provided here further illustrates the previously unappreciated range of morphological and taxonomic diversity present within the upper Elliot Formation. Although rare constituents of earliest Jurassic ecosystems, basal sauropods nonetheless evolved alongside an array of massospondylid and stem sauropodiform taxa, only surpassing the latter in numerical abundance and ecological dominance towards the end of the Early Jurassic.

Nonetheless, the incompleteness of the *Pulanesaura* assemblage restricts elucidation of this process to the limited anatomical information preserved. This in turn precludes further assessment of the differential rates of change experienced by various parts of the skeleton (i.e., whether the early evolution of the sauropod *bauplan* was accomplished via a series of correlated anatomical changes, or through the episodic transformations of individual skeletal modules [e.g., axial vs forelimb vs hindlimb]). This also highlights continued uncertainties about sauropod evolution generally, with certain anatomical regions (particularly the skull and manus) maintaining a sampling gap of nearly twenty-million-years. Unfortunately, any future amelioration of this particular issue will depend primarily upon continued taxonomic sampling of a notoriously poor early sauropod record.

Another future issue obtains when considering if the currently favoured phylo-taxonomic definitions are appropriate for capturing our continually shifting ideas as to the inclusivity of the sauropod clade. Whether Sauropoda is delimited with respect to an ecological/evolutionary "event", or via reflexive dependency on a previously established "node" is an epistemological issue, especially insofar as the rationale behind labelling any portion of a cladogram is concerned. A less conceptually stringent approach may be warranted in future explorations of the underlying, causal criteria of the sauropod condition, especially when determining the efficacy and relative explanatory power of processual or pattern-based interpretations.

6.3. *KIRKWOOD SAUROPODS*

Fossil sampling throughout the Mesozoic is highly irregular, with some periods relatively well represented, e.g., the earliest and latest Jurassic, whereas others preserve only scant

clues as to the faunal constituency of their respective ecosystems, e.g., the earliest Cretaceous. Within the Gondwanan context, this latter period is especially underrepresented, with only two recognized terrestrial deposits known from the southern Continents (Upchurch et al., 2015). It is thus not surprising that, following the latest Jurassic (a period represented by the famously fossiliferous rocks of the Morrison and Tendaguru formations), recent research strongly suggests a sharp decline in sauropod diversity at the outset of the Cretaceous (e.g., Mannion et al., 2011)

The discovery of several diagnostic sauropod vertebrae from the Early Cretaceous Kirkwood Formation therefore provides a much-needed insight into southern Gondwanan sauropod diversity during this poorly known period. The identification of at least four distinct, morphologically disparate forms of sauropod dinosaur highlights the degree to which our dependence on a highly incomplete fossil record obfuscates attempts at estimating comparative faunal diversities throughout time. Moreover, noted similarities between the Kirkwood assemblage and those of Late Jurassic formations such as the Morrison, Tendaguru, and Lourinhã further confirms that the Jurassic–Cretaceous boundary was not co-incident with abrupt changes in sauropod faunal dynamics; instead presenting a more gradual turn-over whereby non-rebbachisaurid dipolodocoids and brachiosaurid titanosauriforms were replaced by rebbachisaurid and somphospondylan taxa throughout the duration of the Early Cretaceous.

However, as most estimates of diversity are built on databases which count valid species as the base unit of comparison, and because the earliest Cretaceous record is still largely composed of fragmentary specimens which do not bear names, its constituent formations (e.g., the Kirkwood Formation and Wealden Group) appear to have superficially low

diversity. Although the results of the present study show that even in the absence of taxonomic precision we can assess the diversity of the early Cretaceous, the recovery of additional well-understood OTUs (operational taxonomic units) is a problem that is only likely to improve with further sampling. However, given the relatively low fossil yield of the Kirkwood Formation, along with the near-absence of articulated remains, this is unlikely to be a situation that will improve any time soon.

A further issue pertains to the dating of the Kirkwood Formation. Although it was argued within that the fossil-bearing strata of the formation is best considered as Early Cretaceous, this is based primarily upon invertebrate data from the over-lying/laterally-equivalent Sundays River Formation. This is problematic for two reasons: 1) the precise stratigraphic relationships between the Kirkwood and Sundays River formations remains unresolved and 2) all temporal inferences have thus far relied on relative, as opposed to absolute, dating methods. Given the importance of the Kirkwood Formation to our understanding of the Jurassic–Cretaceous boundary, more precise temporal control is required in order to firmly establish if the abundance of 'Jurassic-type' sauropods represents their survival into the Cretaceous, or if the Kirkwood is simply contemporaneous with other Late Jurassic sauropod-bearing lenses, particularly geographically proximate ones like the Tendaguru beds. The analyses of detrital zircon populations from the relevant, specimen-bearing localities may assist in this, along with the correlation of these populations to bentonite lenses recently discovered in coeval Kirkwood sediment to basins west of the Algoa Basin.

6.4. *A HYPER ROBUST ILIUM*

Although represented by a single, autapomorphic ilium lacking in both collection and provenance data, NMQR 4125 nonetheless has important implications for the diversity of locomotory strategies exhibited by the sauropodomorphs of the Elliot Formation (and basal Sauropodomorpha generally).

In the past it was generally held that the locomotory habits of sauropodomorph dinosaurs moved in a relatively linear evolutionary progression from bipedal through 'semi-bipedal' to the fully quadrupedal gait of Sauropoda (e.g., Brusatte et al., 2010). Although our current phylogenetic hypotheses suggest this trajectory is to some extent correct, it represents a marked simplification of the myriad ways in which Sauropodomorpha managed the inherited behavioural and biomechanical challenges of increasing body-size, hyper herbivory (Barrett and Upchurch, 2007), and a forelimb primarily adapted for use in a bipedal context (Remes, 2008). Whereas the *Pulanesaura* study suggested the ecological and selective circumstances within which a fully quadrupedal locomotory habit may have been advantageous, the majority of non-sauropodan sauropodomorph taxa can be regarded as still – if only facultatively – dependent on some degree of bipedality. The uniquely robust morphology of NMQR 4125 may potentially allude to an early, evolutionary divergent solution to the problem of maintaining a (semi-) bipedal locomotory habit at increased body sizes. In this capacity, the dramatic lateral expansion of the supracetabular crest suggests the development of an unparalleled form of stance-phase hindlimb stabilization at the base of Sauropodomorpha.

However, although large, NMQR 4125 is still relatively modest in absolute size when compared to the unrivaled gigantism of later sauropods. Nonetheless, no sauropod taxon displays a similarly expanded acetabular region relative the dorsoventral height of the iliac blade. This underscores the manner in which, on rare occasions, historical constraints (in this case the retention of a bipedal locomotory habit) can lead to the adoption of a robust skeletal anatomy independent of the acquisition of gigantic size. This also highlights issues pertaining to the current trend within basal sauropodomorph studies to treat "robusticity" as phylogenetic shorthand for a close affinity to Sauropoda. An in-depth examination of current data matrices and the effects that character formulations primarily expressing shifts in body size and/or robusticity have on tree topology is therefore long overdue.

7. SYNTHESIS and CONCLUDING REMARKS

The analyses presented above contribute novel information to our understanding of South Africa's inimitable sauropodomorph record. A recurring theme of these analyses is the importance of this record in capturing the two major temporal transitions of the Mesozoic, namely, the Triassic–Jurassic boundary at 200 million-years-ago and sediments pertaining to the very earliest Cretaceous 55 million years later. The first transition is a period of key relevance to reconstructing the processes surrounding the early radiation and subsequent diversification of the dominant dinosaurian herbivores of the Mesozoic. The sauropodomorph record of the Elliot Formation is therefore highly germane to research efforts focused on various aspects of basal sauropodomorph palaeoecology and phylogeny – especially insofar as these relate to the ultimate divergence of Sauropoda.

Specifically, this thesis has underscored the range of sauropodomorph morphological and taxonomic diversity present across both the upper and lower subunits of the Elliot Formation, as well as emphasizing the possible ecological constraints contributing to the observed *bauplan* morphology of each specimen discussed within. In addition to an exploration of the varied ways in which basal Sauropodomorpha responded to the combined challenges of increasing dependency on low-quality vegetable matter, the attendant dramatic increase in body size, and the historically-conditioned reliance on bipedality, this thesis also represents an attempt to elucidate the manner in which one particular lineage "broke" with tradition and took the first step towards becoming columnar-limbed, fully quadrupedal sauropods. The continued taxonomic uncertainties discussed above should be interpreted as the rich potential for a further refinement of these hypotheses as more fossil material comes to light.

The second major transition captured within the Mesozoic sediments of South Africa – that of the Jurassic–Cretaceous – appears slightly more cryptic than the above, earlier one. This is due, in part, to this thesis finding that the diversity of sauropods in the Kirkwood Formation is surprisingly similar to that of Late Jurassic deposits in Tanzania and the western USA. This conclusion casts doubt on either the age assessment of the Kirkwood's terrestrial strata, or on the end-Jurassic selective extinction of sauropod lineages. Nonetheless, that sauropodomorph fossils remain the most commonly-occurring faunal proxy within the Kirkwood Formation underscores the continuing ecological dominance that Sauropodomorpha exerted over the large-bodied herbivore niche – a dominance that went unchallenged well into the late Mesozoic.

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