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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 of 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; see also Martínez et al., (2015)). 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., 2004a; 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 postcranial 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, Bordy, 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,

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Blikanasaurus therefore represents one of the few remaining departures from the conservative lower Elliot *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: BP, Evolutionary Studies institute, Johannesburg, South Africa (formerly Bernard Price Institute); IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; MB.R., Museum für Naturkunde—Leibniz-Institut für Evolutions und Biodiversitätsforschung an der Humboldt-Universität zu Berlin; NHMUK-PV, Natural History Museum, Palaeontology Vertebrates, London, United Kingdom; 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* [Santa 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 characterized 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; Sciscio and Bordy, 2016). 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 (Table 1). 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]), 0.35 (e.g., *Massospondylus* [BP/1/4693]; *Riojasaurus* [PVL 3808]), and 0.43 (*Lufengosaurus* [IVPP V15]). 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

Table 1
Measurements for NMQR 4125 (in mm).

Maximum anteroposterior length of dorsal iliac blade	560
Transverse width of acetabulum	170
Dorsoventral height of iliac blade above acetabulum	~130
Anteroposterior length of distal surface of pubic peduncle	100
Transverse width of distal surface of pubic peduncle	130
Transverse width of distal surface of ischial peduncle	140
Dorsoventral height of postacetabular process	100
Maximum dorsoventral height of ilium	270