ELSEVIER

Contents lists available at ScienceDirect

# Earth-Science Reviews

journal homepage: www.elsevier.com/locate/earscirev



# A chronostratigraphic framework for the upper Stormberg Group: Implications for the Triassic-Jurassic boundary in southern Africa

Emese M. Bordy<sup>a,\*</sup>, Miengah Abrahams<sup>a</sup>, Glenn R. Sharman<sup>b</sup>, Pia A. Viglietti<sup>c,d,e</sup>, Roger B.J. Benson<sup>c,f</sup>, Blair W. McPhee<sup>c</sup>, Paul M. Barrett<sup>c,g</sup>, Lara Sciscio<sup>a,h</sup>, Daniel Condon<sup>i</sup>, Roland Mundil<sup>j</sup>, Zandri Rademan<sup>k</sup>, Zubair Jinnah<sup>e</sup>, James M. Clark<sup>1</sup>, Celina A. Suarez<sup>b</sup>, Kimberley E.J. Chapelle<sup>c,e</sup>, Jonah N. Choiniere<sup>c</sup>

<sup>a</sup> Department of Geological Sciences, University of Cape Town, Private Bag X3, Rondebosch 7701, South Africa

<sup>i</sup> British Geological Survey (BGS), Keyworth, Nottingham NG12 5GG, United Kingdom

<sup>j</sup> Berkeley Geochronology Center (BGC), 2455 Ridge Road, Berkeley, CA 94709, United States

<sup>k</sup> Department of Earth Science, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

#### ARTICLE INFO

Vertebrate biostratigraphy

U-Pb detrital zircon geochronology

Keywords:

Main Karoo Basin

Elliot Formation

Early dinosaurs

Magnetostratigraphy

ABSTRACT

The upper Stormberg Group (Elliot and Clarens formations) of the main Karoo Basin is well-known for its fossil vertebrate fauna, comprising early branching members of lineages including mammals, dinosaurs, and turtles. Despite 150 years of scientific study, the upper Stormberg Group lacks radioisotopic age constraints and remains coarsely dated via imprecise faunal correlations. Here we synthesise previous litho- and magnetostratigraphic studies, and present a comprehensive biostratigraphic review of the upper Stormberg fauna. We also present the results of the first geochronological assessment of the unit across the basin, using U-Pb dates derived from detrital zircons obtained from tuffaceous sandstones and siltstones, the youngest of which are considered maximum depositional ages. Our results confirm that the Elliot Formation contains the Triassic-Jurassic boundary, making it one of the few fossiliferous continental units that records the effects of the end-Triassic Mass Extinction event. Our work suggests a mid-Norian-Rhaetian age for the lower Elliot Formation and a Hettangian-Sinemurian age for the upper Elliot Formation, although the precise stratigraphic position of the Triassic/Jurassic (Rhaetian/Hettangian) boundary remains somewhat uncertain. A mainly Pliensbachian age is obtained for the Clarens Formation. The new dates allow direct comparison with better-calibrated Triassic-Jurassic faunas of the Western Hemisphere (e.g., Chinle and Los Colorados formations). We show that sauropodomorph, but not ornithischian or theropod, dinosaurs were well-established in the main Karoo Basin ~220 million years ago, and that typical Norian faunas (e.g., aetosaurs, phytosaurs) are either rare or absent in the lower Elliot Formation, which is paucispecific compared to the upper Elliot. While this is unlikely the result of geographic sampling biases, it could be due to historical sampling intensity differences.

#### Motto:

"Africa presents incomparable opportunities for geological studies; the area is vast; the workers are comparatively few. The time has not yet arrived for extremely detailed studies [...] Consequently, a temptation to generalize is ever present; and it is certain that conclusions reached by workers of my and preceding generations will demand constant revision in the light of new knowledge." Sidney Henry Haughton (1888—1982) [in Dunham, K.C., 1983. Sidney Henry Haughton, 7 May 1888—24 May 1982. doi:10.1098/ rsbm.1983.0011]

\* Corresponding author. *E-mail address:* emese.bordy@uct.ac.za (E.M. Bordy).

https://doi.org/10.1016/j.earscirev.2020.103120

Received 25 August 2019; Received in revised form 2 February 2020; Accepted 10 February 2020 Available online 19 February 2020

0012-8252/ © 2020 Elsevier B.V. All rights reserved.

<sup>&</sup>lt;sup>b</sup> Department of Geosciences, University of Arkansas, 340 N. Campus Drive, Fayetteville, AR 72701, United States

<sup>&</sup>lt;sup>c</sup> Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, Wits, 2050 Johannesburg, South Africa

<sup>&</sup>lt;sup>d</sup> Integrative Research Center, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, United States

<sup>&</sup>lt;sup>e</sup> School of Geosciences, University of the Witwatersrand, Private Bag 3, Wits, 2050 Johannesburg, South Africa

<sup>&</sup>lt;sup>f</sup> Department of Earth Sciences, University of Oxford, Oxford OX1 3AN, United Kingdom

<sup>&</sup>lt;sup>8</sup> Department of Earth Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom

<sup>&</sup>lt;sup>h</sup> Department of Geology, University of Johannesburg, Kingsway and Auckland Park, 2006 Johannesburg, South Africa

<sup>&</sup>lt;sup>1</sup>Department of Biological Sciences, The George Washington University, 800 22nd St. NW Suite 6000, Washington, D.C., 20052, United States

# Earth-Science Reviews 203 (2020) 103120

#### 1. Introduction

The Upper Triassic to Lower Jurassic upper Stormberg Group (Elliot and Clarens formations) in the main Karoo Basin (MKB) of southern Africa (Fig. 1) is rich in both vertebrate body and trace fossils and serves as a global standard for Triassic-Jurassic boundary (TJB) studies. This fossil record is critical for understanding early Mesozoic terrestrial vertebrate evolution, and it includes remains of dinosaurs, pseudosuchians, lepidosaurs, stem-group turtles, temnospondyl amphibians, and later-branching therapsids, as well as their tracks and trackways (e.g., Ellenberger et al., 1964; Ellenberger, 1970, 1972, 1974; Kitching and Raath, 1984; Knoll, 2004, 2005). Faunal and sedimentary facies changes informally divide the Elliot Formation (EF) into lower (IEF) and upper (uEF) sections (e.g., Ellenberger et al., 1964; Kitching and Raath, 1984; Bordy et al., 2004a, 2004b, 2004c, 2004d). Historically, the lEF and uEF were both considered to be Upper Triassic (e.g., Haughton, 1924), but more recent work based on intercontinental faunal correlations has proposed that they represent Late Triassic and

Early Jurassic depositional ages, respectively (e.g., Olsen and Galton, 1984; Lucas and Hancox, 2001). If these correlations are correct, then the Elliot Formation is indeed one of the few fossiliferous continental deposits that spans the end-Triassic Mass Extinction event (ETME). This makes it crucially important for understanding shifts in the terrestrial ecosystems of southern Pangaea through the TJB interval. However, these age assessments have not been tested using geochronological methods and, instead, rely on low-precision ichno- and biostratigraphic correlations. This prevents the rich fossil record of the Elliot Formation from being fully used for studying the dynamics of extinction and recovery during the ETME.

Determining the depositional age of clastic sedimentary rocks is challenging, particularly in the absence of widespread and age-specific fossils or interbedded geochronologically datable primary volcanic tuff layers – the products of co-genetic volcanic events. Within the Karoo Supergroup in the main Karoo Basin (Figs. 1 and 2), the Permo-Triassic Beaufort Group is a leading example of a radioisotopically well-dated, highly fossiliferous stratigraphic unit (e.g., Rubidge et al., 2013;



**Fig. 1.** (A) Overview geological map of the upper Karoo Supergroup showing the geographic distribution of the 16 detrital zircon samples presented in this study (see Sections 3 and 4.1 for details). (B) Inset map of the MKB of South Africa and Lesotho showing the position of the Stormberg Group within it. (C) Karoo timewheel showing the relative length of geological time represented by each main stratigraphic unit in the Karoo Supergroup.



**Fig. 2.** The chronostratigraphy of the Upper Triassic–Lower Jurassic Stormberg and Drakensberg groups (Karoo Supergroup), with special focus on the magneto- and lithostratigraphy of the Elliot Formation, and the main body and trace fossil groups in the upper Stormberg Group. Radioisotopic dates are from this study for the upper Stormberg Group and Moulin et al. (2017; K-Ar,  $^{40}$ Ar/ $^{39}$ Ar methods) for the Drakensberg basalts. Unless otherwise marked, the maximum depositional ages are based on the mean U-Pb detrital zircon dates of the youngest two or more grains with overlapping dates at 2 $\sigma$  (see Table 1). The less-than sign next to each MDA indicates that the age of the sample could be younger (i.e., the MDAs are only maximum constraints on the age of deposition). Geological time scale based on the International Chronostratigraphic Chart (v2018/08; ICS, 2018) and Cohen et al. (2013). The Triassic time scale shows both the 'long Norian' and 'short Norian' calibrations of the Late Triassic (see discussion in Lucas, 2018). Note that most lithostratigraphic boundaries are likely to be diachronous, i.e., they are time-transgressive laterally across the basin from south to north and likely from west to east as well. Stormberg Group sample locations are shown in Fig. 1. For the complete geochronologic dataset, see Supplemental Text S1, Table S1 and Fig. S1. For a key to the animal silhouettes and ichnites (mostly from Ellenberger, 1970), see Supplemental Text S1.

Viglietti et al., 2018a). In contrast, radioisotopic dates have not been used to constrain stratigraphic hypotheses for the overlying Stormberg Group, which encompasses the Molteno, Elliot and Clarens formations. Although both groups are globally recognised for their rich continental fossil assemblages and associated record of mass extinctions, the lack of a high-resolution chronology in the Stormberg Group limits its biostratigraphic utility. One reason for this is that the Stormberg Group archives ~50 million years of geological history in <1.3 km of maximum stratal thickness, whereas the Beaufort Group represents ~26 million years of geological history in >4.5 km of thickness in the central MKB (see the Karoo timewheel: Fig. 1c). Regardless of the resolution of the geological archive provided by the Stormberg Group, establishing a modern chronostratigraphic framework for the section that encompasses the TJB in southern Africa is long overdue (Figs. 1 and 2; e.g., Porro et al., 2010; Sciscio et al., 2017a; McPhee et al., 2017).

The depositional ages of the Stormberg Group formations (Fig. 2) are constrained to some extent by biostratigraphy and, to a lesser extent, magnetostratigraphy. The oldest Stormberg Group unit, the Molteno Formation, is assumed to be Carnian, an assignment based on its exceptionally well-preserved and diverse plant fossil assemblages that are dominated by the seed fern Dicroidium (Figs. 2 and 3; Anderson and Anderson, 1970: Anderson et al., 1998: Knoll, 2004: Labandeira et al., 2018). Based on biostratigraphic correlations with better-dated global deposits, the two subdivisions of the unconformably overlying Elliot Formation, the lEF and uEF, are believed to be Norian-Rhaetian and Hettangian-Sinemurian, respectively (for lEF see e.g., Hopson, 1984; Gow and Hancox, 1993; Lucas and Hancox, 2001; Knoll, 2004; McPhee et al., 2017; for the uEF see e.g., Olsen and Galton, 1984; Smith and Kitching, 1997; Lucas and Hancox, 2001; Knoll, 2005). The overall Norian-Sinemurian age for the Elliot Formation has been confirmed recently via magnetostratigraphy (Sciscio et al., 2017a). The youngest Stormberg Group unit, the Clarens Formation, contains a paucispecific assemblage composed of taxa similar or identical to those common in the underlying uEF, and is inferred to be Sinemurian-Pliensbachian. The age of the upper boundary of the Stormberg Group succession is provided by the conformably overlying, Toarcian-aged continental flood basalts, the outpouring of which terminated sedimentation of the Karoo Supergroup (Figs. 2 and 3). Radioisotopic dating of these basalts indicates that the main pulse of this multi-peak volcanic event occurred between 181 and 183 Ma (Duncan et al., 1997; Svensen et al., 2012; Sell et al., 2014; Moulin et al., 2017). Moreover, field and radioisotopic evidence indicate that the outpouring of the first lava flows, at least in the southern MKB, started a few million years earlier in the late Pliensbachian (at ~189 Ma; Fig. 2; Moulin et al., 2017).

Here we present the first chronostratigraphic framework for the upper Stormberg Group, using new age constraints (maximum depositional ages, MDAs) obtained from detrital zircons in tuffaceous sandstones and siltstones via U-Pb geochronological methods (CA-ID-TIMS, LA-ICP-MS). We regard this initial, basin-wide chronostratigraphic framework as an important independent test of previous age determination methods, while acknowledging that it is but a first step in solving a temporally and geographically enormous problem. Our efforts to arrive at the most accurate age interpretations of these newly obtained geochronological dates are informed by our collective lithostratigraphic, sedimentologic, magnetostratigraphic, and biostratigraphic (including ichnologic) perspectives. Therefore, we also present a brief review of the unit on the basis of these multidisciplinary aspects and integrate the new dates into the overall stratigraphy of the Elliot and Clarens formations. While our dating results are circumscribed by the long duration and limited rock volume of the upper Stormberg Group, this synthesis allows us to infer that the duration of the Elliot depositional episode was middle Norian-Sinemurian, whereas the Clarens depositional episode was mostly Pliensbachian, and thus to evaluate paleobiogeographical signals at the onset and recovery from the ETME. Moreover, these new geochronological dates provide initial steps towards a more quantitative understanding of the rates of sediment preservation, basin evolution processes (e.g., sediment sources, dispersal patterns), paleogeographic/climatic changes, and major paleobiological events, including the tempo and mode of early dinosaur, crocodylomorph, turtle and mammalian evolution in southern Pangea during the transition from the Late Triassic to the Early Jurassic.

## 2. Stratigraphic background

The ETME is one of the 'Big Five' biotic crises that are generally thought to have shaped large-scale patterns of Phanerozoic biodiversity, fundamentally reorganising the taxonomic compositions of both continental and marine biogeographic realms (e.g., Raup and Sepkoski, 1982). Studying the effects of this global event in continental ecosystems is difficult because fossiliferous deposits spanning the Late Triassic-Early Jurassic (specifically the post-Carnian to pre-Toarcian interval) are rare and generally poorly dated (e.g., Lucas, 2018). The Elliot and Clarens formations of southern Africa have rich records of tetrapod body and trace fossils resulting from over a century and a half of investigation (e.g., Owen, 1854; Haughton, 1924; Crompton and Jenkins, 1968; Ellenberger, 1970, 1972, 1974; Kitching and Raath, 1984; Warren and Damiani, 1999; Yates and Kitching, 2003; Knoll, 2004, 2005; Butler et al., 2007; Yates, 2007a, 2007b; Yates et al., 2009; McPhee et al., 2014, 2015a, 2015b, 2017, 2018; Dollman et al., 2019). However, the current state of its chronostratigraphic framework leaves the quantification of geological and biological processes uncertain. The lack of absolute age control in the upper Stormberg Group hampers our ability to accurately and precisely correlate the changes that have already been observed in basin development, ancient landscapes, climate, and faunal assemblages with other global records, as well as with regards to the position of the ETME. In the following sections, we review these and additional limitations of the currently weak chronostratigraphic framework, and highlight the recent advancements in the various stratigraphic studies of the Elliot Formation, the unit that contains the Triassic-Jurassic boundary in southern Africa.

## 2.1. Lithostratigraphy

The first modern facies analysis study of the Elliot Formation confirmed that the informal lithostratigraphic subdivisions of the unit (IEF and uEF, respectively) are recognizable on a basinal scale (Figs. 2 and 3; Bordy et al., 2004a, 2004b, 2004c, 2005). These studies also demonstrated mappable regional spatiotemporal changes in facies distribution, thickness, and sediment dispersal patterns (via provenance

Relative abundance: Stratigraphic contact:	Stormberg Group								
High Gradational	Molteno Formation	lower Elliot	§ upper Elliot	Clarens					
Low Vnconformable		S Formation (IEF)	SFormation (uEF)	Formation					
Coarse-grained facies Mud-pebble conglomerate Quartz/quartzite-pebble conglomerate Carbonate nodules conglomerate (+ bone fragments) Clast-rich silty, very fine-grained sandstone Outsized exotic quartzite clasts (pebble-boulder)									
Very fine-grained facies Red-purple, heterogeneous mudstones (massive) Brick-red, maroon to light pink, homogenous Khaki-green-olive-grey mudstones (massive) Organic-rich, dark grey to black mudstones Coal seams Massive siltstone, silty sandstone (?reworked loess) Laminated mudstones			<u>-</u>	<u> </u>					
Colour mottling Desiccation cracks Carbonate nodules Populate				=====					
Bioturbation structures Calcic paleosols				2					
Sandstone facies Coarse, very coarse-grained, granules (glittery) Medium-grained Fine-grained									
Very fine-grained Sublitharenites (and quartz arenites)			-						
Subarkoses–arkoses Very large-scale cross-bedding (paleodunes) Trough cross-stratification Planar cross-stratification									
Massive beds Low-angle cross-stratification									
Planar stratification (horizontal lamination) Ripple cross-lamination									
Soft-sediment deformation structures			-	= _					
Multi-storey sandstone bodies architecture Asymmetrical channel-fill, lateral accretion Tabular, sheet-like bodies Lateral extent <100-150 m Lateral extent <100-150 m				= =					
Sediment supply source	NO BA SER								
From south and southeast From south-west From west									
Feldspatho-quartzose provenance	1								
Stratal stacking pattern across unit Upward-coarsening & upward-thickening				• E 1					
Thickness from S to N within the MKB Decrease No trend	-		-						
Key fossils Dicroidium flora Fossil wood		====							
Insects				= =					
Tetrapod tracks Vertebrate burrows			-						
Paleoenvironment Perennial braided channels Perennial meandering channels Ephemeral channels Extensive floodplain areas Vegetation on floodplain Vegetation along channel banks				= _					
Perennial lakes									
Climate Humid Semi-arid									
Arid									

Fig. 3. Sedimentary facies characteristics and main depositional conditions of the Molteno, IEF, uEF and Clarens formations (Stormberg Group) in the main Karoo Basin of southern Africa. (Data sources: Ellenberger et al., 1964; Bordy et al., 2004a, 2004b, 2004c, 2004d, 2005; Bordy and Head, 2018; Rademan, 2018).

assessment of paleocurrents and source rock composition) in this fluviolacustrine succession. Although lithostratigraphic/sedimentary facies characteristics (summarized in Fig. 3) assist in the straightforward separation of the lEF and uEF, the lateral variability of the stratigraphic architecture at outcrop scale is so high throughout the basin that robust correlation between facies associations is not feasible even in adjacent, high-quality outcrops. Although the correlation of fluvio-lacustrine strata is usually problematic (e.g., Miall, 2013, 2015, 2016), the absence of high-resolution subsurface data (e.g., seismic reflection studies, core data) for the entire Stormberg Group further compound these correlation difficulties.

The lEF is generally characterised by heterogeneous red-purple (ranging from olive-grev to bluish-to-purplish-red) mudstone units with rare colour mottling, and multi-storey, cliff-forming sandstone units with well-developed lateral accretion surfaces and irregular, erosive basal bounding surfaces (Fig. 3; Bordy et al., 2004b, 2004d). The medium-grained, litho-quartzose sandstones in the lEF can be up to ~20 m thick, and have asymmetrical geometry in cross-section perpendicular to paleocurrent directions. The sandstones are often trough and planar cross-bedded and massive (structureless); low-angle crossbedding and planar stratification (horizontal lamination) are rare. Ripple cross-lamination, bioturbation structures and soft-sediment deformation features are all extremely rare. Well-defined, upward-fining successions often begin with mud-pebble conglomerate lags. The mudstones, which are 20-30 m thick on average, rarely display pedogenic alteration features (e.g., irregular mottles, desiccation cracks, carbonate nodules) in contrast to uEF mudstones.

The majority of the uEF comprises very fine- to fine-grained, feldspatho-quartzose sandstones and pedogenically altered mudstones (mostly siltstones) (Fig. 3; Bordy et al., 2004b; McPhee et al., 2018). The diagnostic sedimentary facies of the uEF are intraformational conglomerates, consisting mostly of reworked pedogenic nodules and bone fragments, and clast-rich, massive, silty, very fine-grained sandstones (e.g., Bordy et al., 2004b: pp. 393, 395, 397; Bordy et al., 2017a: pp. 366, 369). The uEF sandstones are tabular, sheet-like bodies with thickness ranges of < 1-6 m that can extend laterally for several hundred metres (Fig. 3). The uEF sandstones contain planar stratification (horizontal lamination), ripple cross-lamination and, less commonly, planar cross-bedding. Soft sediment deformation and bioturbation structures are common. In the uppermost uEF, sandstones are slightly coarser, medium-grained and occur as channel-shaped bodies with rare lateral accretion beds that are up to 15 m in thickness, resulting in an overall upward-coarsening and upward-thickening character. The uEF mudstones are brick-red, maroon to light pink in colour, and regularly show evidence for pedogenic overprinting (e.g., desiccation cracks, in-situ carbonate nodules, rootlets, colour mottling, bioturbation structures) in contrast to the lEF mudstones. Laminated mudstones, appearing dark grey to black, are also present in the uEF. They are rich in organic matter and some bear conchostracans in the uppermost uEF (e.g., Sciscio et al., 2017b; Rampersadh et al., 2018).

Sediment supply patterns prevailed from the south in the lEF but were replaced by transportation directions mainly from west and southwest in the uEF (Fig. 3). Simultaneously, with the reorganization of the sediment supply patterns, the source of the sandstones also shifted from a litho-quartzose provenance in the lEF to a feldspatho-quartzose one in the uEF. Both the lEF and uEF show a decrease in thickness from south to north within the MKB, especially over the southern margin of the Kaapvaal Craton. This south-to-north thinning is particularly distinct in the lEF, which is  $\sim$ 300 m-thick near its type locality in the Barkly Pass, and <10 m-thick in the northernmost region of the basin (e.g., Bordy et al., 2004b, 2004c; Bordy and Eriksson, 2015; McPhee et al., 2017). The uEF has a maximum thickness of  $\sim$ 255 m in the south and a minimum thickness of <30 m in the north.

The marked differences in the architecture of the sedimentary facies (i.e., contrasting sandstone body geometries and associated facies assemblages), sediment supply pattern, petrological composition and

thickness trends at the lEF-uEF contact are explained by changes in fluvial style and regional basin dynamics (Bordy et al., 2004a, 2004b, 2004c, 2004d, 2005). The multi-storey, cliff-forming, asymmetrical channel-fill sandstones of the lEF are interpreted as deposits of a perennial fluvio-lacustrine system that formed under humid to semi-arid climatic conditions. The moderately meandering channels in the lEF were adorned by riparian forests separated from one another by extensive overbank floodplain areas. In contrast to the lEF, the low-energy depositional system in the uEF was prone to cycles of sudden flash flooding and prolonged desiccation under semi-arid climatic conditions. The multi-storey, mostly tabular sandstones in the uEF formed in ephemeral watercourses, which intermittently flowed on vast floodplains with abundant calcic paleosols and shallow, mostly ephemeral lakes. A long-term trend of aridification that started in the uEF (e.g., Bordy et al., 2004b; Bordy and Eriksson, 2015; Sciscio and Bordy, 2016) continued during the deposition of the Clarens Formation (Figs. 2 and 3), which is dominated by massive to large-scale, cross-bedded sandstones that formed in wet and dry deserts with large, down-wind and eastward migrating sand dunes (e.g., Beukes, 1970; Visser, 1984; Eriksson, 1986; Bordy and Head, 2018).

The contrast in fluvial style, provenance and thickness trends across the contact of the IEF and uEF was interpreted by Bordy et al. (2004a, 2004b, 2004c, 2004d, 2005) as a basin-wide unconformity. The duration of this stratigraphic gap was sufficiently long to have allowed the reorganization of regional fluvial depositional style and drainage patterns. Neither the absolute time represented by this regionally mappable paraconformity (essentially a sequence boundary) nor its date of occurrence relative to the TJB have been quantified, mainly because the aforementioned lithostratigraphic and sedimentologic methods are unsuitable for age assessments, except for coarse inferences of relative rates of sediment preservation (e.g., mature paleosols develop during prolonged low rates of clastic sediment accumulation vs flash flood sediments representing sudden high rates of accumulation).

### 2.2. Magnetostratigraphy

Magnetostratigraphy is a stratigraphic correlation and relative dating tool that can provide an autonomous framework for delineating discrepancies between other stratigraphic correlation methods. However, in fluvio-lacustrine units (such as the Elliot Formation), magnetostratigraphy is fraught with uncertainty due to the inherently discontinuous nature and heterogenous stratigraphic architecture of such sedimentary rock successions (e.g., Miall, 2013). To minimize analytical and stratigraphic uncertainties, modern magnetostratigraphic approaches combine detailed litho- and biostratigraphic assessments with robust age constraints, which serve as stratigraphic calibration and anchoring points (e.g., Tauxe, 1998; Langereis et al., 2010).

Paleomagnetic studies in the Mesozoic of southern Africa have relatively low resolution and mostly focus on the Permo-Triassic boundary and Toarcian continental flood basalts (e.g. De Kock and Kirschvink, 2004; Lanci et al., 2013; Moulin et al., 2011, 2012, 2017). Magnetostratigraphic studies on the upper Stormberg Group are less common (e.g., Opdyke, 1964; De Kock, 2003; Sciscio, 2016; Sciscio et al., 2017a), and use magneto- and biostratigraphic correlations to link this succession to its global counterparts in continental settings. For example, Sciscio et al. (2017a) built a 280-m-thick composite magnetostratigraphic section for the Elliot Formation by combining nine stratigraphic sections along a ~350-km-long transect in the MKB (Figs. 1 and 2). This composite section comprises seven polarity pairs (EF2-EF8) and two single polarity intervals (EF1r and EF9n). The lEF contains four normal-reverse polarity intervals (EF2-EF5) and one reverse polarity zone (EF1r). The uEF has three normal-reverse polarity intervals (EF6-EF8) and one normal polarity zone (EF9n). The basal magnetostratigraphic tie is a single  $^{40}\mathrm{Ar}\text{-}^{39}\mathrm{Ar}$  age of  $215\pm3$  Ma (Hälbich et al., 1983), which has been tentatively linked to a

deformation event in the Cape Fold Belt (Catuneanu et al., 1998) and to the unconformable contact between the Molteno and Elliot formations (Bordy et al., 2005). This age has been debated by various authors (e.g., Duane and Brown, 1992; Hansma et al., 2016; Blewett and Phillips, 2016; Blewett et al., 2019), and is generally considered to be unreliable. The uppermost tie point is the radioisotopic age and magnetostratigraphy established for the Toarcian continental flood basalts (e.g., Duncan et al., 1997; Moulin et al., 2011, 2012, 2017). Augmented with biostratigraphic proxies, Sciscio et al. (2017a) also attempted a global correlation of the Elliot Formation to continental sections in the North American Newark APTS, Hartford Basin, Chinle and Moenave formations of the Colorado Plateau (e.g., Nevada, Utah, northern Arizona, western New Mexico), the Argentinian Ischigualasto–Villa Union Basin, and the European St Audrie's Bay (UK) and Paris Basin (France) (e.g., Moreau et al., 2002; Donohoo-Hurley et al., 2010; Olsen et al., 2010; Zeigler and Geissman, 2011; Hüsing et al., 2014; Kent et al., 2014).

Sciscio et al. (2017a) emphasized that the magnetozones have an inconsistent thickness between sections given isopach changes across the basin, which are due to the variable sedimentation rates and the erosional events typical in fluvio-lacustrine environments. Although the basin-wide unconformity between the IEF and uEF is of unknown duration, it has been recognized to have impacted the magnetostratigraphic correlations. Moreover, the main caveat of Sciscio et al. (2017a) is the need for reliable radioisotopic calibration points, and a revision of the current biostratigraphic framework of the Elliot Formation. Therefore, the reliability of the composite magnetostratigraphic section is expected to increase with the addition of new multi-disciplinary datasets.

## 2.3. Biostratigraphy

The Elliot Formation preserves a series of exemplary Late Triassic–Early Jurassic continental faunas (Fig. 2) that have been the subject of several in-depth reviews (e.g., Haughton, 1924; Ellenberger, 1970; Kitching and Raath, 1984; Knoll, 2004, 2005; McPhee et al., 2017; Viglietti et al., 2020a, 2020b). We summarize these below and present the preliminary findings of a quantitative investigation into the geospatial and stratigraphic distributions of upper Stormberg Group vertebrate taxa in Sections 3.2 and 4.2 (see also Viglietti et al., 2020a, 2020b).

The lEF is similarly fossiliferous to, but less taxonomically diverse than, the uEF, and is dominated by early branching sauropodomorph dinosaurs (Fig. 2). Following McPhee et al. (2017), this assemblage includes the following valid sauropodomorph genera: Plateosauravus (Haughton, 1924; Yates, 2003), Eucnemesaurus (Van Hoepen, 1920; Yates, 2007a; McPhee et al., 2015a), and Blikanasaurus (Galton and Van Heerden, 1985; Yates, 2008). Melanorosaurus is provisionally retained as a fourth valid sauropodomorph taxon on the basis of its syntype material (Haughton, 1924; Galton et al., 2005; Yates, 2007b; PMB and JNC, unpublished results), although its taxonomic validity and the referral of key specimens have been questioned (McPhee et al., 2015a, 2015b, 2017). It is clearly in need of substantial revision and this work is currently in progress (PMB and JNC, unpublished results). Additionally, although the recently named Sefapanosaurus (Otero et al., 2015) and Meroktenos (Gauffre, 1993; de Fabrègues and Allain, 2016) have poor provenance data, these might also represent valid IEF taxa. As concluded by McPhee et al. (2017), determining clear morphological boundaries between lEF sauropodomorphs is far from straightforward, with all known taxa possessing medium-to-large bodied, variably robust phenotypes that are currently distinguished by subtle postcranial features (cranial remains are currently unknown for all named species). Although tridactyl theropod trackways are well-known in the IEF (see Section 2.4), the only body fossil evidence for theropods thus far comes from isolated teeth (e.g., Ray and Chinsamy, 2002), which are very difficult to distinguish from those of carnivorous pseudosuchians. There are currently no ornithischian dinosaurs in the lEF (see comments on Eocursor, below and Section 5.4.3).

Therapsids in the lEF are represented by the traversodontid cynodont Scalenodontoides macrodontes (Crompton and Ellenberger, 1957), the youngest known traversodontid occurrence in Gondwana (Abdala and Gaetano, 2018). Recent work added the tritheledontid cynodont Elliotherium kersteni (Sidor and Hancox, 2006) and a possible diademodontid cynodont (Abdala et al., 2007) to this list. However, the diademodontid site has been reassigned to the uEF (Bordy et al., 2017a) and we consider it very likely that the Elliotherium kersteni is from a bed in the lower uEF as this taxa is associated with other fossils and rock types that are typical in the uEF (EMB and PAV, unpublished results). Although the ichnofossil record has hinted at the presence of large dicynodonts in the lEF (see Bordy et al., 2017b for a summary), this was only confirmed recently with the description of Pentasaurus goggai (Kammerer, 2018), and the discovery of new, currently unpublished fragmentary dicynodont material from Eastern Cape Province (JNC, PAV, LS, unpublished data).

Pseudosuchian archosaurs have an enigmatic presence within the lEF. Previous reports of aetosaurs (e.g., Kitching and Raath, 1984) have been shown to be spurious (Tolchard et al., 2019). Maxillary and dentary fragments of likely two species of 'rauisuchians' (i.e., noncrocodylomorph pseudosuchians branching later than aetosaurs) were recently identified by Tolchard et al. (2019), but their exact provenance is unknown. It is possible that isolated occurrences of serrated, recurved teeth indicates the presence of carnivorous pseudosuchians, such as poposauroids or non-crocodylomorph loricatans (e.g., 'Basutodon', von Huene, 1932; see also Tolchard et al., 2019) but, as noted above, a possible theropod identity cannot be discounted. Although never adequately studied, some of the material collected as part of the 'Aliwalia rex' (Galton, 1985) assemblage is possibly non-crocodylomorph pseudosuchian in origin, and could explain why material otherwise referable to Sauropodomorpha might have been incorrectly interpreted as a 'herrerasaurid theropod' (see Yates, 2007a).

The final major tetrapod group within the lEF is temnospondyl amphibians. This fauna was most recently reviewed by Warren and Damiani (1999) who noted the presence of several indeterminate stereospondyls all referable to chigutisaurids, which discounts evidence of capitosaurids from the lEF (Kitching and Raath, 1984). Based on our recent field investigations and consultation with the original collector (B. Battail, personal communication, 2018), we confirm that the stratigraphic position of a gigantic brachyopid stereospondyl mentioned by Steyer and Damiani (2005) originated from the lower uEF near Alwyns Kop in Lesotho.

In contrast to the lEF, the uEF and Clarens Formation sauropodomorph assemblage is morphologically and taxonomically diverse (Fig. 2), and contains the following valid genera: Massospondylus (Cooper, 1981; Gow et al., 1990; Yates and Barrett, 2010; Chapelle and Choiniere, 2018; Barrett et al., 2019), Antetonitrus (Yates and Kitching, 2003; McPhee et al., 2014), Aardonyx (Yates and Barrett, 2010), Pulanesaura (McPhee et al., 2015b; McPhee and Choiniere, 2018), Ngwevu (Chapelle et al., 2019) and Ledumahadi (McPhee et al., 2018). Together these taxa comprise a diverse fauna ranging from gracile massospondylids to multi-tonne lessemsaurids, signalling disparate feeding ecologies supported by distinct biomechanical strategies (McPhee et al., 2015b, 2017, 2018). The discovery of Pulanesaura also indicates the presence of the earliest branching sauropods (McPhee et al., 2015b). Two other genera, Arcusaurus (Yates et al., 2011) and Ignavusaurus (Knoll, 2010) have also been named from the uEF in recent years, but their validity has been questioned (e.g., Yates et al., 2011; McPhee et al., 2017).

Theropod dinosaurs in the uEF and Clarens Formation are represented by fragmentary remains attributed to the southern African coelophysid *Megapnosaurus rhodesiensis* (formerly *Syntarsus rhodesiensis* and *Coelophysis rhodesiensis*, see below; Kitching and Raath, 1984; Smith and Kitching, 1997; Munyikwa and Raath, 1999; Bristowe and Raath, 2004). A larger theropod species, *Dracovenator regenti*, was named from partial cranial material and is possibly related to the North American taxon *Dilophosaurus* (Yates, 2005). Several genera of basal ornithischian dinosaur have been named from the uEF, including some of the earliest global occurrences of the group. *Lesothosaurus diagnosticus* (e.g., Galton, 1972; Butler, 2005; Porro et al., 2015; Barrett et al., 2016; Baron et al., 2017a; Sciscio et al., 2017c) represents the most abundant form (*Stormbergia dangershoeki* is currently thought to be a junior synonym of this taxon: e.g., Baron et al., 2017a; Sciscio et al., 2017c). Several heterodontosaurids are also known (Porro et al., 2010), including: *Heterodontosaurus tucki* (e.g., Crompton and Charig, 1962; Norman et al., 2011; Sereno, 2012), *Abrictosaurus consors* (Thulborn, 1974; Sereno, 2012). *Lycorhinus angustidens* and *Pegomastax africanus* (Butler et al., 2008; Sereno, 2012). *Eocursor parvus*, originally described as a lEF taxon (Butler et al., 2007), has recently been reinterpreted as coming from the uEF (Olsen et al., 2010; McPhee et al., 2017).

The most abundant uEF taxa after dinosaurs are cynodonts, of which both non-mammaliaforms and mammaliaforms are present. Following the recent review of Abdala and Gaetano (2018), the former includes the tritheledontid taxa *Tritheledon, Diarthrognathus* and *Pachygenelus*, and the tritylodontids *Tritylodontoideus* and *Tritylodon*. Mammaliaformes are represented by the morganucodontids *Megazostrodon* and *Erythrotherium*.

The diverse uEF crocodylomorph fauna was recently reviewed by Dollman et al. (2019), with the following taxa recognised currently: the non-crocodyliform crocodylomorphs *Sphenosuchus acutus* and *Litargosuchus leptorhynchus*; and the crocodyliform 'protosuchids' *Protosuchus haughtoni*, *Notochampsa istedana* and *Orthosuchus stormbergi*. Dollman et al. (2019) noted that the majority of crocodylomorph occurrences are restricted to the upper half of the uEF. Non-archosaurian reptiles are represented by the early turtle *Australochelys africanus* (Gaffney and Kitching, 1994) and a specimen of the rhynchocephalian *Clevosaurus* sp. (Sues and Reisz, 1995). As with the lEF, the temnospondyl record of the uEF is restricted to mostly indeterminate remains of chigutisaurid stereospondyls (Warren and Damiani, 1999), one of which is the largest brachyopid stereospondyl documented to-date (Steyer and Damiani, 2005), as noted above.

#### 2.3.1. Biostratigraphic correlations

Global biostratigraphic correlations for Stormberg Group vertebrate faunas are based on weak evidence. Many rely on broad faunal similarities, or 'stage of evolution' arguments, rather than the presence of shared index taxa, leading to low precision, issues of replicability between different workers, and decreased confidence in their results (e.g., Olsen and Sues, 1986; Lucas, 1998; see Rayfield et al., 2009 for a critique of this approach). No species-level taxa in the Stormberg Group are shared with non-African faunas, only four genera are shared, and phylogenies including Stormberg taxa at the species level are either labile, weakly supported, or have not been performed.

The poorly known lEF fauna has been biostratigraphically correlated, often tentatively, with Norian-Rhaetian faunas such those from the 'Middle Keuper' of Germany, the Los Colorados Formation of Argentina, and the Chinle Formation of the USA (Lucas and Hancox, 2001; Knoll, 2004; McPhee et al., 2017). However, the absence of shared index taxa does not allow for a precise correlation with these deposits. The fauna of the uEF and Clarens Formation has been correlated with Early Jurassic faunas, such as the Lower Lufeng Formation of China, the Glen Canyon Group of the USA, and the McCoy Brook Formation of Canada (Olsen and Galton, 1984; Smith and Kitching, 1997; Lucas and Hancox, 2001; Knoll, 2005) and, in this case, some potentially useful shared taxa are present. For example, the close similarity of species within the crocodyliform genus Protosuchus from the uEF (P. haughtoni), the Moenave Formation of the Glen Canyon Group, Arizona (P. richardsoni: Clark, 1986), and the McCoy Brook Formation, Nova Scotia (P. micmac: Sues et al., 1996) does suggest that these

deposits are approximately contemporaneous. These North American strata are currently regarded as Hettangian in age on the basis of a radioisotopic date recovered from basalts underlying the McCoy Brook Formation (Sues and Olsen, 2015) and detrital zircon dating of the Moenave Formation (Suarez et al., 2017). Correlation with the McCoy Brook Formation is further supported by the shared genera Pachygenelus (a trithelodontid cynodont: Shubin et al., 1991) and Clevosaurus (a rhynchocephalian lepidosauromorph: Sues and Reisz, 1995), both of which are absent from the depauperate fauna of the Moenave Formation. The absence of these same genera from the diverse fauna of the Kaventa Formation, which overlies the Moenave Formation, suggests that the fauna of the uEF is older than that of the Kaventa Formation. which has been dated with detrital zircons as no older than late Pliensbachian (Marsh and Rowe, 2018). Protosuchus has been reported from the Hettangian of Poland (Gierliński and Potemska, 1985), providing a potential European correlation, but the latter requires confirmation given the similarities of this material to other 'protosuchian' genera. More promisingly, Clevosaurus has been recorded from several other Early Jurassic faunas, including the Hettangian of the UK (Evans and Kermack, 1994) and the Early Jurassic of China (Luo and Wu, 1994), extending its potential use in global correlations. However, the stratigraphic range of Clevosaurus also extends into the Late Triassic, based on abundant material from the UK, Belgium, Luxembourg and Brazil (Fraser, 1988; Godefroit and Sigogneau-Russell, 1995; Hsiou et al., 2015, 2019). Although these Late Triassic occurrences might offer some support for the proposed Rhaetian age inferred for the lower uEF on the basis of magnetostratigraphy (Sciscio et al., 2017a), it is more likely that they represent species that are temporally distinct (Hsiou et al., 2019), although the monophyly of Clevosaurus has recently been questioned (Herrera-Flores et al., 2018; Hsiou et al., 2019). Finally, coelophysoid theropods have been identified in both the Late Triassic (Norian) Chinle Formation of the USA (Coelophysis bauri; Colbert, 1989) and the uEF (Megapnosaurus rhodesiensis; Munyikwa and Raath, 1999; as 'Syntarsus' rhodesiensis and as 'Coelophysis' rhodesiensis in previous works), although with distinct species in each region. However, anatomically similar coelophysoids are also known from other Lower Jurassic deposits such as the Lufeng Formation of China (You et al., 2014) and the Kayenta Formation of North America (e.g., Rowe, 1989). The inclusion of M. rhodesiensis within Coelophysis was proposed by Bristowe and Raath (2004), and could potentially indicate correlation with the Chinle Formation. However, recent phylogenetic studies question that assignment (e.g., Ezcurra and Brusatte, 2011; Griffin and Nesbitt, 2019; Wang et al., 2017), and we regard the occurrence of coelophysoids in the uEF as consistent with an either Late Triassic or Early Jurassic age (also see Martínez and Apaldetti, 2017).

Biostratigraphic correlations between other Karoo-aged basins in southern and eastern Africa are also weakly supported due to the absence of shared genus- and species-level taxa. Currently, no IEF vertebrate taxa are known outside the main Karoo Basin. However, Megapnosaurus rhodesiensis has been identified in the uEF and the Forest Formation of Zimbabwe (e.g., Raath, 1969; Munyikwa and Raath, 1999), along with more taxonomically tentative records of Clevosaurus (Gow, 1977) and Notochampsa (Raath, 1981). Moreover, occurrences of the basal sauropodomorph dinosaur Massospondylus have been reported in several Zimbabwean basins (e.g., the Mid-Zambezi, Mana Pools, and Tuli basins: Attridge, 1963; Raath et al., 1970; Bond, 1973; Cooper, 1981; Munyikwa, 1997; Rogers et al., 2004) and might provide a direct faunal link, but the material reported from the Zimbabwean localities requires taxonomic reassessment to confirm these proposals (Barrett et al., 2019). A tentative link between the uEF and Karoo-aged strata in the Luangwa Basin of Zambia has been posited on the basis of taxonomically indeterminate sauropodomorph material (Choiniere and Barrett, 2015), but requires additional support.

#### 2.4. Vertebrate ichnology

The Stormberg Group, and in particular its upper part (Fig. 2), contains a diverse and globally important trackway record, with an abundant assemblage of ichnites attributable to herbivorous and carnivorous dinosaurs, dicynodonts, cynodonts, amphibians, crocodylomorphs, and mammaliaforms (e.g., Ellenberger et al., 1964; Ellenberger, 1970, 1972, 1974; Raath et al., 1990; Smith et al., 2009; Wilson et al., 2009; Marsicano et al., 2014; Sciscio et al., 2016, 2017c; Abrahams et al., 2017; Bordy et al., 2017b; Rampersadh et al., 2018).

Paul Ellenberger conducted the pioneering work on this record, erecting a great diversity of tetrapod ichnogenera and ichnospecies in addition to establishing an ichnostratigraphic subdivision for the southern African Upper Triassic to Lower Jurassic (e.g., Ellenberger, 1970, 1972, 1974). This work introduced the first biozonation scheme for the Stormberg Group (e.g., lEF includes zones A1 – A6; uEF and the Clarens Formation zones A7, B1- B7) and underscored the division of the regional ichnofaunas into two broad biozones that reflect a faunal change equivalent to the turnover in skeletal remains both locally and globally during the Late Triassic to Early Jurassic. Ellenberger's seminal work was revised some 35 years ago by Olsen and Galton (1984), who significantly reduced the number of ichnotaxa through synonymization. While this ichnotaxonomic revision was valuable for pointing out several nomina dubia, it also lumped some valid ichnotaxa, which had the unfortunate corollary of decreasing confidence in the value of the southern African ichnofossils for global correlation and regional biodiversity assessments. The shortcomings of this alternative ichnologic framework have to some extent been rectified subsequently by, for example, Lockley et al. (1996, 2004, 2006), Rainforth (2003), Lockley and Gierlinski (2006), D'Orazi Porchetti and Nicosia (2007), and D'Orazi Porchetti et al. (2015, 2017, 2018). Based on these revisions, the currently accepted tetrapod ichnofaunal list for the Upper Triassic IEF includes Tetrasauropus, ?Lavinipes jaquesi, and Pseudotetrasauropus (quadrupedal and bipedal sauropodomorph dinosaurs), Grallator (theropod dinosaur), Pentasauropus (dicynodont), Sauropodopus (probable rauisuchians, with similarities to Chirotherium), Paratetrasauropus (crocodylomorph) and cf. Brachychirotherium (archosauromorph), whereas for the Lower Jurassic uEF and Clarens Formation contains Episcopopus (amphibian), Batrachopus (crocodylomorph), Moyenisauropus and Trisauropodiscus (ornithischians), Ameghinichnus (tritylodontid cynodonts), a great variety of ichnotaxa on the Grallator-Eubrontes plexus and Kayentapus (theropods) as well as tentative Brasilichniumlike (mammaliaforms, ?synapsids) tracks. This list is far from complete, and our ongoing ichnologic work is aimed at updating and refining the Stormberg Group ichnostratigraphic scheme to better reflect the true ichnofaunal diversity and the degree of trackmaker endemism within the Stormberg Group (EMB, unpublished results; Sciscio et al., 2016, 2017c; Abrahams et al., 2017; Bordy et al., 2017b, 2020; Rampersadh et al., 2018).

The vertebrate track record of the Stormberg Group, based on shared ichnofauna elements, has been linked to Late Triassic to Early Jurassic tracks on all continents except Antarctica (for relevant reviews see Olsen and Galton, 1984; D'Orazi Porchetti and Nicosia, 2007; Lucas, 2007: Klein and Lucas. 2010: D'Orazi Porchetti et al., 2015: Citton et al., 2018; Hunt et al., 2018 and references therein). However, the coarse temporal and stratigraphic resolution of the tetrapod footprint record in the upper Stormberg Group, in addition to an outdated regional ichnotaxonomy, limits its utility for fine-scale regional or global correlations, despite the great abundance of ichnites within the succession. As mentioned above, this shortcoming is being addressed systematically by our ongoing research program, and a major review of the upper Stormberg track assemblages, augmented by refined stratigraphic data on existing ichnofossil sites and additional collecting, will be forthcoming. Because the current ichnozonation is in flux, this topic is not discussed further herein.

#### 3. Methodology

#### 3.1. Detrital zircon U-Pb geochronology

Given the dearth of prior radioisotopic constraints for the Stormberg Group, due to the lack of obvious primary volcanic lithologies amenable to radioisotopic dating, we have taken the approach of seeking juvenile zircons from volcanoclastic lithologies. Juvenile zircons, those that show morphological evidence for limited reworking within a sedimentary system, and return ages that are 'close' to the true depositional age (TDA), have been used in similar continental sedimentary rock (e.g., Ramezani et al., 2011) to provide useful maximum age constraints on the timing of sediment accumulation, aiding the revision of the chronostratigraphic frameworks. Detrital zircons were successfully extracted and dated from 16 rock samples taken from the Elliot and Clarens formations in South Africa and Lesotho (Supplemental Table S1). Because primary volcanic tuff layers (i.e., pyroclastics) were not identified in the studied succession, the sampled rocks are exclusively tuffaceous sandstones and siltstones.

Zircons were separated using a modified standard method described by Tucker et al. (2013), which includes rock crushing, panning, and magnetic and heavy liquid separation of minerals. Zircons from each sample were inspected under optical microscopy and showed mixed morphology ranging from rounded, indicating reworking in a sedimentary environment, to acicular and faceted, with medial melt inclusions, typical of volcanic zircon that has not undergone significant reworking. Zircons were then mounted in resin for laser ablation inductively coupled plasma ionization mass spectrometry (LA-ICP-MS) U-Pb dating, with a subset of samples undergoing LA-ICP-MS mounted on tape. The grains from the youngest population were removed for subsequent high-precision chemical abrasion thermal ionization mass spectrometry (CA-ID-TIMS) U-Pb dating (Supplemental Text S1 and Table S1). Both of these geochronological methods have their advantages, as the LA-ICP-MS method allows for a large number of grains to be analysed, increasing the probability of finding the youngest grains, and the CA-ID-TIMS allows for high-precision analyses and treatment for open-system behavior. We have therefore attempted to take advantage of both these methods. Laser ablation spots were selected after the careful consideration of inclusions, textural features, and cracks within the imaged zircon grains. The geochronological dating procedures are further detailed in Supplemental Text 1.

## 3.2. Biostratigraphic methods

We collated, to the best of our ability, all metadata relating to fossil collections of upper Stormberg tetrapods including both South African (e.g., Iziko Museum, Evolutionary Studies Institute, Albany Museum, National Museum) and international repositories (e.g., London Natural History Museum, Muséum National d'Histoire Naturelle Paris, Naturhistorisches Museum Wien Vienna) using a combination of publications, online databases, and collections records and archives of field notes obtained directly from museum collections. We cleaned these data (e.g., removing spelling errors in taxon names) using automated means where possible. Geospatial positions and stratigraphic provenance of specimen occurrences were validated by cross-referencing Google Earth, GIS software, field notes, personal measurements of stratigraphic sections at historic fossiliferous sites, and the collection of new, well-georeferenced fossil material. Collation of this large historic dataset resulted in over 1400 records, about 20% of which are georeferenced with high credibility, and located across the northern, eastern, southern, and western extent of the Elliot and Clarens formations in the MKB (see Data Availability section).

#### Table 1

Summary of the results from the different age estimating methods used in constraining the maximum depositional age (MDA) of the samples from the Elliot and Clarens formations in the upper Stormberg Group.

Sample ID	Method	Lithology & formation	Preferred MDA		YSG Y		YC1σ(2+)		YC2σ(2+	YC2σ(2+)		YC2σ(3+)		Concordia	
			Age	2σ	Age	2σ	Age	2σ	Age	2σ	Age	2σ	Age	Age	2σ
BH-15	ID-TIMS	tsa lEF	204.9	0.88	204.02	0.59	205	1.2	204.9	0.17			205	205	0.64
GV-14	ID-TIMS	tsa lEF	212.1	0,19	212.1	0,19									
HAF	LA-ICP-MS	tsa lEF	209.6	1.4	208.2	2.9	209	1.6	209.6	1.4	209.6	1.4	209	209.7	2.4
HB-15	LA-ICP-MS	tsi lEF	218.2	2	216.5	4.7	518	9.9	218.2	2	518	9.7	520	218.9	10
LEP	LA-ICP-MS	tsa uEF	197.3	2.3	195.7	3.1	239.6	2.7	197.3	2.3	243	1.5	196	197.4	2.3
LGT	ID-TIMS	tsi lEF	209.11	0.20			209.11	0.2	208.01	0.86	208.01	0.86	209	208	0.9
LK-17	LA-ICP-MS	tsi lEF	207	5			207.6	5.1	207	5.1	467	8	207	208.3	4.7
LMO	LA-ICP-MS	tsa uEF	199.9	2.3	193.9	2.9	199.8	2.1	199.9	2.3	232	2	194	200	8.6
MAF	LA-ICP-MS	tsa uEF	201	2.3	199	3	254	2.8	201	2.3	256.4	1.4	256		
MAP	LA-ICP-MS	tsa lEF	215.4	1.9							215.4	1.1			
PHU	LA-ICP-MS	tsa lEF	219.6	2.5	217.6	3.4	242.6	2.2	219.6	2.5	243.1	2	243	219.7	2.5
PS-15	ID-TIMS	tsa uEF	202.33	0.19	202.33	0.19	217.14	0.14	217.21	0.11	217.21	0.11	217	217.2	0.54
Q6	LA-ICP-MS	tsa um uEF	191.1	1.5	190	2.4	193.4	1.2	191.9	1.5	467.4	2.5	193		
QSS1	LA-ICP-MS	tsa lEF	211.5	2.8	207.5	9	211.5	2.9	211.5	2.9	211.5	2.9	213		
SUB	LA-ICP-MS	tsa lEF	216.4	2.4	215.4	3.4	216.4	2.4	216.4	2.4	252	2	216		
UMC	LA-ICP-MS	tsa Clarens	187.5	1.6	185.9	2.2	186.7	1.2	187.5	1	187.5	1	187		

For spatiotemporal distribution of the samples, see Figs. 1, 2, 4 and 5. Abbreviations:  $IEF - Iower Elliot Formation; uEF - upper Elliot Formation; tsa - tuffaceous sandstone; tsi - tuffaceous siltstone; um - uppermost; <math>\sigma$  - internal error. Ages and errors are in millions of years (Ma). Strike-through indicates that the MDA is too young based on stratigraphic constraints. For justification of the preferred MDAs, see Supplemental Text 1.

#### 4. Results

#### 4.1. Appraisal of the detrital zircon U-Pb geochronology methods

To constrain the maximum depositional age (MDA) of the samples from the Elliot and Clarens formations (Table 1), we explore a range of different age calculations for the data obtained from the analysed detrital zircons in order to assess the sensitivity of the age constraints to our chosen interpretive framework. The complete dataset of geochronological measurements is provided in Supplemental Table S1. The relevant measurements for each sample are illustrated in Figs. 2, 4 and 5, and in Supplemental Fig. S1. The latter provides, for each sample, the relative-age-probability plots (or probability density plots; PDPs) for zircons < 500 Ma, concordance diagrams for zircons younger than ~250 Ma and plots of the weighted mean dates (at 95% confidence) for zircons younger than ~250 Ma. The sample-by-sample appraisal of the detrital zircon U-Pb geochronology dates and the justification of the preferred MDAs and true depositional ages (TDAs) are in Supplemental Text 1.

Our preferred method for estimating the MDA (Table 1) is the weighted mean of the youngest cluster comprised of two or more grains overlapping with the youngest one at  $2\sigma$  internal error (YC $2\sigma[2+]$ ). Using two or more analyses instead of the single youngest analysis reduces the chance that the MDA will be younger than the TDA (e.g., as a consequence of Pb-loss; see below). Furthermore, our use of CA-ID-TIMS analyses for a subset of the samples helps deal with this issue - the use of chemical abrasion pre-treatment means that Pb-loss is effectively eliminated, and the higher-precision of the data allow for a more robust assessment of Pb-loss via discordance. Although somewhat subjective, the use of the  $YC2\sigma(2+)$  metric resulted in the MDA calculations being more consistently compatible with other stratigraphic considerations in the study area. The considerations that are used to constrain our age interpretations include: the stratigraphic context of the sample (i.e., its position relative to key stratigraphic contacts and other dated samples in the same section to which a sample must obey the law of superposition); the location of the sample within the Karoo foreland basin; lithostratigraphic characters of the host rocks (i.e., lEF, uEF); and the body and ichnofossil content of the adjacent strata. In several samples, the youngest single grain method (YSG) seems to be the least representative of the TDA, because the measured dates of the youngest grain often seem younger than the expected TDA than what would be

anticipated from other stratigraphic considerations (e.g., samples BH-15, LGT). This is likely due to Pb-loss as explained further in the Supplementary Text 1 (as well as in e.g., Dickinson and Gehrels, 2009; Corfu, 2013; Andersen et al., 2019; Gehrels et al., 2019; Herriott et al., 2019; Rossignol et al., 2019). To put it differently, the YSG method is statistically the least robust, because it focuses on a single data point that is often not reproducible in detrital zircon samples. The MDA calculations based on age clusters are more robust than the YSG because they incorporate multiple data points and account for internal analytical error and the external error of the population (e.g., Dickinson and Gehrels, 2009; Gehrels et al., 2019; Herriott et al., 2019). Although  $YC2\sigma(3+)$  is the second most quoted MDA metric in the literature (e.g., Coutts et al., 2019), our preferred method for interpreting MDA is its modified version, the  $YC2\sigma(2 +)$  metric as explained above. Contrary to the YSG metric, the weighted mean calculated from the youngest grain cluster composed of three or more grains that overlap at  $2\sigma$  uncertainty  $(YC2\sigma[3+])$  often appears to be too conservative, yielding older dates (early Middle Triassic - Ordovician) than the currently accepted age estimates of Late Triassic - Early Jurassic for the upper Stormberg Group (e.g., samples HB-15, LK-17). In these cases, it is likely that the measured dates are significantly older than the TDA, because near-depositional-age zircons were not captured in the sediment during deposition or are too few in the sample for this date-calculation method (e.g., Andersen et al., 2016). For more comprehensive discussions on the various MDA calculations used, including their relative merits, the readers are referred to Dickinson and Gehrels (2009), Andersen et al. (2019), Coutts et al. (2019), Gehrels et al. (2019), Herriott et al. (2019), Johnstone et al. (2019), and Rossignol et al. (2019).

#### 4.2. Biostratigraphic results

Several clear patterns emerge from our database of upper Stormberg tetrapod occurrences (Fig. 6). There is a pronounced turnover across the lEF/uEF contact. No currently valid tetrapod genera cross this boundary, and although it is possible that the dipnoan *Ceratodus* is present in the lEF (EMB, unpublished results) and uEF (Kitching and Raath, 1984), this genus is temporally wide-ranging and the upper Stormberg material is in need of revision. Family level or higher boundary crossers include Sauropodomorpha, Cynodontia, and Chigutisauridae.

Lower Elliot Formation tetrapod occurrences, in general, are as





**Fig. 5.** Simplified stratigraphic sections showing the detrital zircon sample position within the local succession. Sections are arranged from north to south (see inset map for locations). Question marks at the stratigraphic contact of the lEF-uEF indicate a < 10 m thick zone where lack of outcrops obscure the position of the contact. The uncertain position of the TJB is emphasised by the grey band. The less-than sign next to each MDA indicates that the age of the sample could be younger (i.e., the MDAs are only maximum constraints on the age of deposition). For the complete analytical dataset, see Supplemental Text S1, Table S1 and Fig. S1. (Rademan, 2018).

geographically widespread as those in the uEF (Fig. 7), but the lEF has many fewer well-georeferenced records for valid taxa. For example, in the lEF, only Scalenodontoides, Eucnemesaurus, and possibly Melanorosaurus have representative occurrences approximating the geographic range of the overall fossil sample, whereas the uEF has at least five such taxa (Heterodontosaurus, Lesothosaurus, Massospondylus, Protosuchus, Tritylodon). In addition, poor taxonomic data for many lEF tetrapod occurrences lead to insufficient ability to infer stratigraphic ranges for most lEF taxa, with the notable exception of Scalenodontoides (Viglietti et al., 2020a). This traversodontid cynodont is the only lEF tetrapod taxon that is currently taxonomically valid, easy to identify in the field, and known from multiple specimens with well-constrained provenance from several IEF localities across the basin (unlike any of the IEF dinosaur taxa - see e.g., McPhee et al., 2018). In contrast, the uEF is rich in well-georeferenced fossil taxa, providing detailed information for the stratigraphic ranges of most uEF fossil vertebrate lineages (Fig. 7). We also observe a similar trend to that noted by Kitching and Raath (1984), where a sudden increase in the relative abundance of fossils occurs above the lower quarter of the uEF and at the contact of the uEF and Clarens Formation.

Dinosaur lineage diversity increases markedly in the uEF (Fig. 6). Sauropodomorpha are present and relatively abundant in both the lEF and uEF (Fig. 8), although more species are currently known from the uEF. In contrast, ornithischians and non-dental theropod remains are absent from the lEF, indicating that they were either rare or absent. Both groups have their first definite occurrences low in the uEF. Many other tetrapod lineages also make their first appearance in the uEF, with the first crocodylomorphs, probainagnathians (including trithelodontids and tritylodontids), and turtles appearing relatively low in the uEF and the first mammaliaforms definitively appearing closer to the contact of the uEF and Clarens Formation (Fig. 6).

#### 5. Discussion

#### 5.1. Detrital zircon U-Pb geochronology

In continental rock successions that are lacking pyroclastics (i.e., primary volcaniclastic rocks), utilizing the U-Pb radioisotopic dates from detrital zircons is an effective approach for inferring the maximum depositional ages (MDAs) of strata (e.g., Dickinson and Gehrels, 2009; Ramezani et al., 2011; Coutts et al., 2019; Rossignol et al., 2019). It should be emphasized that the ages of the youngest detrital zircons in any given sedimentary rock sample only provides a maximum constraint on the depositional age; the sample will be younger than the MDA if the detrital zircons are recycled from older sediment sources. The extent to which the youngest detrital zircons provide precise estimates of the true depositional age (TDA) depends on the availability of syn-depositional zircons in the depositional system, typically supplied via windblown volcanic ash or from erosion of active volcanic sources. In some cases, MDA calculations can be older than the TDA even in volcaniclastic sediment due to the presence of antecrystic, epicrystic, and xenocrystic zircon that formed prior to the most recent eruption (Rossignol et al., 2019).

Our detrital zircons were recovered from sandstones and tuffaceous siltstones, and both lithologies show evidence of reworking. In this context, the extent to which detrital zircons provide meaningful age constraints depends on: (1) the extent to which autocrystic (syn-eruptive) zircon is present, and (2) the time lag between the zircon crystallisation in the original magma chamber and final deposition in the upper Stormberg Group (e.g., Spencer et al., 2016; Andersen et al., 2019; Gehrels et al., 2019; Herriott et al., 2019; Rossignol et al., 2019). Given that both assumptions cannot be independently constrained, we assume that all zircon is recycled and that MDA calculations provide only a *maximum* constraint on the TDA (i.e., the TDA is younger or equal to the MDA). By integrating MDA calculations with existing age constraints from bio-, litho-, and magnetostratigraphic considerations, we show that, in many cases, the youngest detrital zircons provide meaningful age constraints on the age of the upper Stormberg Group. In the following sections, we discuss the implications of the new detrital zircon U-Pb ages for the geological history of the TJB-bearing Elliot Formation in southern Africa from various from litho-, magneto- and biostratigraphic aspects.

#### 5.2. New radioisotopic dates and basin evolution

#### 5.2.1. Lithostratigraphic considerations

Based on our new geochronological dataset, obtained from U-Pb radioisotopic dates of detrital zircons in the Elliot and Clarens formations (Figs. 1, 2 and 4), the upper Stormberg Group probably spans ~40 Ma, and we infer that this represents a sedimentation record from the middle Norian to early Toarcian. In particular, the TJB-bearing Elliot Formation represents a ~30-million-year-long depositional episode (from ~220 to ~190 Ma ago), of which the lEF and uEF account for ~20 and ~10 Ma, respectively.

These new age-constraints help us understand the resolution and completeness of the geological history captured in the late stages of MKB evolution. The completeness of the depositional record is variable across the MKB, as evidenced by the fact that the Elliot Formation. which was deposited in  $\sim$  30 million years, is  $\sim$  500-m-thick in the south and less than 30-m-thick in the north. Assuming that the unit's stratigraphic contacts are isochronous across the MKB, the ~30 Ma worth of rock record of the Elliot Formation can imply that this unit: (1) was deposited under low sediment preservation conditions (i.e., accumulation rates of  $\sim$ 1.5-27.5 m/Ma), (2) contains cryptic stratigraphic gaps, which are possibly long but rarer in the south, and short but more abundant in the north of the basin, and (3) is separated from the underlying Carnian Molteno Formation by a regional stratigraphic gap of  $\sim$ 6–7 Ma. In foreland basins, low sediment preservation conditions are normally favourable for mature paleosol development (e.g., DeCelles, 2012; Miall, 2016), whereas regional unconformities are typically associated with flexural tectonics driven largely by mountain building events (e.g., Catuneanu et al., 1998; Catuneanu, 2004; Bordy et al., 2004a, 2005). Moreover, the newly obtained dates also suggest that: (1) the relative resolution of the rock record is higher in the uEF compared to the lEF (Fig. 1c); and (2) the overall resolution of the Elliot rock record is modest to very low, especially in the northern part of the basin, where the thickness of the Elliot Formation is rarely >100 m.

Our radioisotopic age estimates are an important critical test of previous assessments based on relative chronostratigraphy. Nevertheless, they largely uphold those previous assertions, albeit with more nuance. While the results currently lack the spatial resolution required to precisely identify the position of the TJB at the sampling sites and for the entire basin, both vertically and laterally, these new results nonetheless support previous proposals that the TJB is close to the geological transition from lEF to uEF facies, and lay the foundation for quantifying the vertical distance between these key chrono- and lithostratigraphic boundaries (Fig. 3).

Determining the position of the TJB relative to this major stratigraphic contact will require much denser sampling of radioisotopic ages in multiple vertical sections throughout the basin. In addition to









Fig. 8. Proportional representation of the key vertebrate higher taxa in the lEF (left), and uEF and Clarens formations (right) in the MKB. These relative abundances only show occurrences that are identified at generic level or lower. Silhouettes not to scale.

maximum depositional ages from juvenile detrital zircons, radioisotopic dating of authigenic mineral phases (e.g., feldspars, phosphates, carbonates, especially from the abundant pedogenic carbonates in the uEF) may provide useful minimum depositional ages (e.g., Wang et al., 1998; Tabor and Myers, 2015). Such high-density geochronological sampling campaign at selected sites could also assist in reliably answering key geological questions, such as: (1) how much time is represented by the unconformity currently thought to separate the lEF from the uEF; (2) whether this stratigraphic gap is diachronous or isochronous across the basin (i.e., are there lateral changes in the size of the gap at regional and subregional scales); (3) what is the frequency and magnitude of smaller stratigraphic gaps in the lEF and uEF; and (4) what were the regional depositional dynamics in the late foreland basin history of the MKB (i.e., differential sedimentation/preservation rates from site-tosite across the basin; residence time of zircons in the dynamic fluvial setting of the Elliot depositional episode). Establishing a higher resolution age framework in the Elliot Formation could refine the depositional history of this unit, placing its high lateral facies variability into context. It would also facilitate judicious short-range, local correlation of strata (see Section 2.1, above). The latter, in turn, could also assist with robust answers to key paleobiological questions, many of which have global relevance (see Section 5.4, below).

## 5.2.2. Sediment provenance considerations

Primary volcanic tuff layers (i.e., pyroclastics) that are suitable for robust chronostratigraphic age determinations remain elusive in the studied part of the MKB upper Stormberg succession. Such non-recycled air-fall tuffs are also commonly lacking in other Upper Triassic–Lower Jurassic continental deposits worldwide (e.g., Lucas, 2018). In the MKB, we tentatively attribute the lack of primary volcaniclastics to a combination of geological processes: (1) sediment recycling and other dynamics of continental sedimentation in foreland basins, where deep lakes, similar to those in the extensional Fundy (Canada) and Newark (USA) basins, are lacking; and (2) a potential volcanic ash fall gap in the rocks due to either a) relative inactivity or dormancy of the regional volcanic arcs in the Late Triassic to Early Jurassic or b) the site of continental deposition in the final stages of the MKB evolution was distal to major, contemporaneous volcanic eruption centres, i.e., the primary source of datable, syn-sedimentary zircon grains were located in faraway sectors of the incipiently fragmenting Pangean supercontinent (e.g., Pankhurst et al., 2006, 2014; Schiuma and Llambias, 2008; Muravchik et al., 2011; Spikings et al., 2016).

Notwithstanding the lack of primary ash fall deposits (i.e., pyroclastics), the newly acquired dataset of the detrital zircons, especially the older part of the age spectra in each sample, provides new avenues for interpreting the difference in provenance characteristics of the lEF vs uEF, and thus the depositional history of the Elliot Formation in the MKB. By tapping into this dataset, a deeper understanding of the sedimentary recycling regime and detrital zircon budget of southern Africa in the Mesozoic may be achieved, especially if this is thoughtfully combined with documented (and newly measured) sediment transport directions within the Stormberg Group (e.g., Bordy et al., 2004c, 2004d, 2005). The most notable difference (Supplemental Table S1) between the detrital zircon populations of the lEF and uEF is that Neoproterozoic grains (~35%) are the dominant single population in the lEF, whereas Palaeozoic grains are the dominant single population in the uEF (49%), and the single Clarens Formation sample included in this study (59%). The lEF detrital zircon signature is expected from the recycling of rocks in the south from the Cape Fold Belt as well as the lower Karoo rocks (Dwyka and Ecca groups; Fig. 1). The uEF detrital zircon signature, sourced from the west and south and dominated by Palaeozoic grains, suggests a proximal source area of mostly pre-Stormberg Karoo and Cape Fold Belt rocks (Fig. 1), with little or no input from older Precambrian terranes (e.g., western Kaapvaal Craton).

#### 5.3. New radioisotopic dates and implications for magnetostratigraphy

Using paleomagnetism and the close phylogenetic affinities of several prosauropod dinosaurs, Sciscio et al. (2017a) correlated the lowermost lEF to the Los Colorados Formation (Kent et al., 2014). Given the detrital zircon ages herein (Figs. 2, 4 and 5), the basal magnetozone EF1r in the lEF (Fig. 2) can now be more firmly tied to the LC5r magnetozone in the Los Colorados Formation. Maximum depositional ages from the lowermost lEF, specifically samples PHU, HB-15, SUB (<219.6, <218.2, and <216.4, respectively; Figs. 2, 4 and 5), increase the credibility of tying the lEF (EF1r) to the Los Colorados Formation (LC5r). By extension, these new maximum depositional ages further support correlation to the radiometrically dated upper Blue Mesa and lower Sonsela members in the Chinle Formation in the USA (Ramezani et al., 2011, 2014; Kent et al., 2018), although recycling of older detrital zircons in these members has been reported by Gehrels et al. (2019) and Kent et al. (2019). The correlation does still serve to reduce the uncertainty of the most likely basal age of the lEF to within  $\sim 3$ million years, and places it into the early middle Norian (i.e., within the Adamanian holochron, which has an estimated age range between ~224-215 Ma in the USA; Martz and Parker, 2017). Correlation of the Newark-Hartford APTS E11r-E12r, lower Chinle PF7r-PF6r and associated relative ages (~221.47 and 219.29 Ma, respectively; Kent et al., 2017, 2019) with the magnetozone LC5 of the Los Colorados Formation (Kent et al., 2014) and therefore EF1r of the lEF complements the above statements.

Biostratigraphically, magnetozones EF2 and EF3 of the middle lEF (Fig. 2) can be correlated to the upper third of the Los Colorados Formation (~La Esquina assemblage), with magnetozone EF2n tied to LC8n (Sciscio et al., 2017a). This, in turn, links EF2 to Newark APTS E15/E16 at ~213-212 Ma (Kent et al., 2017, 2018). Furthermore, correlation of the upper Chinle Formation chronostratigraphy (Ramezani et al., 2011, 2014; Gehrels et al., 2019; Kent et al., 2018, 2019) to the middle lEF and the upper Los Colorados Formation suggest that the EF2 may be correlated with upper Sonsela and lower Petrified Forest members. This is corroborated by the middle lEF maximum depositional ages, which range from <215.4 to <211.5 Ma (samples MAP, GV-14 and QSS1 Figs. 2, 4 and 5). In contextualising the EF2 magnetozone, EF3 is likely younger than ~210 Ma, and the lEF maximum depositional ages suggest an age range between <209.6 and < 207 Ma (samples HAF, LGT, LK-17) for EF3. Thus, a more meaningful approximation can be made between the magnetostratigraphic and depositional ages of the Petrified Forest/Painted Desert and Owl Rock members (particularly PF2r, PF1r: 210.08±0.22 Ma -<207.8 Ma; Ramezani et al., 2011, 2014; Kent et al., 2018, 2019) relative to the lEF EF2 and EF3 magnetozones. While the maximum depositional ages across this lEF interval improve and support previous assertions of Sciscio et al. (2017a), they do not firmly constrain this interval beyond <210-~205 Ma, which approximates the age of the Revueltian holochron estimated by Martz and Parker (2017).

Elliot Formation magnetochrons EF4 –EF9n (Fig. 2) are more difficult to correlate globally based on: (i) poorly constrained taxon range zone(s), (ii) lack of shared and/or diagnostic taxa with global distributions, and (iii) limited radioisotopic ages (see Section 5.2). The interval of the lEF represented by the EF5–EF6.2n magnetozones yielded one datable sample (BH-15) with a maximum depositional age of <204.9 Ma (Figs. 2, 4 and 5). Based on this age and the magnetostratigraphic correlation of Sciscio et al. (2017a), it is possible that lEF EF4–EF6.1r magnetozones straddle the Norian-Rhaetian boundary at ~205.7 Ma (Wotzlaw et al., 2014; Maron et al., 2015), and the Newark magnetozones E20r.2r, E21n and E21r.1r (and their relative ages at ~206.03 Ma, 204.65 Ma, ~204.12 Ma, respectively; Kent et al., 2017). It should be noted that the lEF sample BH-15 is from a single locality in the northern part of the basin, and the Newark ages are inferred from astrochronology cyclostratigraphy.

In refining the placement of the TJB in the Elliot Formation, the

current maximum depositional ages for the uEF do not improve upon previous evidence from bio- and magnetostratigraphy. Sciscio et al. (2017a) considered it plausible that the TJB may lie within the lower uEF, either within the normal polarity chron EF6.2n or higher in the Elliot magnetostratigraphic composite sequence (i.e., within EF7n; Fig. 2). The Upper Triassic-Lower Jurassic Moenave Formation was previously correlated with the Elliot EF4-EF8 magnetozones based on bio- and magnetostratigraphy, and suggests an Early Jurassic age for the EF7 magnetozone (EF7 = M3 magnetozone; Donohoo-Hurley et al., 2010; Whiteside et al., 2011; Kirkland et al., 2014; Martz and Parker, 2017). Magnetozones EF5–EF6 have not been sampled for detrital zircon-bearing samples in this study, and therefore the radioscopic age of this interval remains uncertain. However, because of the occurrence of Protosuchus in the lower-middle uEF (Dollman et al., 2019) shared with the lower Dinosaur Canyon Member (Moenave Formation, USA; Suarez et al., 2017) and the Rhaetian McCoy Brook Formation (Nova Scotia, Canada) could suggest that magnetozones EF5-EF6 may be latest Triassic in age, could straddle the ETE, and be a reflection of the Apachean holochron (Martz and Parker, 2017). Thus, the first lower Jurassic rocks of the Elliot Formation may be, potentially, within the EF7 magnetozone, and therefore above the lEF/uEF boundary. However, this correlation is only weakly supported by a single uEF sample (MAF) with a maximum depositional age of <201 Ma (Figs. 2, 4 and 5). The pattern and number of the polarity pairs in the uppermost uEF (EF7, EF8 and EF9n; Fig. 2) are not distinctive enough for firm magnetostratigraphic correlations to other basins. Based on biostratigraphic argument alone, Sciscio et al. (2017a) tied these magnetochrons to the Hartford H24r-H27 and the St Audrie's Bay/East Quantoxhead composite AQ1r-AQ3r providing a Hettangian-Sinemurian age for the upper half of the uEF. The new maximum depositional ages in this study do not assist in validating this correlation, because of the limited number of productive detrital zircon-bearing samples in the uEF (e.g., Q6: <191.9 Ma; LEP: <197.3 Ma, LMO: <199.9 Ma, MAF: <201 Ma; Figs. 2, 4 and 5).

## 5.4. New radioisotopic dates and implications for biostratigraphy

#### 5.4.1. Biostratigraphic discussion

The striking differences in tetrapod diversity between the uEF and IEF have long been noted but have been relatively understudied. The geospatial studies undertaken here show that species-area effects (Close et al., 2017) are a poor explanatory model for this difference in diversity, as the geographic spread of lEF and uEF localities is nearly identical (Fig. 7). Sampling intensity may provide a partial explanation, because the uEF has many more collections records than the lEF. Our database currently contains 128 generically-determined records of lEF vertebrate body fossils, of which 42 have precise stratigraphic occurrence data, compared to 618 from the uEF (131 with precise stratigraphic data). In the case of sauropodomorphs, a number of well-provenanced records in the IEF are confounded by taxonomic uncertainty, and continued revision of lEF taxa will undoubtedly improve our knowledge of the stratigraphic distributions of those dinosaurs. However, a sufficient sample exists in the lEF to infer that theropod and ornithischian dinosaurs, as well as crocodylomorphs, later-branching cynodonts, and turtles were either rare components of Norian-Rhaetian ecosystems in the MKB or absent. This contrasts with the presence and abundance of these groups in the uEF, and is suggestive of a marked faunal change during the Triassic-Jurassic transition.

Our chronostratigraphic data show that the thicker IEF represents a longer period of time than the thinner uEF (Fig. 1, 2 and 4; see Section 5.1), meaning that it had longer periods of non-deposition or more frequent/longer periods of erosion. This likely has the effect of compressing the vertical range of IEF taxa, confounding our efforts to establish meaningful biozonation. However, recent biostratigraphic investigations (Viglietti et al., 2020a) suggest that IEF taxa, particularly *Scalenodontoides*, have a fairly wide stratigraphic distribution at least in

the lower parts of the lEF, especially in the southern part of the basin (Fig. 7). This may reflect heterogeneity in depositional rates or in basinal subsidence patterns, or possibly an abnormally long duration of that genus. Targeted future collection efforts are necessary to test these hypotheses. In addition, the strong thickness variation of the lEF (see Section 5.1; Bordy et al., 2004a, 2004b, 2004d; Bordy and Eriksson, 2015) may indicate that significant parts of the section are missing in different portions of the basin, providing fewer options to sample the entire lEF record for its tetrapod diversity.

## 5.4.2. Taxon sampling in the Norian-Rhaetian lEF

Our new age assessment of the Elliot and Clarens formations provides more robust temporal correlations with increasingly well-dated vertebrate faunas in the Western Hemisphere (e.g., Langer et al., 2018). In particular, we can more confidently state that the lEF overlaps in time with the well-studied faunas of the Chinle and Los Colorados formations, potentially including those from famous localities like the *Placerias* and Hayden Quarries and the La Esquina fauna.

Given that we can now confirm a Late Triassic (Norian–Rhaetian) age for the lEF, it is surprising that this unit has not yielded body fossils of the many diverse terrestrial tetrapod taxa present in other Late Triassic faunas worldwide. Representatives of small-bodied lineages that are known from Late Triassic deposits globally are absent, including mammaliaforms, rhynchocephalians, drepanosauromorphs, recumbirostrans, and pterosaurs. These absences are most likely explained by taphonomic or collector biases, which are currently uncharacterised and unexplained. However, it is unlikely that small-bodied yrough groups that are widespread in other Late Triassic assemblages are more likely to reflect genuine absence, or rarity, including those of phytosaurs and several pseudosuchian lineages (such as poposauroids; see review in Knoll, 2004).

In the case of the aquatic phytosaurs, it had been suggested that their absence from southern Africa might be due to a clade-specific paleotropical preference, as all known localities were situated between ~30°N and ~30°S (Olsen and Galton, 1984; Shubin and Sues, 1991). However, discoveries of phytosaur material in the Baltic region of Europe (approximately 45° N during the Late Triassic: Brusatte et al., 2013) and in the Tashinga Formation of the Mid-Zambezi Basin, Zimbabwe (paleolatitude of approximately 40°S: Barrett et al., 2020) demonstrate conclusively that they were not constrained to the paleotropics. Although phytosaurs would have been confined to regions with perennial lakes or rivers, placing limits on their geographic range (Buffetaut, 1993), IEF paleoenvironments were seasonally wet and supported large, permanent rivers (e.g., Smith et al., 1993; Bordy et al., 2004b, 2004d), so their absence from the MKB remains unexplained. Interestingly, phytosaurs are also absent from the La Esquina fauna of the Los Colorados Formation.

A general explanation for the scarcity of pseudosuchians in the Elliot Formation might relate to latitudinal temperature gradients. This group, which includes extant crocodylians, has well-defined pattern of high abundance and diversity at low latitudes, and low abundance or absence at high latitudes, and has done since its origin in the Triassic (Markwick, 1998; Mannion et al., 2015). The MKB represents a relatively high paleolatitude assemblage at approximately 50° south, and this potentially explains both the relatively low abundance of pseudosuchians in the lEF, and the under-representation of pseudosuchian clades (other than crocodylomorphs). Nevertheless, this does not provide a good explanation of the abundance of crocodylomorphs in the uEF.

Until recently, dicynodont synapsids were considered to be absent from the lEF fauna (although possible trackways had been reported: Ellenberger, 1955, 1970, 1972; Ellenberger and Ellenberger, 1958; Bordy et al., 2017b), but their presence has now been demonstrated with the description of *Pentasaurus*, which also records the first known association of large-bodied dicynodonts with sauropodomorph dinosaurs from anywhere in the world (Kammerer, 2018). This occurrence provides additional evidence that placeriine dicynodonts had a Pangean distribution (Kammerer, 2018), contrary to earlier paleobiogeographic hypotheses (Kammerer et al., 2013).

## 5.4.3. Implications for the early evolution of Dinosauria

Revisions to the stratigraphy and age of key upper Stormberg Group vertebrate localities have major implications for our understanding of early dinosaur evolution, and particularly for understanding the diversification of Ornithischia. The early ornithischian dinosaur Eocursor was originally reported as from the lEF and thus inferred to be of Late Triassic (Norian) age (Butler et al., 2007). Late Triassic ornithischian material has been considered to be very rare (Irmis et al., 2007) and this taxon was therefore important in calibrating divergence times within ornithischian phylogeny and in elucidating the nature of the early ornithischian bauplan. However, more recent work at the Eocursor type locality demonstrated that this material pertains to the uEF and is more likely earliest Jurassic in age (Olsen et al., 2010; McPhee et al., 2017). This revision, alongside stratigraphic and taxonomic revisions of other purported Late Triassic ornithischians, has now removed all known evidence for Late Triassic ornithischians from the global record (e.g. Irmis et al., 2007; Olsen et al., 2010; Irmis, 2011; Agnolín and Rozadilla, 2018; Baron et al., 2017b; Baron, 2019). This leaves an extensive ghost lineage between the earliest confirmed ornithischians from the earliest Jurassic and their Late Triassic sister-group (either Theropoda or Saurischia; compare phylogenies of Baron et al., 2017b, 2017c; Langer et al., 2017), which suggests that their early history took place in a currently unsampled area. Alternatively, this 'ornithischian gap' might represent a genuine absence that could indicate a relatively late derivation of ornithischians from within Theropoda (Padian, 2013; Baron, 2019), although this idea has not gained wide acceptance. Nevertheless, the uEF currently provides the best available window on early ornithischian evolution, possessing not only a diversity of taxa from across the tree (Abrictosaurus, Eocursor, Heterodontosaurus, Lesothosaurus, Lycorhinus), but an abundance of material for functional and paleoecological, as well as phylogenetic, analysis (e.g., Butler, 2005, 2010; Butler et al., 2007, 2008; Knoll, 2008; Knoll et al., 2010; Maidment and Barrett, 2011; Porro et al., 2010, 2015; Norman et al., 2011; Sereno, 2012; Galton, 2014; Barrett et al., 2016; Baron et al., 2017b, 2017c; Sciscio et al., 2017c). The presence of a diverse ornithischian fauna in the uEF coincides with their widespread appearance in the global fossil record at this time (e.g., Irmis, 2011; Barrett et al., 2014; Raven et al., 2019; earliest Jurassic of China, Venezuela, the UK, and USA) and clear evidence of phenotypic divergence in body size, stance, and dental morphology (Benson et al., 2014; Benson, 2018). Taken together, these observations demonstrate that ornithischians radiated rapidly in the wake of the ETME.

Our results also enhance the understanding of the early evolution of sauropodomorph dinosaurs. Abundant fossil discoveries from the Elliot Formation have been central to the development of knowledge on early sauropodomorph evolution, and complement the rich record found elsewhere, particularly that from South America. Sauropodomorphs are by far the dominant vertebrate taxa in our collection records for the Norian-Rhaetian lEF (Fig. 8), echoing their relative abundances in the penecontemporaneous and latitudinally nearly equivalent Los Colorados Formation of South America (Martínez et al., 2015). During this time, sauropodomorphs underwent key morphological transitions, including the evolution of giant body size (Apaldetti et al., 2018) and the first instances of quadrupedalism (McPhee et al., 2018) and much of our understanding of these transitions results from the systematic study of the uEF body fossil record (e.g., Huxley, 1867; Haughton, 1924; Galton and Van Heerden, 1985; Yates and Kitching, 2003; Bonnan and Yates, 2007; Yates, 2007b; Yates and Barrett, 2010; McPhee et al., 2015a, 2015b, 2017, 2018). Body fossil specimens of sauropodomorphs from the lEF are generally less complete, and have yielded fewer direct insights into sauropodomorph evolution. For example, although limb

proportions within the problematic Plateosauravus syntype (Haughton, 1924; Yates, 2003; McPhee et al., 2017) are suggestive of a quadrupedal locomotor habit for that taxon, unequivocally quadrupedal sauropodomorphs have yet to be identified from the lEF-despite their presence in the Norian deposits of South America (Riojasaurus, Bonaparte, 1969; Lessemsaurus and Ingentia, Apaldetti et al., 2018). Nonetheless, quadrupedal trackways (i.e., Paratetrasauropus seakensis, Sauropodopus antiquus, ?Lavinipes jaquesi, Tetrasauropos unguiferus, Ellenberger, 1970, 1972; D'Orazi Porchetti and Nicosia, 2007) are common in the lEF (Fig. 2). Some of these trackways are attributed to quadrupedal sauropodomorphs, and are present within the first 15 m of the lEF (e.g., at our PHU sample site), and continue throughout that section (for example, at our MAP and HAF sample sites with MDAs 215.4 and 209.6 Ma, respectively; Figs. 4 and 5). Moreover, some quadrupedal trackways (e.g., ?Lavinipes jaquesi - D'Orazi Porchetti and Nicosia, 2007 occur alongside the bipedal sauropodomorph trackway Pseudotetrasauropous bipedoida, Ellenberger, 1970, 1972; D'Orazi Porchetti and Nicosia, 2007) at our PHU sample site (Fig. 5), which has a MDA of 219.6 Ma. Therefore, we confidently infer the presence of quadrupedal sauropodomorphs in southern Africa by between  $\sim 220$ and ~216 Ma. The first known multi-tonne Elliot sauropodomorphs only appear in the lower part of the uEF (Ledumahadi; McPhee et al., 2018), postdating their first appearance in South America (Apaldetti et al., 2018). However, undescribed specimens of lEF sauropodomorphs in the South African collections record are of enormous size. Future research will likely show that both gigantic body size and quadrupedalism appeared at similar times in sauropodomorphs of the Norian of South America and southern Africa.

Mass accumulations of vertebrate fossil material have great potential to improve our knowledge of IEF faunas, especially those in the middle Norian. To-date, two major bone beds have been documented from the lower IEF, both occurring within 50 m of the lower contact of the unit. The first one, containing abundant sauropodomorph remains, was discovered in the 1950s at Maphutseng (Lesotho) (e.g., Ellenberger, 1955; Ellenberger and Ginsburg, 1966), and is located <20 m below our sample MAP (with an MDA of 215.4 Ma; Figs. 4 and 5). The second, found < 20 km south of the Maphutseng site, is a recent discovery made by the local community near Qhemegha, a village in Eastern Cape Province, South Africa and is a multi-taxic assemblage including dinosaurs, dicynodonts, cynodonts, and possibly other taxa (JNC, PMB, RBJB, PAV, LS, EMB, unpublished results). Moreover, with one exception, all other significant IEF sauropodomorph taxa that were provenanced by McPhee et al. (2017; see their fig. 5) occur within the first ~50 m of the lEF. Considering the MDAs of strata from adjacent beds in the lEF, the two major lEF bone beds and other sauropodomorphbearing strata in the lowermost lEF appear to have formed in the middle Norian (i.e., between ~216 and ~220 Ma), in the first 6-7 Ma after the end of the Carnian (Fig. 2).

## 6. Concluding remarks

The increasing sophistication (i.e., accuracy, precision) and affordability of modern dating techniques, combined with more systematic and higher density sampling efforts, will profoundly improve our understanding of the geological history of the upper Stormberg Group, a key Mesozoic terrestrial succession in the upper Karoo Supergroup of South Africa. In turn, this will increase its utility for decoding not only southern Pangean paleogeographic and ecological changes during the final stages of MKB development, but will also enhance its impact on studies of the ETME and ensuing global biodiversity changes.

Our study, which contains the first-ever and long-overdue radioisotopic assessment of the upper Stormberg Group, provides a solid initial framework for these future efforts. However, some important questions remain unanswered at this time, such as the length of the depositional hiatus between the lEF and the uEF and the stratigraphic position of the TJB and ETME. This is largely due to our relatively low number of analysed samples and applied radioisotopic methods, which were dictated by the rock types suitable for age dating and resources available to us as a group of multidisciplinary researchers, mostly based in the Global South. Nonetheless, our basin-wide study of the upper Stormberg Group gives a clear exposition of the status quo, whilst it also substantially advances knowledge on the age, litho-, magneto- and biostratigraphy of this important unit. Future efforts must, therefore, focus on obtaining high-precision dates for stratigraphic sections that traverse the lEF–uEF boundary, using an intensive, densely spaced sampling regime and high-precision geochronological methods like CA-ID-TIMS. Ideally, these focus areas should be in places with abundant vertebrate fossils.

By expanding our chronostratigraphic research to potentially correlatable continental successions in southern Africa (e.g., the Mid-Zambezi Basin), we will gain a better understanding of geographic controls on Triassic–Jurassic biodiversity in southern Africa. Indeed, work in that area is already underway (Viglietti et al., 2018b; Barrett et al., 2020), but more comprehensive surveys, with integrated sedimentology, biostratigraphy, magnetostratigraphy, and absolute dating methods, are needed of all upper Karoo units across southern Africa.

Finally, by integrating stable isotope geochemistry in this research (e.g., C-isotope excursions), we can potentially link major climatic changes with faunal differences on an absolute timescale – and in doing so help set a world standard for understanding landscape changes and basin development in southwestern Gondwana during the Late Triassic and Early Jurassic.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.earscirev.2020.103120.

## Declaration of competing interest

None.

## Acknowledgements

We would like to extend our sincere gratitude to Akhil Rampersadh, Maposholi Mokhethi, Howard Head, Robert Muir, Mhairi Reid, and T'Nielle Haupt who assisted us during geological fieldwork. Staff at the U-(Th)-Pb Geochronology Division in the Central Analytical Facilities of Stellenbosch University are acknowledged for guidance with detrital zircon data processing and reduction. We thank Barry Shaulis for assistance with laser ablation at the University of Arkansas TRAIL facility. Assistance with the GIS components of the research was provided by Michelle Clack and Simon Wills. Members of various field parties assisting with paleontological field work in South Africa, especially Kathleen Dollman, Casey Staunton, Katherine Clayton, Simon Wills, Cory Dinter, Cebisa Mdekazi, Gilbert Mokgethoa, James Neenan, Rick Tolchard, Wilfred Bilankulu and Matt Baron, are also acknowledged. Bernhard Zipfel, Sifelani Jirah, Zaituna Skosan, Claire Browning, Elize Butler, Jennifer Botha-Brink, Rose Prevec, William J. de Klerk, Heidi Fourie provided access to specimens and specimen records in their care in South Africa. We also thank staff at the London Natural History Museum, and Muséum National d'Histoire Naturelle Paris, and Naturhistorisches Museum Wien Vienna for assistance with the respective specimen records.

# Funding

We gratefully acknowledge the following funding sources: National Research Foundation (NRF) of South Africa [Competitive Programme for Rated Researches (CPRR); African Origins Programme (AOP); research funding 93544, 113394, 98825 to EMB; 98906, 98800 and 118794 to JNC; postgraduate funding to MA, LS, ZR]; Department of Science and Technology (DST) and NRF of South Africa [Centre of Excellence in Palaeosciences (COE PAL); operational support funding in 2015, 2019 to EB; 2015–2018 to JNC; postgraduate and postdoctoral funding to MA, LS, PAV, BWM, KEJC (2015–2019)]; National Research Foundation (NRF) of South Africa [Incentive funding; grants to EB and JNC from 2015–2018]; Palaeontological Scientific Trust (PAST) of South Africa [research funding to JNC from 2013–2015, 2017; postgraduate funding to ZR (2016–2018), BWM (2015), KEJC (2016-2019)]; National Science Foundation (NSF) of the USA [Division of Earth Sciences (EAR) Sedimentary Geology and Paleobiology (SGP); research fund 1761576 to CAS and GRS]; Claude Leon Foundation of South Africa [postdoctoral fellowship funding to LS (2019)]; Royal Society of London of UK [research funding to PMB]; Natural History Museum, London of UK [Earth Sciences Departmental Investment Fund; research funding to PMB]; National Geographic Society of the USA [research fund CP-033R-2017 to JMC (PI), EMB and JNC].

The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. Opinions expressed and conclusions arrived at are those of the authors and are not necessarily to be attributed to the CoE in Palaeosciences, NRF, PAST or any other sponsor listed above. The authors have declared that no competing interests exist.

#### Data availability

South African Heritage regulations stipulate that the biostratigraphic database must reside with a collections manager or curator. The database used in this contribution is available for all bonafide requests by emailing either bernhard.zipfel@wits.ac.za or sifelani.jirah@wits.ac.za, or the current University Curator of Collections at the University of the Witwatersrand.

All other datasets mentioned as Supplementary Materials in the text of this article can be found at doi:10.6084/m9.figshare.9730100, an open-source online data repository hosted at Figshare (Bordy et al., 2019).

[dataset] Bordy et al., Dating of the upper Stormberg Group: Datasets and Supplementary Materials, 2019, Figshare, v1, https://dx. doi.org/10.6084/m9.figshare.9730100

#### References

- Abdala, F., Gaetano, L.C., 2018. The Late Triassic record of cynodonts: time of innovations in the mammalian lineage. In: The Late Triassic World. Springer, Cham, pp. 407–445.
- Abdala, F., Damiani, R., Yates, A., Neveling, J., 2007. A non-mammaliaform cynodont from the Upper Triassic of South Africa: a therapsid Lazarus taxon. Palaeontol. Afr. 42, 17–23.
- Abrahams, M., Bordy, E.M., Sciscio, L., Knoll, F., 2017. Scampering, trotting, walking tridactyl bipedal dinosaurs in southern Africa: ichnological account of a Lower Jurassic palaeosurface (upper Elliot Formation, Roma Valley) in Lesotho. Hist. Biol. 29 (7), 958–975.
- Agnolín, F.L., Rozadilla, S., 2018. Phylogenetic reassessment of *Pisanosaurus mertii* Casamiquela, 1967, a basal dinosauriform from the Late Triassic of Argentina. J. Syst. Palaeontol. 16 (10), 853–879.
- Andersen, T., Elburg, M., Cawthorn-Blazeby, A., 2016. U–Pb and Lu–Hf zircon data in young sediments reflect sedimentary recycling in eastern South Africa. J. Geol. Soc. 173 (2), 337–351. https://doi.org/10.1144/jgs2015-006.
- Andersen, T., Elburg, M.A., Magwaza, B.N., 2019. Sources of bias in detrital zircon geochronology: discordance, concealed lead loss and common lead correction. Earth Sci. Rev. 197, 102899.
- Anderson, H.M., Anderson, J.M., 1970. A preliminary review of the biostratigraphy of the uppermost Permian, Triassic and lowermost Jurassic of Gondwanaland. Palaeontol. Afr. 13, 1–22.
- Anderson, J.M., Anderson, H.M., Cruickshank, A.R., 1998. Late Triassic ecosystems of the Molteno/Lower Elliot biome of southern Africa. Palaeontology 41 (3), 387–421.
- Apaldetti, C., Martínez, R.N., Cerda, I.A., Pol, D., Alcober, O., 2018. An early trend towards gigantism in Triassic sauropodomorph dinosaurs. Nat. Ecol. Evol. 2, 1227–1232.
- Attridge, J., 1963. The Upper Triassic Karroo deposits and fauna of southern Rhodesia. S. Afr. J. Sci. 59 (5), 242–247.
- Baron, M.G., 2019. Pisanosaurus mertii and the Triassic ornithischian crisis: could phylogeny offer a solution? Hist. Biol. 31, 967–981. https://doi.org/10.1080/08912963. 2017.1410705.

Baron, M.G., Norman, D.B., Barrett, P.M., 2017a. Postcranial anatomy of Lesothosaurus

*diagnosticus* (Dinosauria: Ornithischia) from the Lower Jurassic of southern Africa: implications for basal ornithischian taxonomy and systematics. Zool. J. Linnean Soc. 179 (1), 125–168. https://doi.org/10.1111/zoj.12434.

- Baron, M.G., Norman, D.B., Barrett, P.M., 2017b. A new hypothesis of dinosaur relationships and early dinosaur evolution. Nature 543 (7646), 501. https://doi.org/ 10.1038/nature21700.
- Baron, M.G., Norman, D.B., Barrett, P.M., 2017c. Untangling the dinosaur family tree reply. Nature 551 (7678), E4–E5. https://doi.org/10.1038/nature24012.
- Barrett, P.M., Butler, R.J., Mundil, R., Scheyer, T.M., Irmis, R.B., Sánchez-Villagra, M.R., 2014. A palaeoequatorial ornithischian and new constraints on early dinosaur diversification. Proc. R. Soc. B Biol. Sci. 281 (1791), 20141147. https://doi.org/10. 1098/rspb.2014.1147.
- Barrett, P.M., Butler, R.J., Yates, A.M., Baron, M.G., Choiniere, J.N., 2016. New specimens of the basal ornithischian dinosaur *Lesothosaurus diagnosticus* Galton, 1978 from the Early Jurassic of South Africa. Palaeontol. Afr. 50, 48–63.
- Barrett, P.M., Chapelle, K.E., Staunton, C.K., Botha, J., Choiniere, J.N., 2019. Postcranial osteology of the neotype specimen of *Massospondylus carinatus* Owen, 1854 (Dinosauria: Sauropodomorpha) from the upper Elliot formation of South Africa. Palaeontol. Afr. 53, 114–178.
- Barrett, P.M., Sciscio, L., Viglietti, P.A., Broderick, T.J., Suarez, C.A., Sharman, G.A., Jones, A.S., Munyikwa, D., Edwards, S.F., Chapelle, K.E.J., Dollman, K.N., Zondo, M., Choiniere, J.N., 2020. The age of the Tashinga Formation (Karoo Supergroup) in the Mid-Zambezi Basin, Zimbabwe and the first phytosaur from sub-Saharan Africa. Gondwana Res. 81, 445–460.
- Benson, R.B.J., 2018. Dinosaur macroevolution and macroecology. Annu. Rev. Ecol. Evol. Syst. 49, 379–408.
- Benson, R.B.J., Campione, N.E., Carrano, M.T., Mannion, P.D., Sullivan, C., Upchurch, P., Evans, D.C., 2014. Rates of dinosaur body mass evolution indicate 170 million years of sustained ecological innovation on the avian stem lineage. PLoS Biol. 12 (5) e1001853.
- Beukes, N.J., 1970. Stratigraphy and sedimentology of the Cave Sandstone stage, Karoo System. In: Haughton, S.H. (Ed.), Proceedings 2nd IUGS Symposium on Gondwana Stratigraphy and Palaeontology. CSIR, Pretoria, pp. 321–341.
- Blewett, S.C., Phillips, D., 2016. An overview of Cape Fold Belt Geochronology: implications for sediment provenance and the timing of Orogenesis. In: Origin and Evolution of the Cape Mountains and Karoo Basin. Springer, Verlag, pp. 45–55. https://doi.org/10.1007/978-3-319-40859-0\_5.
- Blewett, S.C., Phillips, D., Matchan, E.L., 2019. Provenance of Cape Supergroup sediments and timing of Cape Fold Belt orogenesis: constraints from high-precision 40Ar/39Ar dating of muscovite. Gondwana Res. 70, 201–221. https://doi.org/10.1016/j.gr. 2019.01.009.
- Bonaparte, J.F., 1969. Dos nuevas "faunas" de reptiles Triásicos de Argentina. Ameghiniana 10 (1), 89–102.
- Bond, G., 1973. The palaeontology of Rhodesia. Rhod. Geol. Surv. Bull. 70, 1-121.
- Bonnan, M.F., Yates, A.M., 2007. A new description of the forelimb of the basal sauropodomorph *Melanorosaurus*: implications for the evolution of pronation, manus shape and quadrupedalism in sauropod dinosaurs. Spec. Pap. Palaeontol. 77, 157–168
- Bordy, et al., 2019. Dating of the upper Stormberg Group: Datasets and Supplementary Materials, Figshare v1. https://doi.org/10.6084/m9.figshare.9730100.
- Bordy, E.M., Eriksson, P., 2015. Lithostratigraphy of the Elliot Formation (Karoo Supergroup), South Africa. S. Afr. J. Geol. 118 (3), 311–316. https://doi.org/10. 2113/gssajg.118.3.311.
- Bordy, E.M., Head, H.V., 2018. Lithostratigraphy of the Clarens Formation (Stormberg Group, Karoo Supergroup), South Africa. S. Afr. J. Geol. 121 (1), 119–130.
- Bordy, E.M., Hancox, P.J., Rubidge, B.S., 2004a. Basin development during the deposition of the Elliot Formation (Late Triassic – Early Jurassic), Karoo Supergroup, South Africa. S. Afr. J. Geol. 107, 395–410.
- Bordy, E.M., Hancox, P.J., Rubidge, B.S., 2004b. Fluvial style variations in the Late Triassic – Early Jurassic Elliot Formation, main Karoo Basin, South Africa. J. Afr. Earth Sci. 38, 383–400.
- Bordy, E.M., Hancox, P.J., Rubidge, B.S., 2004c. Provenance Study of the Late Triassic Early Jurassic Elliot Formation, main Karoo Basin, South Africa. S. Afr. J. Geol. 107, 587–602.
- Bordy, E.M., Hancox, P.J., Rubidge, B.S., 2004d. A description of the sedimentology and palaeontology of the Late Triassic–Early Jurassic Elliot Formation in Lesotho. Palaeontol. Afr. 40, 43–58.
- Bordy, E.M., Hancox, P.J., Rubidge, B.S., 2005. The contact of the Molteno and Elliot formations through the main Karoo Basin, South Africa: a second-order sequence boundary. S. Afr. J. Geol. 108, 349–362.
- Bordy, E.M., Sciscio, L., Abdala, F., McPhee, B.W., Choiniere, J.N., 2017a. First Lower Jurassic vertebrate burrow from southern Africa (upper Elliot Formation, Karoo Basin, South Africa). Palaeogeogr. Palaeoclimatol. Palaeoecol. 468, 362–372.
- Bordy, E.M., Abrahams, M., Sciscio, L., 2017b. The Subeng vertebrate tracks: stratigraphy, sedimentology and a digital archive of a historic Upper Triassic palaeosurface (lower Elliot Formation), Leribe, Lesotho (southern Africa). Boll. Soc. Paleontol. Ital. 56 (2), 181–198. https://doi.org/10.4435/BSPI.2017.12.
- Bordy, E.M., Rampersadh, A., Abrahams, M., Lockley, M.G., Head, H.V., 2020. Tracking the Pliensbachian–Toarcian Karoo firewalkers: trackways of quadruped and biped dinosaurs and mammaliaforms. PLoS One 15 (1). https://doi.org/10.1371/journal. pone.0226847. e0226847.
- Bristowe, A., Raath, M.A., 2004. A juvenile coelophysoid skull from the Early Jurassic of Zimbabwe, and the synonymy of *Coelophysis* and *Syntarsus* (USA). Palaeontol. Afr. 40, 31–41.
- Brusatte, S.L., Butler, R.J., Niedźwiedzki, G., Sulej, T., Bronowicz, R., Satkūnas, J., 2013. First record of Mesozoic terrestrial vertebrates from Lithuania: phytosaurs (Diapsida:

Archosauriformes) of probable Late Triassic age, with a review of phytosaur biogeography. Geol. Mag. 150 (1), 110–122.

Buffetaut, E., 1993. Phytosaurs in time and space. Paleontol. Lombarda Nuova Ser. 2, 39–44.

- Butler, R.J., 2005. The 'fabrosaurid'ornithischian dinosaurs of the upper Elliot Formation (Lower Jurassic) of South Africa and Lesotho. Zool. J. Linnean Soc. 145 (2), 175–218.
- Butler, R.J., 2010. The anatomy of the basal ornithischian dinosaur Eocursor parvus from the lower Elliot Formation (Late Triassic) of South Africa. Zool. J. Linnean Soc. 160 (4), 648–684.
- Butler, R.J., Smith, R.M., Norman, D.B., 2007. A primitive ornithischian dinosaur from the Late Triassic of South Africa, and the early evolution and diversification of Ornithischia. Proc. R. Soc. B Biol. Sci. 274 (1621), 2041–2046. https://doi.org/10. 1098/rspb.2007.0367.
- Butler, R.J., Porro, L.B., Norman, D.B., 2008. A juvenile skull of the primitive ornithischian dinosaur *Heterodontosaurus tucki* from the 'Stormberg' of southern Africa. J. Vertebr. Paleontol. 28 (3), 702–711. https://doi.org/10.1671/0272-4634(2008) 28[702:AJSOTP]2.0.CO;2.
- Catuneanu, O., 2004. Basement control on flexural profiles and the distribution of foreland facies: the Dwyka Group of the Karoo Basin, South Africa. Geology 32 (6), 517–520.
- Catuneanu, O., Hancox, P.J., Rubidge, B.S., 1998. Reciprocal flexural behaviour and contrasting stratigraphies: a new basin development model for the Karoo retroarc foreland system, South Africa. Basin Res. 10 (4), 417–439.
- Chapelle, K.E., Choiniere, J.N., 2018. A revised cranial description of Massospondylus carinatus Owen (Dinosauria: Sauropodomorpha) based on computed tomographic scans and a review of cranial characters for basal Sauropodomorpha. PeerJ 6, e4224.
- Chapelle, K.E.J., Barrett, P.M., Botha, J., Choiniere, J.N., 2019. Ngwevu intloko: a new early sauropodomorph dinosaur from the Lower Jurassic Elliot Formation of South Africa and comments on cranial ontogeny in Massospondylus carinatus. PeerJ 7 (e7240 https://doi.org/1.7717/peerj.7240).

Choiniere, J.N., Barrett, P.M., 2015. A sauropodomorph dinosaur from the Early Jurassic of Lusitu, Zambia. Palaeontol. Afr. 49, 42–52.

- Citton, P., Díaz-Martínez, I., de Valais, S., Cónsole-Gonella, C., 2018. Triassic pentadactyl tracks from the Los Menucos Group (Río Negro province, Patagonia Argentina): possible constraints on the autopodial posture of Gondwanan trackmakers. PeerJ 6 e5358. https://doi.org/10.7717/peerj.5358.
- Clark, J.M., 1986. Phylogenetic Relationships of the Crocodylomorph Archosaurs. [Ph. D. dissertation]. University of Chicago, Chicago, Illinois.

Close, R.A., Benson, R.B.J., Upchurch, P., Butler, R.J., 2017. Controlling for the speciesarea effect supports constrained long-term Mesozoic terrestrial vertebrate diversification. Nat. Commun. 8, 15381.

Cohen, K.M., Finney, S.C., Gibbard, P.L., Fan, J.-X., 2013. International chronostratigraphic chart of the international commission on stratigraphy (v2018/08). Episodes 36, 199–204. (updated). http://www.stratigraphy.org/ICSchart/ ChronostratChart2018-08.jpg.

Colbert, E.H., 1989. The Triassic dinosaur Coelophysis. Mus. Nort. Ariz. 57, 1-160.

- Cooper, M.R., 1981. The prosauropod dinosaur Massospondylus carinatus Owen from Zimbabwe: its biology, mode of life and phylogenetic significance. Occas. Pap. Nat. Mus. Monum. Rhod. Ser. B Nat. Sci. 6 (10), 690–840.
- Corfu, F., 2013. A century of U-Pb geochronology: the long quest towards concordance. Bulletin 125 (1–2), 33–47.
- Coutts, D.S., Matthews, W.A., Hubbard, S.M., 2019. Assessment of widely used methods to derive depositional ages from detrital zircon populations. Geosci. Front. https:// doi.org/10.1016/j.gsf.2018.11.002.
- Crompton, A.W., Charig, A.J., 1962. A new ornithischian from the Upper Triassic of South Africa. Nature 196 (4859), 1074.
- Crompton, A.W., Ellenberger, F., 1957. On a new cynodont from the Molteno Beds and the origin of the tritylodontids. Ann. S. Afr. Mus. 44 (1), 1–13.
- Crompton, A.W., Jenkins, F.A., 1968. Molar occlusion in Late Triassic mammals. Biol. Rev. 43 (4), 427–458.
- D'Orazi Porchetti, S., Nicosia, U., 2007. Re-examination of some large early Mesozoic tetrapod footprints from the African collection of Paul Ellenberger. Ichnos 14, 219–245.
- de Fabrègues, C.P., Allain, R., 2016. New material and revision of *Melanorosaurus tha*banensis, a basal sauropodomorph from the Upper Triassic of Lesotho. PeerJ 4, e1639.
- De Kock, M.O., 2003. Selected Magnetostratigraphic Studies in the Main Karoo Basin (South Africa): Implications for Mass Extinction Events and the Supercontinent of Pangea. Masters dissertation. University of Johannesburg.
- De Kock, M.O., Kirschvink, J.L., 2004. Paleomagnetic constraints on the Permian-Triassic boundary in terrestrial strata of the Karoo Supergroup, South Africa: implications for causes of the end-Permian extinction event. Gondwana Res. 7 (1), 175–183.
- DeCelles, P.G., 2012. Foreland basin systems revisited: Variations in response to tectonic settings. Tectonics Sediment. Basins Recent Adv. 405–426.
- Dickinson, W.R., Gehrels, G.E., 2009. Use of U–Pb ages of detrital zircons to infer maximum depositional ages of strata: a test against a Colorado Plateau Mesozoic database. Earth Planet. Sci. Lett. 288 (1–2), 115–125.
- Dollman, K.N., Viglietti, P.A., Choiniere, J.N., 2019. A new specimen of Orthosuchus stormbergi (Nash 1968) and a review of the distribution of Southern African Lower Jurassic crocodylomorphs. Hist. Biol. 31 (5), 653–664.
- Donohoo-Hurley, L.L., Geissman, J.W., Lucas, S.G., 2010. Magnetostratigraphy of the uppermost Triassic and lowermost Jurassic Moenave Formation, western United States: correlation with strata in the United Kingdom, Morocco, Turkey, Italy, and eastern United States. Geol. Soc. Am. Bull. 122 (11–12), 2005–2019.

D'Orazi Porchetti, S., Mocke, H.B., Latiano, M., Wagensommer, A., 2015. First record of *Otozoum* from Namibia. Lethaia 48 (1), 72–82.

D'Orazi Porchetti, S., Bertini, R.J., Langer, M.C., 2017. Walking, running, hopping:

analysis of gait variability and locomotor skills in *Brasilichnium elusivum* Leonardi, with inferences on trackmaker identification. Palaeogeogr. Palaeoclimatol. Palaeoecol. 465. 14–29.

- D'Orazi Porchetti, S., Bertini, R.J., Langer, M.C., 2018. Proposal for ichnotaxonomic allocation of therapsid footprints from the Botucatu Formation (Brazil). Ichnos 25 (2–3), 192–207.
- Duane, M.J., Brown, R.W., 1992. Geochemical open-system behaviour related to fluid flow and metamorphism in the Karoo Basin. In: Inversion Tectonics of the Cape Fold Belt, Karoo and Cretaceous Basins of Southern Africa. 127. AA Balkema, Rotterdam, The Netherlands, pp. 137.
- Duncan, R.A., Hooper, P.R., Rehacek, J., Marsh, J., Duncan, A.R., 1997. The timing and duration of the Karoo igneous event, southern Gondwana. J. Geophys. Res. Solid Earth 102 (B8), 18127–18138. https://doi.org/10.1029/97JB00972.
- Ellenberger, P., 1955. Note preliminaire sur les pistes et les restes osseux de vertebres du Basutoland (Afrique-Du-Sud). C. R. Seances Acad. Sci. 240 (8), 889–891.
- Ellenberger, P., 1970. The fossil-bearing strata associated with the earliest appearance of mammals in South Africa and their ichnology: establishment of detailed stratigraphic zones in the Stormberg of Lesotho, South Africa, Upper Triassic to Jurassic. In: Proceedings and Papers of the Second Gondwanaland Symposium on Gondwana Stratigraphy and Palaeontology. Council for Scientific & Industrial Research, Pretoria, pp. 343–370.
- Ellenberger, P., 1972. Contribution to the classification of Triassic vertebrate trackways: types found in the Stormberg Series of South Africa (I). In: Palaeo-vertebrata, Memoire Extraordinaire, Montpellier, pp. 134.
- Ellenberger, P., 1974. Contribution à la classification des pistes de vertébrés du Trias: les types du Stormberg d'Afrique du Sud (IIème partie: Le Stormberg superieur). Laboratoire de paléontologie des vertébrés. In: Palaeo-vertebrata, Memoire Extraordinaire, Montpellier, pp. 142.
- Ellenberger, F., Ellenberger, P., 1958. Main types of vertebrate footprints in the Stormberg beds of Basutoland (South Africa). (Preliminary note). CR Somm. Soc. Géol. Fr. 65–67.
- Ellenberger, F., Ginsburg, L., 1966. Le gisement de dinosauriens triasiques de Maphutseng (Basutoland) et lorigine des sauropodes. C. R. Seances Acad. Sci. Ser. D 262 (4), 444–447.
- Ellenberger, F., Ellenberger, P., Fabre, J., Ginsburg, L., Mendrez, C., 1964. The Stormberg Series of Basutoland (South Africa). In: Reports of the 22nd International Geological Congress. 9. pp. 320–330.
- Eriksson, P.G., 1986. Aeolian dune and alluvial fan deposits in the Clarens Formation of the Natal Drakensberg. Trans. Geol. Soc. S. Afr. 89, 389–394.
- Evans, S.E., Kermack, K.A., 1994. Assemblages of small tetrapods from the Early Jurassic of Britain. In: Fraser, N.C., Sues, H.-D. (Eds.), In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods. Cambridge University Press, pp. 271–283.
- Ezcurra, M.D., Brusatte, S.L., 2011. Taxonomic and phylogenetic reassessment of the early neotheropod dinosaur *Camposaurus arizonensis* from the Late Triassic of North America. Palaeontology 54 (4), 763–772.
- Fraser, N.C., 1988. The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida). Philos. Trans. R. Soc. Lond. B Biol. Sci. 321 (1204), 125–178.
- Gaffney, E.S., Kitching, J.W., 1994. The most ancient African turtle. Nature 369, 55–58. Galton, P.M., 1972. Classification and evolution of ornithopod dinosaurs. Nature 239
- (5373), 464.
- Galton, P.M., 1985. The poposaurid thecodontian *Teratosaurus suevicus v*. Meyer, plus referred specimens mostly based on prosauropod dinosaurs, from the Middle Stubensandstein (Upper Triassic) of Nordwürttemberg. Stuttg. Beitr. Naturkunde Ser. B Geol. Paläontol. 116, 1–29.
- Galton, P.M., 2014. Notes on the postcranial anatomy of the heterodontosaurid dinosaur *Heterodontosaurus tucki*, a basal ornithischian from the Lower Jurassic of South Africa. Rev. Paléobiol. 33 (1), 97–141.
- Galton, P.M., Van Heerden, J., 1985. Partial hindlimb of *Blikanasaurus cromptoni* n. gen. and n. sp., representing a new family of prosauropod dinosaurs from the Upper Triassic of South Africa. Geobios 18 (4), 509–516.
- Galton, P.M., Van Heerden, J., Yates, A.M., 2005. Postcranial anatomy of referred specimens of the sauropodomorph dinosaur *Melanorosaurus* from the Upper Triassic of South Africa. In: Tidwell, V., Carpenter, K. (Eds.), Thunder-Lizards: The Sauropodomorph Dinosaurs. Indiana University Press, Bloomington, pp. 1–37.
- Gauffre, F.-X., 1993. The most recent Melanorosauridae (Saurischia, Prosauropoda), Lower Jurassic of Lesotho, with remarks on the prosauropod phylogeny. N. Jb. Geol. Paläont. 11, 648–654.
- Gehrels, G., Giesler, D., Olsen, P., Kent, D., Marsh, A., Parker, W., Rasmussen, C., Mundil, R., Irmis, R., Geissman, J., Lepre, C., 2019. LA-ICPMS U-Pb geochronology of detrital zircon grains from the Coconino, Moenkopi, and Chinle Formations in the Petrified Forest National Park (Arizona). Geochronol. Discuss. https://doi.org/10.5194/ gchron-2019-12. (in review).
- Gierliński, G., Potemska, A., 1985. Protosuchus sp. z dolnej jury północnego obrzeżenia Gór Świętokrzyskich. Prz. Geol. 33 (10), 567–570.
- Godefroit, P., Sigogneau-Russell, D., 1995. Cynodontes et Mammiferes primitifs du Trias Superieur, en region Lorraine et Luxembourgeoise. Bull. Soc. Géol. 104, 9–21.
- Gow, C.E., 1977. Fossil vertebrate studies in Rhodesia: sphenodontid remains from the Upper Trias of Rhodesia. Palaeontol. Afr. 20, 121–122.
- Gow, C.E., Hancox, P.J., 1993. First complete skull of the Late Triassic Scalenodontoides (Reptilia, Cynodontia) from southern Africa. N. M. Mus. Nat. Hist. Sci. Bull. 3, 161–168.
- Gow, C.E., Kitching, J.W., Raath, M.A., 1990. Skulls of the prosauropod dinosaur Massospondylus carinatus Owen in the collections of the Bernard Price Institute for Palaeontological Research. Palaeontol. Afr. 27, 45–58.
- Griffin, C.T., Nesbitt, S.J., 2019. Does the maximum body size of theropods increase across the Triassic-Jurassic boundary? Integrating ontogeny, phylogeny, and body

size. Anat. Rec. https://doi.org/10.1002/ar.24130.

- Hälbich, I.W., Fitch, F.J., Miller, J.A., 1983. Dating the Cape orogeny. In: Sohnge, A.P.G.,
  Hälbich, I.W. (Eds.), Geodynamics of the Cape Fold Belt. 12. pp. 149–164 Special
  Publication of the Geological Society of South Africa.
- Hansma, J., Tohver, E., Schrank, C., Jourdan, F., Adams, D., 2016. The timing of the Cape Orogeny: new 40Ar/39Ar age constraints on deformation and cooling of the Cape Fold Belt, South Africa. Gondwana Res. 32, 122–137. https://doi.org/10.1016/j.gr. 2015.02.005.
- Haughton, S.H., 1924. The fauna and stratigraphy of the Stormberg Series. Ann. S. Afr. Mus. 12 (8), 323–497.
- Herrera-Flores, J.A., Stubbs, T.L., Elsler, A., Benton, M.J., 2018. Taxonomic reassessment of *Clevosaurus latidens* Fraser, 1993 (Lepidosauria, Rhynchocephalia) and rhynchocephalian phylogeny based on parsimony and Bayesian inference. J. Paleontol. 92 (4), 734–742. https://doi.org/10.1017/jpa.2017.136.
- Herriott, T.M., Crowley, J.L., Schmitz, M.D., Wartes, M.A., Gillis, R.J., 2019. Exploring the law of detrital zircon: LA-ICP-MS and CA-TIMS geochronology of Jurassic forearc strata, Cook Inlet, Alaska, USA. Geology 47 (11), 1044–1048.
- Hopson, J.A., 1984. Late Triassic traversodont cynodonts from Nova Scotia and southern Africa. Palaeontol. Afr. 25, 181–201.
- Hsiou, A.S., De França, M.A.G., Ferigolo, J., 2015. New data on the *Clevosaurus* (Sphenodontia: Clevosauridae) from the Upper Triassic of southern Brazil. PLoS One 10 (9). https://doi.org/10.1371/journal.pone.0137523. e0137523.
- Hsiou, A.S., Nydam, R.L., Simões, T.R., Pretto, F.A., Onary, S., Martinelli, A.G., Liparini, A., Martínez, P.R.R.D.V., Soares, M.B., Schultz, C.L., Caldwell, M.W., 2019. A new clevosaurid from the triassic (carnian) of Brazil and the Rise of Sphenodontians in Gondwana. Sci. Rep. 9, 11821.
- Hunt, A.P., Lucas, S.G., Klein, H., 2018. Late Triassic nonmarine vertebrate and invertebrate trace fossils and the pattern of the Phanerozoic record of vertebrate trace fossils. In: The Late Triassic World. Springer, Cham, pp. 447–544.
- Hüsing, S.K., Beniest, A., van der Boon, A., Abels, H.A., Deenen, M.H.L., Ruhl, M., Krijgsman, W., 2014. Astronomically-calibrated magnetostratigraphy of the Lower Jurassic marine successions at St. Audrie's Bay and East Quantoxhead (Hettangian–Sinemurian; Somerset, UK). Palaeogeogr. Palaeoclimatol. Palaeoecol. 403, 43–56. https://doi.org/10.1016/j.palaeo.2014.03.022.
- Huxley, T.H., 1867. On the remains of large dinosaurian reptiles from the Stormberg Mountains, South Africa. Q. J. Geol. Soc. 23, 1–6.

Irmis, R.B., 2011. Evaluating hypotheses for the early diversification of dinosaurs. Earth Environ. Trans. R. Soc. Edinb. 101, 397–426.

- Irmis, R.B., Parker, W.G., Nesbitt, S.J., Liu, J., 2007. Early ornithischian dinosaurs: the Triassic record. Hist. Biol. 19 (1), 3–22.
- Johnstone, S.A., Schwartz, T.M., Holm-Denoma, C.S., 2019. A stratigraphic approach to inferring depositional ages from detrital geochronology data. Front. Earth Sci. 7, 57. https://doi.org/10.3389/feart.2019.00057.
- Kammerer, C.F., 2018. The first skeletal evidence of a dicynodont from the lower Elliot Formation of South Africa. Palaeontol. Afr. 52, 102–128.
- Kammerer, C.F., Fröbisch, J., Angielczyk, K.D., 2013. On the validity and phylogenetic position of *Eubrachiosaurus browni*, a kannemeyeriiform dicynodont (Anomodontia) from Triassic North America. PLoS One 8 (5). https://doi.org/10.1371/journal.pone. 0064203. e64203.
- Kent, D.V., Malnis, P.S., Colombi, C.E., Alcober, O.A., Martínez, R.N., 2014. Age constraints on the dispersal of dinosaurs in the Late Triassic from magnetochronology of the Los Colorados Formation (Argentina). Proc. Natl. Acad. Sci. 111 (22), 7958–7963. https://doi.org/10.1073/pnas.1402369111.
- Kent, D.V., Olsen, P.E., Muttoni, G., 2017. Astrochronostratigraphic polarity time scale (APTS) for the Late Triassic and Early Jurassic from continental sediments and correlation with standard marine stages. Earth Sci. Rev. 166, 153–180. https://doi.org/ 10.1016/j.earscirev.2016.12.014.
- Kent, D.V., Olsen, P.E., Rasmussen, C., Lepre, C., Mundil, R., Irmis, R.B., Gehrels, G.E., Giesler, D., Geissman, J.W., Parker, W.G., 2018. Empirical evidence for stability of the 405-kiloyear Jupiter–Venus eccentricity cycle over hundreds of millions of years. Proc. Natl. Acad. Sci. 115 (24), 6153–6158. https://doi.org/10.1073/pnas. 1800891115.
- Kent, D.V., Olsen, P.E., Lepre, C., Rasmussen, C., Mundil, R., Gehrels, G.E., Giesler, D., Irmis, R.B., Geissman, J.W., Parker, W.G., 2019. Magnetochronology of the entire Chinle Formation (Norian age) in a scientific drill core from Petrified Forest National Park (Arizona, USA) and implications for regional and global correlations in the Late Triassic. Geochem. Geophys. Geosyst. 20, 4654–4664. https://doi.org/10.1029/ 2019GC008474.
- Kirkland, J.I., Milner, A.R.C., Olsen, P.E., Hargrave, J.E., 2014. The Whitmore Point Member of the Moenave Formation in its type area in Northern Arizona and its age and correlation with the section in St. George, Utah: evidence for two major lacustrine sequences. Geol. Utah Far South Utah Geol. Assoc. Publ. 43, 321–356.
- Kitching, J.W., Raath, M.A., 1984. Fossils from the Elliot and Clarens Formations (Karoo Sequence) of the North-eastern Cape, Orange Free State and Lesotho, and a suggested biozonation based on tetrapods. Palaeontol. Afr. 25, 111–125.
- Klein, H., Lucas, S.G., 2010. Tetrapod footprints-their use in biostratigraphy and biochronology of the Triassic. Geol. Soc. Lond., Spec. Publ. 334 (1), 419–446.
  Knoll, F., 2004. Review of the tetrapod fauna of the "Lower Stormberg Group" of the main
- Knoll, F., 2004. Review of the tetrapod fauna of the "Lower Stormberg Group" of the main Karoo Basin (southern Africa): implication for the age of the Lower Elliot Formation. Bull. Soc. Géol. Fr. 175 (1), 73–83.
- Knoll, F., 2005. The tetrapod fauna of the Upper Elliot and Clarens formations in the main Karoo Basin (South Africa and Lesotho). Bull. Soc. Géol. Fr. 176 (1), 81–91.
- Knoll, F., 2008. Buccal soft anatomy in *Lesothosaurus* (Dinosauria: Ornithischia). N. Jb. Geol. Paläont. (Abh.) 248 (3), 355–364.
- Knoll, F., 2010. A primitive sauropodomorph from the upper Elliot Formation of Lesotho. Geol. Mag. 147 (6), 814–829.

- Knoll, F., Padian, K., de Ricqlès, A., 2010. Ontogenetic change and adult body size of the early ornithischian dinosaur Lesothosaurus diagnosticus: implications for basal ornithischian taxonomy. Gondwana Res. 17 (1), 171–179.
- Labandeira, C.C., Anderson, J.M., Anderson, H.M., 2018. Expansion of arthropod herbivory in Late Triassic South Africa: the Molteno Biota, Aasvoëlberg 411 site and developmental biology of a gall. In: The Late Triassic World. Springer, Cham, pp. 623–719.
- Lanci, L., Tohver, E., Wilson, A., Flint, S., 2013. Upper Permian magnetic stratigraphy of the lower Beaufort Group, Karoo Basin. Earth Planet. Sci. Lett. 375, 123–134.
- Langer, M.C., Ezcurra, M.D., Rauhut, O.W., Benton, M.J., Knoll, F., McPhee, B.W., Novas, F.E., Pol, D., Brusatte, S.L., 2017. Untangling the dinosaur family tree. Nature 551 (7678), E1.
- Langer, M.C., Ramezani, J., Da Rosa, Á.A., 2018. U-Pb age constraints on dinosaur rise from south Brazil. Gondwana Res. 57, 133–140.
- Langereis, C.G., Krijgsman, W., Muttoni, G., Menning, M., 2010. Magnetostratigraphy–concepts, definitions, and applications. Newsl. Stratigr. 43 (3), 207–233.
- Lockley, M.G., Gierlinski, G.D., 2006. Diverse vertebrate ichnofaunas containing Anomoepus and other unusual trace fossils from the Lower Jurassic of the western United States: implications for paleoecology palichnostratigraphy. The Triassic–Jurassic Terrestrial Transition. N. M. Mus. Nat. Hist. Sci. Bull. 37, 176–191.
- Lockley, M.G., Meyer, C.A., dos Santos, V.F., 1996. Megalosauripus, Megalosauropus and the concept of megalosaur footprints. In: The Continental Jurassic: Symposium Volume: Museum of Northern Arizona Bulletin. vol. 60. pp. 113–118.
- Lockley, M.G., Lucas, S.G., Gaston, R., Hunt, A.P., 2004. Ichnofaunas from the Triassic-Jurassic boundary sequences of the Gateway area, Western Colorado: implications for faunal composition and correlations with other areas. Ichnos 11, 89–102.
- Lockley, M.G., Lucas, S.G., Hunt, A.P., 2006. Eosauropus, a new name for a Late Triassic track: further observations on the Late Triassic ichnogenus *Tetrasauropus* and related forms, with notes on the limits of interpretation. The Triassic–Jurassic Terrestrial Transition. N. M. Mus. Nat, Hist. Sci. Bull. 37, 192–198.
- Lucas, S.G., 1998. Global Triassic tetrapod biostratigraphy and biochronology. Palaeogeogr. Palaeoclimatol. Palaeoecol. 143 (4), 347–384.
- Lucas, S.G., 2007. Tetrapod footprint biostratigraphy and biochronology. Ichnos 14 (1–2), 5–38.
- Lucas, S.G., 2018. The late triassic world: earth in a time of transition. In: Tanner, L.H. (Ed.), The Late Triassic World: Earth in a Time of Transition. Springer International Publishing, Cham, pp. 1–25.
- Lucas, S.G., Hancox, P.J., 2001. Tetrapod-based correlation of the nonmarine Upper Triassic of southern Africa. Albertiana 25, 5–9.
- Luo, Z.X., Wu, X.C., Fraser, N.C., Sues, H.-D., 1994. The small tetrapods of the lower Lufeng Formation, Yunnan, China. In: The Shadow of the Dinosaurs: Early Mesozoic Tetrapods. Cambridge University Press, pp. 251–270.Maidment, S.C., Barrett, P.M., 2011. The locomotor musculature of basal ornithischian
- Maidment, S.C., Barrett, P.M., 2011. The locomotor musculature of basal ornithischian dinosaurs. J. Vertebr. Paleontol. 31 (6), 1265–1291.
- Mannion, P.D., Benson, R.B.J., Carrano, M.T., Tennant, J.P., Judd, J., Butler, R.J., 2015. Climate constrains the evolutionary history and biodiversity of crocodilians. Nat. Commun. 6, 8438.
- Markwick, P.J., 1998. Crocodilian diversity in space and time: the role of climate in paleoecology and its implication for understanding K/T extinctions. Paleobiology 24, 470–497.
- Maron, M., Rigo, M., Bertinelli, A., Katz, M.E., Godfrey, L., Zaffani, M., Muttoni, G., 2015. Magnetostratigraphy, biostratigraphy, and chemostratigraphy of the Pignola-Abriola section: new constraints for the Norian-Rhaetian boundary. Bulletin 127 (7-8), 962–974.
- Marsh, A.D., Rowe, T.B., 2018. Anatomy and systematics of the sauropodomorph Sarahsaurus aurifontanalis from the Early Jurassic Kayenta Formation. PLoS One 3 (10). https://doi.org/10.1371/journal.pone.0204007. e0204007.
- Marsicano, C.A., Wilson, J.A., Smith, R.M., 2014. A temnospondyl trackway from the early mesozoic of western Gondwana and its implications for basal tetrapod locomotion. PLoS One 9 (8) e103255.
- Martínez, R.N., Apaldetti, C., 2017. A Late Norian—Rhaetian Coelophysid Neotheropod (Dinosauria, Saurischia) from the Quebrada Del Barro Formation, Northwestern Argentina. Ameghiniana 54 (5), 488–506.
- Martínez, R.N., Apaldetti, C., Correa, G., Colombi, C.E., Fernández, E., Santi Malnis, P., Praderio, A., Abelín, D., Benegas, L.G., Aguilar-Cameo, A., Alcober, O.A., 2015. A new Late Triassic vertebrate assemblage from northwestern Argentina. Ameghiniana 52, 379–390.
- Martz, J.W., Parker, W.G., 2017. Revised formulation of the Late Triassic Land Vertebrate "Faunachrons" of western North America: recommendations for codifying nascent systems of vertebrate biochronology. In: Zeigler, K.E., Parker, W. (Eds.), Terrestrial Depositional Systems: Deciphering Complexities Through Multiple Stratigraphic Methods. Elsevier, pp. 39–125. https://doi.org/10.1016/B978-0-12-803243-5. 00002-9.
- McPhee, B.W., Choiniere, J.N., 2018. The osteology of Pulanesaura eocollum: implications for the inclusivity of Sauropoda (Dinosauria). Zoological Journal of the Linnean Society 182 (4), 830–861.
- McPhee, B.W., Yates, A.M., Choiniere, J.N., Abdala, F., 2014. The complete anatomy and phylogenetic relationships of *Antetonitrus ingenipes* (Sauropodiformes, Dinosauria): implications for the origins of Sauropoda. Zool. J. Linnean Soc. 171 (1), 151–205.
- McPhee, B.W., Choiniere, J.N., Yates, A.M., Viglietti, P.A., 2015a. 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). J. Vertebr. Paleontol. 35 (5) p.e980504.
- McPhee, B.W., Bonnan, M.F., Yates, A.M., Neveling, J., Choiniere, J.N., 2015b. A new basal sauropod from the pre-Toarcian Jurassic of South Africa: evidence of niche-

partitioning at the sauropodomorph-sauropod boundary? Sci. Rep. 5, 13224.

- McPhee, B.W., Bordy, E.M., Sciscio, L., Choiniere, J.N., 2017. The sauropodomorph biostratigraphy of the Elliot Formation of southern Africa: tracking the evolution of Sauropodomorpha across the Triassic–Jurassic boundary. Acta Palaeontol. Pol. 62 (3), 441–465. https://doi.org/10.4202/app.00377.2017.
- McPhee, B.W., Benson, R.B., Botha-Brink, J., Bordy, E.M., Choiniere, J.N., 2018. A giant dinosaur from the earliest Jurassic of South Africa and the transition to quadrupedality in early sauropodomorphs. Curr. Biol. 28 (19), 3143–3151.
- Miall, A.D., 2013. Sophisticated stratigraphy. The web of geological sciences: advances, impacts and interactions. Geol. Soc. Am. Spec. Pap. 500, 169–190.
- Miall, A.D., 2015. Updating uniformitarianism: stratigraphy as just a set of 'frozen accidents' Geol. Soc. Lond., Spec. Publ. 404 (1), 11–36.
- Miall, A.D., 2016. The valuation of unconformities. Earth Sci. Rev. 163, 22-71.
- Moreau, M.G., Bucher, H., Bodergat, A.M., Guex, J., 2002. Pliensbachian magnetostratigraphy: new data from Paris Basin (France). Earth Planet. Sci. Lett. 203 (2), 755–767.
- Moulin, M., Fluteau, F., Courtillot, V., Marsh, J., Delpech, G., Quidelleur, X., Gérard, M., Jay, A.E., 2011. An attempt to constrain the age, duration, and eruptive history of the Karoo flood basalt: Naude's Nek section (South Africa). J. Geophys. Res. Solid Earth 116 (B7). https://doi.org/10.1029/2011JB008210.
- Moulin, M., Courtillot, V., Fluteau, F., Valet, J.P., 2012. The "van Zijl" Jurassic geomagnetic reversal revisited. Geochem. Geophys. Geosyst. 13 (3), Q03010. https:// doi.org/10.1029/2011GC003910.
- Moulin, M., Fluteau, F., Courtillot, V., Marsh, J., Delpech, G., Quidelleur, X., Gérard, M., 2017. Eruptive history of the Karoo lava flows and their impact on early Jurassic environmental change. J. Geophys. Res. Solid Earth 122 (2), 738–772.
- Munyikwa, D., 1997. Faunal analysis of Karoo-aged sediments in the northern Limpopo Valley, Zimbabwe. Arnoldia Zimb. 10 (13), 129–139.
- Munyikwa, D., Raath, M.A., 1999. Further material of the ceratosaurian dinosaur Syntarsus from the Elliot Formation (Early Jurassic) of South Africa. Palaeontol. Afr. 35, 55–59.
- Muravchik, M., D'Elia, L., Bilmes, A., Franzese, J.R., 2011. Syn-eruptive/inter-eruptive relations in the syn-rift deposits of the Precuyano Cycle, Sierra de Chacaico, Neuquén Basin, Argentina. Sediment. Geol. 238 (1-2), 132–144.
- Norman, D.B., Crompton, A.W., Butler, R.J., Porro, L.B., Charig, A.J., 2011. The Lower Jurassic ornithischian dinosaur *Heterodontosaurus tucki* Crompton & Charig, 1962: cranial anatomy, functional morphology, taxonomy, and relationships. Zool. J. Linnean Soc. 163 (1), 182–276.
- Olsen, P.E., Galton, P.M., 1984. A review of the reptile and amphibian assemblages from the Stormberg of southern Africa, with special emphasis on the footprints and the age of the Stormberg. Palaeontol. Afr. 25, 87–110.
- Olsen, P.E., Sues, H.D., 1986. Correlation of continental Late Triassic and Early Jurassic sediments, and patterns of the Triassic–Jurassic tetrapod transition. In: The Beginning of the Age of Dinosaurs. Cambridge University Press, Cambridge, pp. 321–351.
- Olsen, P.E., Kent, D.V., Whiteside, J.H., 2010. Implications of the Newark Supergroupbased astrochronology and geomagnetic polarity time scale (Newark-APTS) for the tempo and mode of the early diversification of the Dinosauria. Earth Environ. Sci. Trans. R. Soc. Edinb. 101 (3-4), 201–229. https://doi.org/10.1017/ \$1755691011020032.
- Opdyke, N.D., 1964. The paleomagnetism of some Triassic red beds from Northern Rhodesia. J. Geophys. Res. 69 (12), 2495–2497.
- Otero, A., Krupandan, E., Pol, D., Chinsamy, A., Choiniere, J.N., 2015. A new basal sauropodiform from South Africa and the phylogenetic relationships of basal sauropodomorphs. Zool. J. Linnean Soc. 174, 589–634.
- Owen, R., 1854. Descriptive Catalogue of the Fossil Organic Remains of Reptilia and Pisces Contained in the Museum of the Royal College of Surgeons of England. p. 184. Taylor and Francis, London.
- Padian, K., 2013. The problem of dinosaur origins: integrating three approaches to the rise of Dinosauria. Earth Environ. Sci. Trans. R. Soc. Edinb. 103 (3-4), 423–442. https://doi.org/10.1017/S1755691013000431.
- Pankhurst, R.J., Rapela, C.W., Fanning, C.M., Márquez, M., 2006. Gondwanide continental collision and the origin of Patagonia. Earth Sci. Rev. 76 (3-4), 235–257.
- Pankhurst, R.J., Rapela, C.W., De Luchi, M.L., Rapalini, A.E., Fanning, C.M., Galindo, C., 2014. The Gondwana connections of northern Patagonia. J. Geol. Soc. 171 (3), 313–328.
- Porro, L.B., Butler, R.J., Barrett, P.M., Moore-Fay, S., Abel, R.L., 2010. New heterodontosaurid specimens from the Lower Jurassic of southern Africa and the early ornithischian dinosaur radiation. Earth Environ. Sci. Trans. R. Soc. Edinb. 101 (3-4), 351–366. https://doi.org/10.1017/S175569101102010X.
- Porro, L.B., Witmer, L.M., Barrett, P.M., 2015. Digital preparation and osteology of the skull of *Lesothosaurus diagnosticus* (Ornithischia: Dinosauria). PeerJ 3 p.e1494. Raath, M.A., 1969. A new coelurosaurian dinosaur from the Forest Sandstone of
- Rhodesia. Arnoldia 4 (28), 1–25.
- Raath, M.A., 1981. A protosuchid crocodilian from the Forest Sandstone Formation (upper Karoo) of Zimbabwe. Palaeontol. Afr. 24, 69–174.
- Raath, M.A., Smith, C.C., Bond, G., 1970. A new Upper Karroo dinosaur fossil locality on the lower Angwa River, Sipolilo District, Rhodesia. Arnoldia 4 (35), 1–10.
- Raath, M.A., Kitching, J.W., Shone, R.W., Rossouw, G.J., 1990. Dinosaur tracks in Triassic Molteno sediments: the earliest evidence of dinosaurs in South Africa? Palaeontol. Afr. 27, 89–95.
- Rademan, Z., 2018. Radiometric Dating and Stratigraphic Reassessment of the Elliot and Clarens Formations; Near Maphutseng and Moyeni, Kingdom of Lesotho, Southern Africa. MSc thesis. Stellenbosch University. http://hdl.handle.net/10019.1/ 104888.
- Rainforth, E.C., 2003. Revision and re-evaluation of the Early Jurassic dinosaurian ichnogenus Otozoum. Palaeontology 46, 803–838.

- Ramezani, J., Hoke, G.D., Fastovsky, D.E., Bowring, S.A., Therrien, F., Dworkin, S.I., Atchley, S.C., Nordt, L.C., 2011. High-precision U-Pb zircon geochronology of the Late Triassic Chinle Formation, Petrified Forest National Park (Arizona, USA): temporal constraints on the early evolution of dinosaurs. Bulletin 123 (11-12), 2142–2159.
- Ramezani, J., Fastovsky, D.E., Bowring, S.A., 2014. Revised chronostratigraphy of the lower Chinle Formation strata in Arizona and New Mexico (USA): high-precision U-Pb geochronological constraints on the Late Triassic evolution of dinosaurs. Am. J. Sci. 314 (6), 981–1008.
- Rampersadh, A., Bordy, E.M., Sciscio, L., Abrahams, M., 2018. Dinosaur behaviour in an Early Jurassic palaeoecosystem–uppermost Elliot Formation, Ha Nohana, Lesotho. Ann. Soc. Geol. Pol. 88 (2), 163–179.
- Raup, D.M., Sepkoski, J.J., 1982. Mass extinctions in the marine fossil record. Science 215 (4539), 1501–1503.
- Raven, T.J., Barrett, P.M., Xu, X., Maidment, S.C.R., 2019. A reassessment of the purported ankylosaurian dinosaur *Bienosaurus lufengensis* from the Lower Lufeng Formation of Yunnan, People's Republic of China. Acta Palaeontol. Pol. 64, 335–342. https://doi.org/10.4202/app.00577.2018.
- Ray, S., Chinsamy, A., 2002. A theropod tooth from the Late Triassic of southern Africa. J. Biosci. 27 (3), 295–298.
- Rayfield, E.J., Barrett, P.M., Milner, A.R., 2009. Utility and validity of Middle and Late Triassic 'land vertebrate faunachrons' J. Vertebr. Paleontol. 29 (1), 80–87.
- Rogers, R.R., Rogers, K.C., Munyikwa, D., Terry, R.C., Singer, B.S., 2004. Sedimentology and taphonomy of the upper Karoo-equivalent Mpandi Formation in the Tuli Basin of Zimbabwe, with a new 40Ar/39Ar age for the Tuli basalts. J. Afr. Earth Sci. 40 (3-4), 147–161.
- Rossignol, C., Hallot, E., Bourquin, S., Poujol, M., Jolivet, M., Pellenard, P., Ducassou, C., Nalpas, T., Heilbronn, G., Yu, J., Dabard, M.P., 2019. Using volcaniclastic rocks to constrain sedimentation ages: to what extent are volcanism and sedimentation synchronous? Sediment. Geol. 381, 46–64. https://doi.org/10.1016/j.sedgeo.2018.12. 010.
- Rowe, T., 1989. A new species of the theropod dinosaur *Syntarsus* from the Early Jurassic Kayenta Formation of Arizona. J. Vertebr. Palaeontol. 9, 125–136.
- Rubidge, B.S., Erwin, D.H., Ramezani, J., Bowring, S.A., de Klerk, W.J., 2013. Highprecision temporal calibration of Late Permian vertebrate biostratigraphy: U-Pb zircon constraints from the Karoo Supergroup, South Africa. Geology 41 (3), 363–366.
- Schiuma, M., Llambias, E.J., 2008. New ages and chemical analysis on Lower Jurassic volcanism close to the dorsal de Huincul, Neuquen. Rev. Asoc. Geol. Argent. 63, 644–652.
- Sciscio, L., 2016. Position of the Triassic-Jurassic Boundary in South Africa and Lesotho: A Multidisciplinary Approach Aimed at Improving the Chronostratigraphy and Biostratigraphy of the Elliot Formation, Stormberg Group. Doctoral dissertation. University of Cape Town. http://hdl.handle.net/11427/20847.
- Sciscio, L., Bordy, E.M., 2016. Palaeoclimatic conditions in the Late Triassic-Early Jurassic of southern Africa: a geochemical assessment of the Elliot Formation. J. Afr. Earth Sci. 119, 102–119.
- Sciscio, L., Bordy, E.M., Reid, M., Abrahams, M., 2016. Sedimentology and ichnology of the Mafube dinosaur track site (Lower Jurassic, eastern Free State, South Africa): a report on footprint preservation and palaeoenvironment. PeerJ 4 p.e2285.
- Sciscio, L., de Kock, M., Bordy, E., Knoll, F., 2017a. Magnetostratigraphy across the Triassic-Jurassic boundary in the main Karoo Basin. Gondwana Res. 51, 177–192. https://doi.org/10.1016/j.gr.2017.07.009.
- Sciscio, L., Bordy, E.M., Abrahams, M., Knoll, F., McPhee, B.W., 2017b. The first megatheropod tracks from the Lower Jurassic upper Elliot Formation, Karoo Basin, Lesotho. PLoS One 12 (10), e0185941. https://doi.org/10.1371/journal.pone. 0185941.

Sciscio, L., Knoll, F., Bordy, E.M., de Kock, M.O., Redelstorff, R., 2017c. Digital reconstruction of the mandible of an adult *Lesothosaurus diagnosticus* with insight into the tooth replacement process and diet. PeerJ 5 p.e3054.

- Sell, B., Ovtcharova, M., Guex, J., Bartolini, A., Jourdan, F., Spangenberg, J.E., Vicente, J.C., Schaltegger, U., 2014. Evaluating the temporal link between the Karoo LIP and climatic–biologic events of the Toarcian Stage with high-precision U–Pb geochronology. Earth Planet. Sci. Lett. 408, 48–56.
- Sereno, P.C., 2012. Taxonomy, morphology, masticatory function and phylogeny of heterodontosaurid dinosaurs. ZooKeys 226, 1–225.
- Shubin, N.H., Sues, H.D., 1991. Biogeography of early Mesozoic continental tetrapods: patterns and implications. Paleobiology 17 (3), 214–230.
- Shubin, N.H., Crompton, A.W., Sues, H.D., Olsen, P.E., 1991. New fossil evidence on the sister-group of mammals and early Mesozoic faunal distributions. Science 251 (4997), 1063–1065. https://doi.org/10.1126/science.251.4997.1063. PMID:17802092.
- Sidor, C.A., Hancox, P.J., 2006. Elliotherium kersteni, a new tritheledontid from the lower Elliot Formation (Upper Triassic) of South Africa. J. Paleontol. 80 (2), 333–342.
- Smith, R., Kitching, J., 1997. Sedimentology and vertebrate taphonomy of the *Tritylodon* Acme Zone: a reworked palaeosol in the Lower Jurassic Elliot Formation, Karoo Supergroup, South Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 131 (1-2), 29–50.
- Smith, R.M.H., Eriksson, P.G., Botha, W.J., 1993. A review of the stratigraphy and sedimentary environments of the Karoo-aged basins of Southern Africa. J. Afr. Earth Sci. 16 (1-2), 143–169.
- Smith, R.M., Marsicano, C.A., Wilson, J.A., 2009. Sedimentology and paleoecology of a diverse Early Jurassic tetrapod tracksite in Lesotho, southern Africa. Palaios 24 (10), 672–684.

Spencer, C.J., Kirkland, C.L., Taylor, R.J., 2016. Strategies towards statistically robust interpretations of in situ U–Pb zircon geochronology. Geosci. Front. 7, 581–589.

Spikings, R., Reitsma, M.J., Boekhout, F., Mišković, A., Ulianov, A., Chiaradia, M., Gerdes,

A., Schaltegger, U., 2016. Characterisation of Triassic rifting in Peru and implications for the early disassembly of western Pangaea. Gondwana Res. 35, 124–143.

- Steyer, J.S., Damiani, R., 2005. A giant brachyopoid temnospondyl from the Upper Triassic or Lower Jurassic of Lesotho. Bulletin de la Société Géologique de France 176 (3), 243–248.
- Suarez, C.A., Knobbe, T.K., Crowley, J.L., Kirkland, J.I., Milner, A.R., 2017. A chronostratigraphic assessment of the Moenave Formation, USA using C-isotope chemostratigraphy and detrital zircon geochronology: implications for the terrestrial end Triassic extinction. Earth Planet. Sci. Lett. 475, 83–93.
- Sues, H.D., Olsen, P.E., 2015. Stratigraphic and temporal context and faunal diversity of Permian-Jurassic continental tetrapod assemblages from the Fundy rift basin, eastern Canada. Atl. Geol. 51, 139–205. https://doi.org/10.4138/atlgeol.2015.006.
- Sues, H.D., Reisz, R.R., 1995. First record of the early Mesozoic sphenodontian *Clevosaurus* (Lepidosauria: Rhynchocephalia) from the Southern Hemisphere. J. Paleontol. 69 (1), 123–126. https://doi.org/10.1017/s0022336000026974.
- Sues, H.D., Shubin, N.H., Olsen, P.E., Amaral, W.W., 1996. On the cranial structure of a new protosuchid (Archosauria: Crocodyliformes) from the McCoy Brook Formation (Lower Jurassic) of Nova Scotia, Canada. J. Vertebr. Paleontol. 16 (1), 34–41. https://doi.org/10.1080/02724634.1996.10011281.
- Svensen, H., Corfu, F., Polteau, S., Hammer, Ø., Planke, S., 2012. Rapid magma emplacement in the Karoo large igneous province. Earth Planet. Sci. Lett. 325, 1–9. https:// doi.org/10.1016/j.epsl.2012.01.015.
- Tabor, N.J., Myers, T.S., 2015. Paleosols as indicators of paleoenvironment and paleoclimate. Annu. Rev. Earth Planet. Sci. 43, 333–361.
- Tauxe, L., 1998. Paleomagnetic Principles and Practice Modern Approaches in Geophysics. Kluwer Academic Publisher, Dordrecht, Netherlands, pp. 309.
- Thulborn, R.A., 1974. A new heterodontosaurid dinosaur (Reptilia: Ornithischia) from the Upper Triassic Red Beds of Lesotho. Zool. J. Linn. Soc. Lond. 55, 151–175.
- Tolchard, F., Nesbitt, S.J., Desojo, J., Viglietti, P., Butler, R.J., Choiniere, J.N., 2019. 'Rauisuchian' material from the lower Elliot Formation of South Africa: implications for Late Triassic biogeography and biostratigraphy. J. Afr. Earth Sci. 160, 103610.
- Tucker, R.T., Roberts, E.M., Hu, Y., Kemp, A.I., Salisbury, S.W., 2013. Detrital zircon age constraints for the Winton Formation, Queensland: contextualizing Australia's Late Cretaceous dinosaur faunas. Gondwana Res. 24 (2), 767–779. https://doi.org/10. 1016/j.gr.2012.12.009.
- Van Hoepen, E.C.N., 1920. Contributions to the knowledge of the reptiles of the Karoo Formation. 6. Further dinosaurian material in the Transvaal Museum. Ann. Transv. Mus. 7, 93–140.
- Viglietti, P.A., Frei, D., Rubidge, B.S., Smith, R.M., 2018a. U-Pb detrital zircon dates and provenance data from the Beaufort Group (Karoo Supergroup) reflect sedimentary recycling and air-fall tuff deposition in the Permo-Triassic Karoo foreland basin. J. Afr. Earth Sci. 143, 59–66.
- Viglietti, P.A., Barrett, P.M., Broderick, T.J., Munyikwa, D., MacNiven, R., Broderick, L., Chapelle, K., Glynn, D., Edwards, S., Zondo, M., Broderick, P., Choiniere, J.N., 2018b. Stratigraphy of the *Vulcanodon* type locality and its implications for regional correlations within the Karoo Supergroup. J. Afr. Earth Sci. 137, 149–156. https://doi.org/ 10.1016/j.jafrearsci.2017.10.015.
- Viglietti, P.A., McPhee, B.W., Bordy, E.M., Sciscio, L., Barrett, P.M., Benson, R.B., Wills, S., Tolchard, F., Choiniere, J.N., 2020a. Biostratigraphy of the Scalenodontoides Assemblage Zone (Stormberg Group, Karoo Supergroup), South
- Africa, S. Afr. J. Geol in press. Viglietti, P.A., McPhee, B.W., Bordy, E.M., Sciscio, L., Barrett, P.M., Benson, R.B., Wills,
- Viglietti, P.A., McPhee, B.W., Bordy, E.M., Sciscio, L., Barrett, P.M., Benson, K.B., Wills, S., Chapelle, K.J.E., Dollman, K.N., Mdekazi, C., Choiniere, J.N., 2020b.

Biostratigraphy of the *Massospondylus* Assemblage Zone (Stormberg Group, Karoo Supergroup), South Africa. S. Afr. J. Geol in press.

- Visser, J.N.J., 1984. A review of the Stormberg Group and Drakensberg volcanics in southern Africa. Palaeontol. Afr. 25, 5–27.
- von Huene, F., 1932. Die fossile Reptil-Ordung Saurischia, ihre Entwicklung und Geschichte. Monographien zur Geologie und Palaeontologie Leipzig, Verlag von Gebrüder Borntraeger. Serie I Heft 4 Teil I 361.
- Wang, Z.S., Rasbury, E.T., Hanson, G.N., Meyers, W.J., 1998. Using the U-Pb system of calcretes to date the time of sedimentation of clastic sedimentary rocks. Geochim. Cosmochim. Acta 62 (16), 2823–2835.
- Wang, S., Stiegler, J., Amiot, R., Wang, X., Du, G.H., Clark, J.M., Xu, X., 2017. Extreme ontogenetic changes in a ceratosaurian theropod. Curr. Biol. 27 (1), 144–148. https://doi.org/10.1016/j.cub.2016.10.043.
- Warren, A., Damiani, R., 1999. Stereospondyl amphibians from the Elliot Formation of South Africa. Palaeontol. Afr. 35, 45–54. http://hdl.handle.net/10539/1646.
- Whiteside, J.H., Olsen, P.E., Eglinton, T., Brookfield, M.E., Sambrotto, R.N., 2011. Compound-specific carbon isotopes from EarthTs largest flood basalt eruptions directly linked to the end-Triassic mass extinction. PNAS 107 (15), 6721–6725. https:// doi.org/10.1073/pnas.1001706107.
- Wilson, J.A., Marsicano, C.A., Smith, R.M., 2009. Dynamic locomotor capabilities revealed by early dinosaur trackmakers from Southern Africa. PLoS One 4 (10), e7331.
- Wotzlaw, J.F., Guex, J., Bartolini, A., Gallet, Y., Krystyn, L., McRoberts, C.A., Taylor, D., Schoene, B., Schaltegger, U., 2014. Towards accurate numerical calibration of the Late Triassic: High-precision U-Pb geochronology constraints on the duration of the Rhaetian. Geology 42 (7), 571–574. https://doi.org/10.1130/G35612.1.
- Yates, A.M., 2003. A definite prosauropod dinosaur from the lower Elliot Formation (Norian: Upper Triassic) of South Africa. Palaeontol. Afr. 39, 63–68.
- Yates, A.M., 2005. A new theropod dinosaur from the Early Jurassic of South Africa and its implications for the early evolution of theropods. Palaeontol. Afr. 41, 105–122.
- Yates, A.M., 2007a. Solving a dinosaurian puzzle: the identity of *Aliwalia rex* Galton. Hist. Biol. 19, 93–123.
- Yates, A.M., 2007b. The first complete skull of the Triassic dinosaur *Melanorosaurus* Haughton (Sauropodomorpha: Anchisauria). Spec. Pap. Paleontol. 77, 9–55.
- Yates, A.M., 2008. A second specimen of *Blikanasaurus* (Dinosauria: Sauropoda) and the biostratigraphy of the lower Elliot Formation. Palaeontol. Afr. 43, 39–43.
- Yates, A.M., Barrett, P.M., 2010. Massospondylus carinatus Owen 1854 (Dinosauria: Sauropodomorpha) from the Lower Jurassic of South Africa: proposed conservation of the usage by designation of a neotype. Palaeontol. Afr. 45, 7–10.
- Yates, A.M., Kitching, J.W., 2003. The earliest known sauropod dinosaur and the first steps towards sauropod locomotion. Proc. R. Soc. Lond. Ser. B Biol. Sci. 270 (1525), 1753–1758.
- Yates, A.M., Bonnan, M.F., Neveling, J., Chinsamy, A., Blackbeard, M.G., 2009. A new transitional sauropodomorph dinosaur from the Early Jurassic of South Africa and the evolution of sauropod feeding and quadrupedalism. Proc. R. Soc. B Biol. Sci. 277 (1682), 787–794.
- Yates, A.M., Bonnan, M.F., Neveling, J., 2011. A new basal sauropodomorph dinosaur from the Early Jurassic of South Africa. J. Vertebr. Paleontol. 31, 610–625.
   You, H.-L., Azuma, Y., Wang, T., Wang, Y.-M., Don, Z.-M., 2014. The first well-preserved
- You, H.-L., Azuma, Y., Wang, T., Wang, Y.-M., Don, Z.-M., 2014. The first well-preserved coelophysoid theropod dinosaur from Asia. Zootaxa 3873, 233–249.
- Zeigler, K.E., Geissman, J.W., 2011. Magnetostratigraphy of the Upper Triassic Chinle Group of New Mexico: Implications for regional and global correlations among Upper Triassic sequences. Geosphere 7 (3), 802–829.