Biostratigraphy of the *Scalenodontoides* Assemblage Zone (Stormberg Group, Karoo Supergroup), South Africa

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Abstract

The *Scalenodontoides* Assemblage Zone (SAZ) is the oldest fossil tetrapod biozone of the Stormberg Group (Karoo Supergroup) and preserves the oldest dinosaur bearing deposits in the Karoo Basin. The SAZ represents a revision of the '*Euskelosaurus*' Range Zone, whose taxonomic basis has been undermined because '*Euskelosaurus*' is well demonstrated to be a *nomen dubium*. Recent qualitative and quantitative investigations into the biostratigraphy of the Elliot and Clarens formations have resulted in the first biostratigraphic review of all lower Elliot Formation (lEF) taxa in nearly 40 years. Thus, we replace the '*Euskelosaurus*' Range Zone with a new biostratigraphic assemblage zone, the *Scalenodontoides* Assemblage Zone (SAZ). Named after the traversodontid cynodont *Scalenodontoides macrodontes*, which co-occurs with the sauropodomorphs *Blikanasaurus cromptoni* and *Melanorosaurus readi*. The SAZ is currently accepted to range in age between the upper Norian and Rhaetian. Our new biozone, which reaches a maximum thickness of ~200 m, is wholly contained within the lower Elliot Formation (Stormberg Group, Karoo Supergroup).

Name

Scalenodontoides Assemblage Zone (SAZ).

Proposer of name

The original proposers of a lower Elliot Formation biozone, the '*Euskelosaurus*' Range Zone, were Kitching and Raath (1984) in their landmark paper on the biozonation of the Late Triassic to Early Jurassic rocks of southern Africa (South Africa and Lesotho). The *Scalenodontoides* Assemblage Zone (SAZ) is defined in this contribution as a clarification and re-definition of the former '*Euskelosaurus*' Range Zone.

Stratigraphic position

Biostratigraphic position

The SAZ overlies the Molteno Formation, a unit devoid of vertebrate bones, but rich in fossil floras (Anderson et al., 1998). The SAZ underlies the *Massospondylus* Assemblage Zone.

Lithostratigraphic position

The entire SAZ lies within the lower Elliot Formation (Stormberg Group, Karoo Supergroup), which is regarded as spanning the lower Norian to uppermost Rhaetian. Initially, the Elliot Formation was subdivided into informal lower, middle and upper units by Kitching and Raath (1984). Subsequently, the lithostratigraphy of the formation was redefined to contain only the informal lower Elliot Formation (lEF) and the unconformably overlying upper Elliot Formation (uEF; Bordy et al., 2004a, b and c; Bordy and Eriksson, 2015). The lEF remains unchanged with respect to the original subdivisions of the Elliot Formation, but the uEF incorporates the middle and upper Elliot formations of Kitching and Raath (1984).

As with its predecessor (the '*Euskelosaurus*' Range Zone), the SAZ is confined within the lEF. However, by proposing the SAZ we incorporate a series of updates to the stratigraphic ranges of lEF taxa, revising some of these for the first time since the compilation of Kitching and Raath (1984). Although recent magnetostratigraphic data (Sciscio et al., 2017) tentatively places the Triassic/Jurassic boundary within the lower uEF (rather than at the boundary of the lEF and uEF as assumed traditionally), the lack of lEF faunal components in the uEF (and *vice versa*), and the general paucity of fossils from the lower part of the uEF, cautions us against extending the latest Triassic (and SAZ) beyond the lEF upper boundary at this stage.

Derivation of name

The SAZ is derived from an easily identified, locally common vertebrate taxon in this biozone, the traversodontid cynodont *Scalenodontoides macrodontes* in co-occurrence with the sauropodomorphs *Melanorosaurus readi* and *Blikanasaurus cromptoni* (Figure 1).

Historical background

The upper Karoo units were first named the "Stormberg formation" by Wyley, Huxley and Dunn (Rogers and Du Toit, 1909), but it was Du Toit (1903, 1905) who laid the foundation for the first stratigraphic investigations and later influenced Haughton's (1924) work on the "Stormberg series" fossil fauna. The first officially accepted biostratigraphic range zones for the Elliot and Clarens formations were proposed by Kitching and Raath (1984). Ellenberger and co-workers (Ellenberger et al., 1964; Ellenberger, 1970) made attempts to subdivide the "Stormberg Series" into several zones, based primarily on the stratigraphic distributions of vertebrate ichnofossils. However, this initial zonation was inconsistent with accepted stratigraphic observations. Kitching and Raath's (1984) biostratigraphic zonation defined the '*Euskelosaurus*' and *Massospondylus* Range Zones based on the stratigraphic distributions of two sauropodomorph taxa: '*Euskelosaurus browni*' and *Massospondylus carinatus*.

'*Euskelosaurus*' and its constituent species ('*E. africanus*' and the genotype '*E. browni*') have been shown to be nomina dubia, and thereafter been used as wastebasket taxa for taxonomically indeterminate remains of large non-sauropodan sauropodomorph dinosaurs (e.g., Yates, 2003, 2007; Yates and Kitching, 2003; Yates et al., 2004; McPhee et al., 2017). Therefore, the taxonomic basis for the '*Euskelosaurus*' Range Zone has

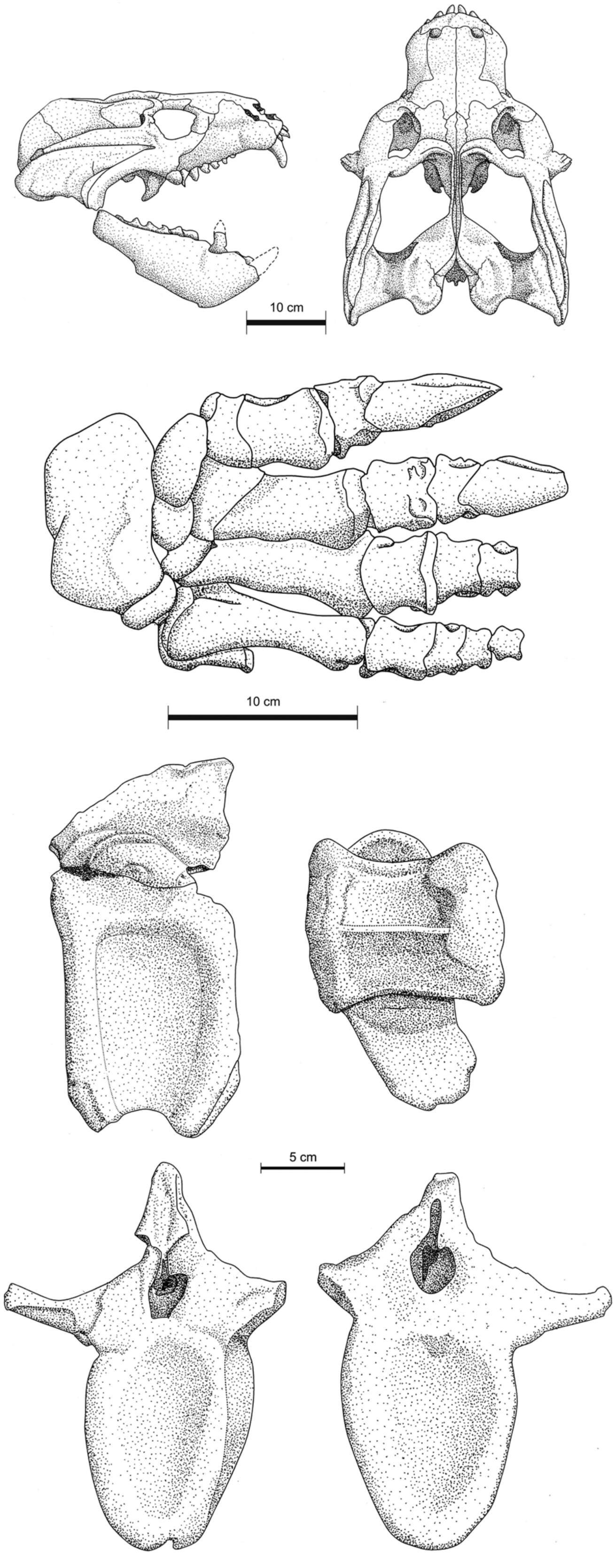

Figure 1. *Lateral and dorsal views of the biozone defining fossils of the* Scalenodontoides *Assemblage Zone. (Top),* Scalenodontoides macrodontes *skull (modified after Gow and Hancox, 1993); (middle),* Blikanasaurus cromptoni *dorsal view of left pes (modified after Galton and Van Heerden, 1985), and (bottom), proximal caudal vertebra of* Melanorosaurus readi *viewed from left lateral (top left) ventral (top right) anterior (bottom left) and posterior (bottom right) aspects (modified after Yates, 2004).*

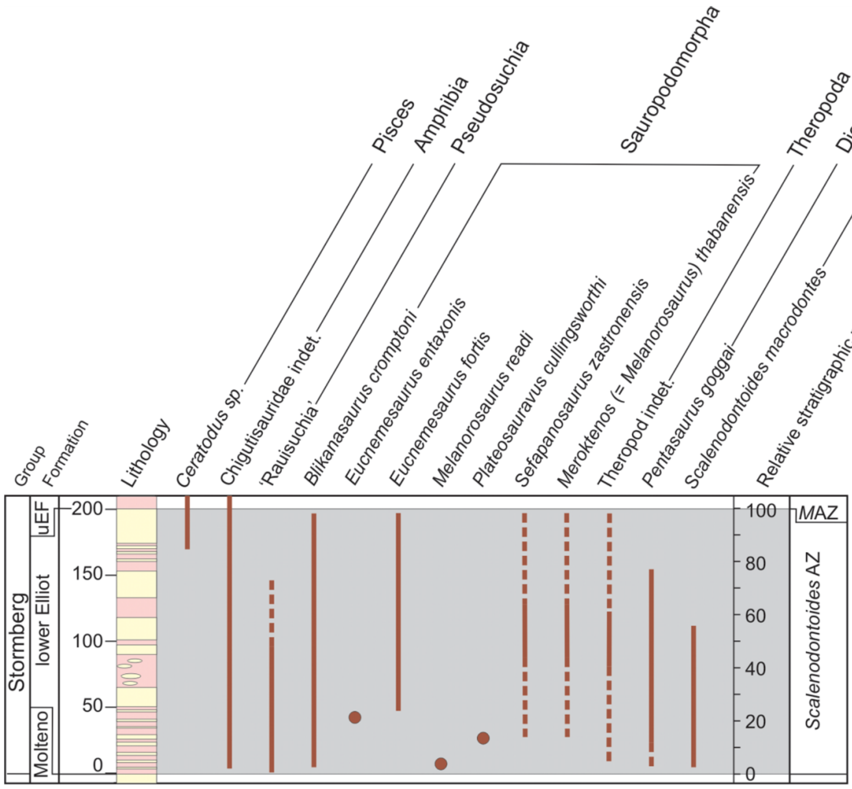

Figure 2. *Stratigraphic section showing the ranges of vertebrate taxa (relative position, %) present in the* Scalenodontoides *Assemblage Zone. The generalized and simplified lithological section is based on the holostratotype of the lower Elliot Formation at Barkly Pass (Eastern Cape Province; modified from Bordy and Eriksson (2015). uEF=upper Elliot Formation, MAZ=Massospondylus Assemblage Zone.*

been undermined, necessitating its re-definition. Recent biostratigraphic and taxonomic revisions of Elliot Formation sauropodomorphs conducted by McPhee et al. (2017) demonstrated that previous biostratigraphic correlations based on the referral of specimens to '*Euskelosaurus*', which have implied equivalent stratigraphic positions between lower Elliot localities, are potentially spurious. Using these findings, and new biostratigraphic data collected during work on the Karoo Collections Database, we propose a redefined assemblage zone for the lEF.

Excluding '*Euskelosaurus'* leaves five other potentially valid sauropodomorph taxa from the lEF: *Plateosauravus cullingsworthi, Melanorosaurus readi, Eucnemesaurus entaxonis, Eucnemesaurus fortis*, and *Blikanasaurus cromptoni*. *Antetonitrus ingenipes* was originally described as a lEF taxon, but McPhee et al. (2017) demonstrated that it occurs in the uEF within the *Massospondylus* Range Zone. McPhee et al. (2015, 2017) also questioned the taxonomic validity of *Plateosauravus,* and here we regard that genus as provisionally valid but pending revision. Although *Eucnemesaurus entaxonis* is valid, the provenance of *Eucnemesaurus fortis* (the genotype) is poorly constrained within the lEF (see McPhee et al., 2017). *Blikanasaurus* is known from distinctive type material (Galton and Van Heerden, 1985), but is based on a very limited hypodigm and its anatomy is largely unknown (Yates, 2008). Finally, the validity of *Melanorosaurus* has also been questioned (e.g., McPhee et al., 2015, 2017), but is likely valid based on the presence of diagnostic material in the syntype series (Yates, 2007). Because of the questionable validity of many lEF sauropodomorph taxa, we consider them unsuitable for use as the main index fossil for this stratigraphic interval.

We propose instead the traversodontid cynodont *Scalenodontoides macrodontes* subfamily *Gomphodontosuchinae* (Watson and Romer, 1956; sensu Liu and Abdala, 2014), as the main index fossil for this interval. It has well-represented skull material and is identifiable from relatively complete specimens, including teeth (Crompton and Ellenberger, 1957; Crompton, 1972; Hopson, 1984; Gow and Hancox, 1993; Battail, 2005). Furthermore, it is the only large-bodied cynodont so far recognized from the Elliot Formation, which makes it easy to identify in the field. Currently, occurrences of *Scalenodontoides* are restricted to the lower half of the lEF. It is therefore possible that another assemblage zone could be needed, spanning the upper part of the lEF (above the last appearance of *Scalenodontoides*) following further fossil collection and stabilisation of Elliot Formation sauropodomorph taxonomy.

Palaeontology

Description of Assemblage Zone

An assemblage zone characterised by the occurrence of the cynodont *Scalenodontoides macrodontes* and the sauropodomorphs *Melanorosaurus readi* and *Blikanasaurus cromptoni*, all of which first appear at the base of the lEF.

Taphonomic notes on fossil occurrences

Well-preserved fossils occur in lEF mudstones and are usually found as isolated specimens. Partial articulation or associated disarticulated elements are the most common types of preservation. Skull material is less common than postcranial material, which is the opposite of the fossil preservation trends in the Beaufort Group, likely due to the differences in skull fusion between synapsids and archosaurs. Fossil bones are commonly purplish-grey in colour, and those encased in calcareous nodules often have better preservation. Kitching and Raath (1984) describe most of the fossil bones as displaying "sun-cracked" pre-burial weathering. The fossil bones are also frequently compacted and covered by a hard, thick (~10 mm) coating of haematite (Kitching and Raath, 1984). Rocks in the lEF are commonly contact metamorphosed by dolerite intrusions, which can alter the properties (e.g., colour, texture, competence) of the rocks and enclosed fossils and enhance preservation.

List of fossils

See Figure 2 for ranges of vertebrate genera, which are shown in the range chart as relative position (% of overall stratigraphic height) rather than as meter notation in the generalized and simplified lithological section of the lEF. This relative position information is necessary because of the extreme thickness variation of the SAZ across the main Karoo Basin. Taxa listed below are derived from: Van Hoepen (1920); Haughton (1924); Du Toit (1927); Huene (1932a and b); Ellenberger (1970, 1972); Turner (1972); Kitching (1977); Galton and Van Heerden (1985); Anderson et al. (1998); Warren and Damiani (1999); Bamford (2004); Knoll (2004); Barbolini (2014); Otero et al. (2015); Rubidge et al. (2016); McPhee et al. (2017); Kammerer (2018); and Tolchard et al. (2019).

Recent collecting and re-assignment of the stratigraphic position of previously collected specimens has led to updated ranges for some lEF taxa. *'Euskelosaurus africanus'*, *'Euskelosaurus browni'* (Yates, 2003, 2007), and *'Basutudon ferox'* (Knoll, 2004) are now considered *nomina dubia*. Recently named lEF taxa inferred to reliably occur in the SAZ include *Eucnemesaurus entaxonis* (McPhee et al., 2015) and *Pentasaurus goggai* (Kammerer, 2018). The non-sauropodan sauropodomorphs *Meroktenos thabanensis* (de Fabrègues and Allain, 2016) and *Sefapanosaurus zastronensis* (Otero et al., 2015) are tentatively placed in the lEF (McPhee et al., 2017), although their provenance data are poorly constrained. In addition, recent taxonomic and biostratigraphic reviews of South African 'Rauisuchia' by Tolchard et al. (2019) report two definitive pseudosuchian taxa. Intriguingly, confirmed theropod fossils remain unknown in the lEF, although footprints (on the *Grallator-Anchisauripus-Eubrontes* plexus) and recurved serrated teeth (e.g., SAM-PK-K10013: Ray and Chinsamy-Turan, 2002) have been used to infer their presence. Moreover, tridactyl prints attributed to theropods have been documented by Raath et al. (1990) in the underlying Molteno Formation. However, given growing evidence that potentially bipedal pseudosuchians were present in the lEF ('Rauisuchia' *sensu* Tolchard et al., 2019), it is possible the trackways and isolated teeth could also be attributed to these taxa.

Vertebrates		
	Pisces	*Ceratodus* sp.
	Amphibia	*Chigutisauridae* indet.
	Amniota	
	Eureptilia	
	Archosauromorpha	
	Pseudosuchia	'Rauisuchia'
	Ornithodira	
	Sauropodomorpha	*Blikanasaurus cromptoni*
		Eucnemesaurus entaxonis
		Eucnemesaurus fortis
		Melanorosaurus readi
		Plateosauravus cullingsworthi
		Sefapanosaurus zastronensis
		Meroktenos (= Melanorosaurus) thabanensis
	Theropoda	Theropod indet.
	Synapsida	
	Therapsida	
	Anomodontia	*Pentasaurus goggai*
	Cynodontia	*Scalenodontoides macrodontes*
Trace fossils		
	Vertebrate	*Eubrontes* isp.
		Grallator isp.
		Paratetrasauropus isp.
		Pentasauropus isp.
		Pseudotetrasauropus isp.
		Sauropodopus isp.
		Tetrasauropus isp.
		Trisauropodiscus isp.
Plants	Sphenophytes	*Equisetites* sp.
	Bennettitaleans	*Otozamites* sp.
	Conifers	*Sphenolepidiurn* sp.
		Pinus sp.
	Seed Ferns	*Dicroidium* sp.
	Incertae sedis	*Phoenicopsis* sp.
	Wood	*Agathoxylon* sp.
	Pollen and spores	*Dictyophyllidites mortonii*
		Lacrimasporonites levis
		Uvaesporites verrucosus

Geological description

Thickness of biozone

As with the underlying biostratigraphic zones of the Beaufort Group, the upper Stormberg Group biozones decrease in thickness from south to north within the main Karoo Basin. This thickness decrease is particularly distinct for the SAZ-hosting lEF, which reaches a maximum thickness of ~200 m near its type locality at Barkly Pass (Bordy et al., 2004a, b and c; Bordy and

Eriksson, 2015: fig. 3), and a minimum thickness of ~30 m in the north of the basin. However, in some rare instances the SAZ has been reported as <10 m thick in the northernmost region (around Ladybrand and Clarens) (see stratigraphic sections in Bordy et al., 2004b; McPhee et al., 2017).

Lithology

The lower Elliot Formation is generally characterised by heterogeneous red-purple (ranging from olive-grey 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 (Bordy et al., 2004b, c). The sandstone units, which can be up to 20 m thick, are medium-grained and have asymmetrical geometry in cross-sections perpendicular to palaeocurrent directions. The sandstones contain trough and planar cross-stratification, massive beds and less commonly low-angle cross-stratification, and planar stratification (horizontal lamination). Ripple cross-lamination, bioturbation structures and soft-sediment deformation structures are all extremely rare. Well-defined, upward-fining successions commonly begin with mud-pebble conglomerate lags. The mudstones are 20 to 30 m thick on average, rarely display pedogenic alteration features (e.g., irregular mottles, desiccation cracks, and carbonate nodules) which contrasts with uEF mudstones (Bordy et al., 2004b and c). In the southern outcrop area of the lEF, where the unit is ~200 m in thickness, the strong differential weathering of the sandstones and mudstones results in terraced hillslopes (Bordy et al., 2004a).

Depositional history

Based on sedimentological and palaeontological evidence, the depositional setting of the lEF is interpreted as a perennial fluvio-lacustrine system that developed under humid to semi-arid climatic conditions (Bordy et al., 2004b; Sciscio and Bordy, 2016). The multi-storey, cliff-forming sandstones are interpreted as deposits of moderately meandering channels flanked by riparian forests, whereas the mudstone-dominated facies represent proximal and distal overbank floodplain areas (Bordy et al., 2004b).

Boundaries

Lower boundary

The lower boundary of the SAZ is defined by the first appearance of a vertebrate fauna including *Scalenodontoides macrodontes* at the sharp contact between the Molteno and Elliot formations, which was interpreted as a regional unconformity by Bordy et al. (2005). The lowermost *Scalenodontoides* specimens are the holotype (MNHN 1957-23) and a referred specimen (SAM-PK-K00336) both found at the Molteno-lEF contact by Crompton and Ellenberger (1957) on Morobong Hill in southwestern Lesotho in 1957 (Turner, 1972; Battail, 2005).

Upper boundary

As with the original definition of the '*Euskelosaurus*' Range Zone, the upper boundary of the SAZ coincides with the lithostratigraphic boundary between the lEF and uEF. This lithostratigraphic boundary has been interpreted as a regional unconformity (Bordy et al., 2004a and b) (Figure 2).

Lateral boundaries

The SAZ has no lateral transitions in the main Karoo Basin, where its outcrop area is between 28 to 31° south and 26 to 28° east as defined by post-Karoo erosion (Figure 3).

Subdivisions

No formal subdivision is proposed for the SAZ.

Regional aspects

Geographic distribution

Examples of SAZ outcrops in the main Karoo Basin can be seen at Barkly Pass, Dordrecht, and Sterkspruit (South Africa), and at Alwyns Kop and Maphutseng (western Lesotho). The same stratigraphic interval has not been identified in any of the other Karoo-aged basins in northern South Africa (i.e., Tuli, Tshipise, Ellisras, Springbok Flats and Lebombo basins; Bordy and Catuneanu, 2002; Bordy et al., 2004a and b).

Lateral and vertical variation

The faunal content in the SAZ shows no lateral variation. The host lEF is also devoid of regional facies changes, although lateral thickness reduction from South to North is documented in the lEF (Bordy et al., 2004a; Bordy and Eriksson, 2015).

Correlation

The absence of SAZ index fossils and sedimentary facies associations typical of the lEF elsewhere in southern Africa make it unlikely that coeval deposits occur in considerable thicknesses in the neighbouring Karoo-aged basins (Bordy and Catuneanu, 2002; Bordy et al., 2004a and b; 2010; Viglietti et al., 2018). In addition, current taxonomic issues with lEF sauropodomorphs (McPhee et al., 2017) and 'Rauisuchia' undermines their use in extrabasinal correlations, but the former remains useful at the faunal composition level. For example, the general similarities between the sauropodomorph assemblages of the Norian-age Los Colorados Formation of Argentina and the lEF have been noted by numerous workers, with the Los Colorados genus *Riojasaurus incertus* and the lEF genus *Eucnemesaurus* spp. resolved as sister taxa in several recent phylogenetic treatments (Yates, 2003; McPhee et al., 2015). *Scalenodontoides macrodontes* also provides a potential biostratigraphic correlation with the Upper Triassic Wolfville Formation (Fundy Group, Newark Supergroup), Nova Scotia, Canada. Here, a large traversodont bearing many similarities to *Scalenodontoides* was found (Hopson, 1984;

originally referred to *Scalenodontoides plemmyridon*), although it was later made the type species of a distinct genus, *Arctotraversodon plemmyridon* (Sues et al., 1992; Battail, 2005). *Scalenodontoides* is morphologically like its sister-taxon, *Exaraetodon* spp. which is known from Carnian and Norian deposits in Argentina, Brazil and India (Chatterjee, 1982; Abdala et al., 2002; Langer et al., 2018). Finally, Pavanatto et al., (2018) described *Siriusgnathus niemeyerorum* from the Niemeyer Site from the Triassic of Brazil (Santa Maria Supersequence), which also is morphologically similar. In recent phylogenetic analyses, the relationships between *Siriusgnathus*, *Exaeretodon* and *Scalenodontoides* are unresolved, but they share a common ancestor to the exclusion of other gomphodont taxa.

Age

The SAZ was hypothesized to range in age from late Norian to latest Rhaetian (e.g., Kitching and Raath, 1984; Olsen and Galton, 1984; Lucas and Hancox, 2001; Knoll, 2004; McPhee et al., 2017). This age assessment was originally based on biostratigraphic correlations and later supported by magnetostratigraphic evidence (Sciscio et al., 2017). Recent geochronological assessment of the maximum depositional age for the upper Stormberg Group confirms an approximately Norian to Rhaetian total age range for the SAZ. However, its lower contact may be slightly older than previous recognised, extending down to the middle Norian (Bordy et al., 2020).

Based on this new information, it is possible that the SAZ could be temporally correlated (without shared index taxa) to the upper parts of the Chinle Formation (i.e., Blue Mesa, Sonsela, Petrified Forest, Owl Rock and Rock Point members: Dubiel et al., 1991; Parker, 2005; Irmis et al., 2011) and Upper Triassic of the Newark Basin (USA); the Los Colorados Formation in Argentina (Arcucci et al., 2004); the Westbury Formation in the UK (Galton, 1985, 1998); the Fleming Fjord Formation of northeastern Greenland (Sulej et al., 2014;

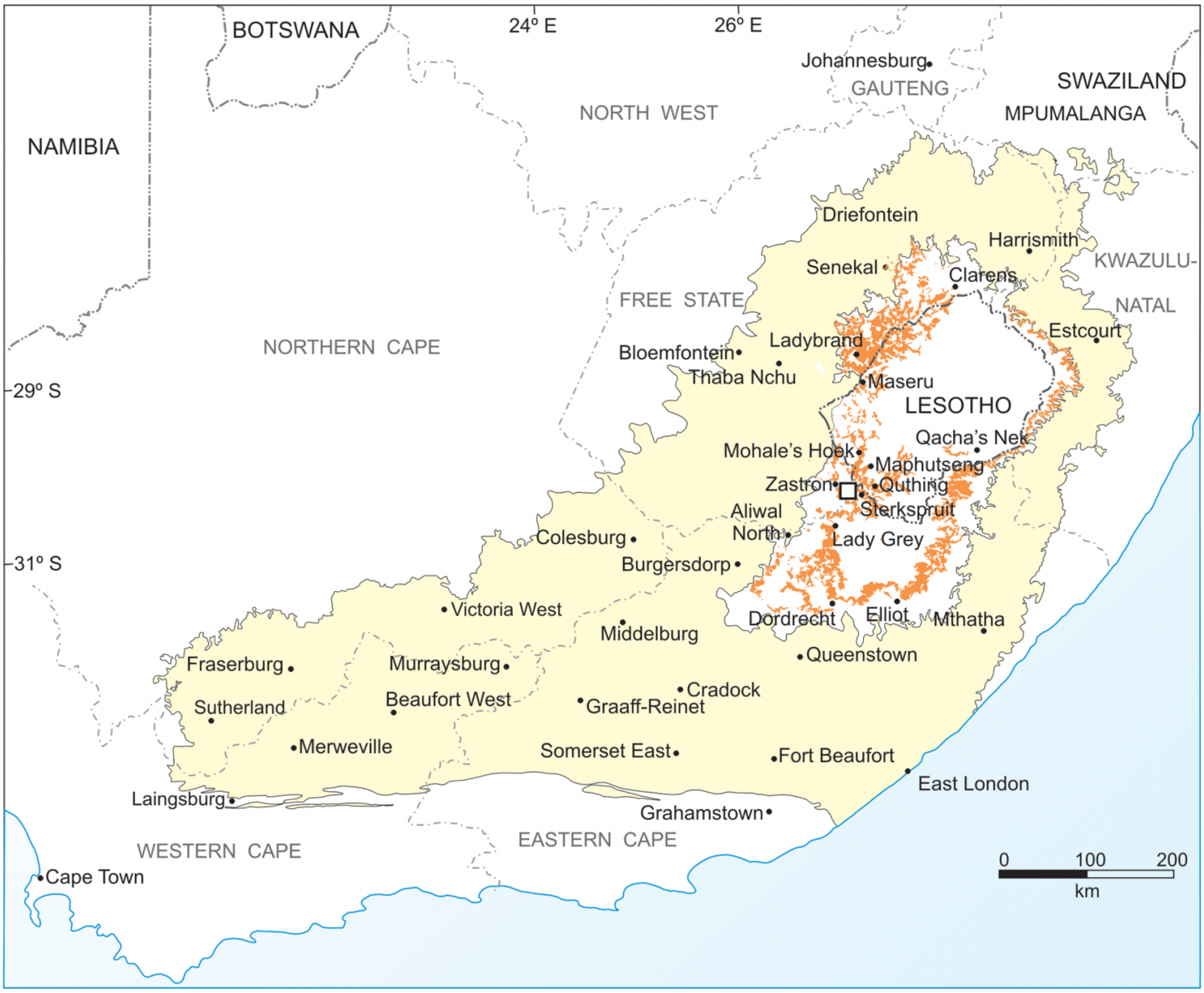

Figure 3. *Distribution map of the* Scalenodontoides *Assemblage Zone (SAZ) within the main Karoo Basin of South Africa and Lesotho with position of the SAZ type locality shown by open square. Light yellow shading = Beaufort Group, white area within yellow shading = Stormberg and Drakensberg groups.*

Clemmensen et al., 2016; Lallensack et al., 2017), and the Trossingen Formation in Germany (Dodson et al., 2004). The uppermost portion of the SAZ might also be correlated to the beds exposed at Lisowice in Poland (Sulej and Niedźwiedzki, 2019).

Type locality

The biozone type locality is on the northwestern portion of Vegkop (adjoining Vegkopwes 6 and Regina 55 farms), immediately east of Zastron in the southeastern Free State Province of South Africa (-30.278096S, 27.168582E; Figure. 4). One of the Elliot Formation's reference stratotypes is from the SAZ type locality (see Bordy and Eriksson, 2015: fig. 4B). The holostratotype of the lEF is at Barkly Pass (Eastern Cape Province, South Africa; -31.256389S, 27.829167E; see Bordy and Eriksson, 2015: fig. 3).

Acknowledgements

We thank James Neenan, Emma Dunne, Kathleen Dollman, Kimberley Chapelle, Daniel Cashmore, Cebisa Mdekazi, Gilbert Mokgethoa, Cory Dinter, Marie-Claire Koschowitz, Gavin Dollman, Stephan Spiekman, Hannie and Nellie Van Heerden (Driefontein farm), Ben Maclennan and Gillian Warren-Brown (Skilderskrans farm), Sginyane James Ralane and Themba Jikajika (Qhemegha) for their assistance in the field. We are grateful to staff at the Evolutionary Studies Institute (Sifelani Jirah, Bernhard Zipfel, Charlton Dube, Gerry Germishuizen, Wilfred Bilankulu, Pepson Mukanela, Thilivhali Nemavhundi), Iziko South African Museum (Roger Smith, Zaituna Skosan, Claire Browning), National Museum (Jennifer Botha, Elize Butler) and Albany Museum (Rose Prevec, Billy de Klerk) for access to specimens in their care and/or helped with logistics, accessioning and preparation of fossils that made this research possible. We also thank Roger Smith and Sterling Nesbitt for reviewing a previous version of this manuscript. The Centre of

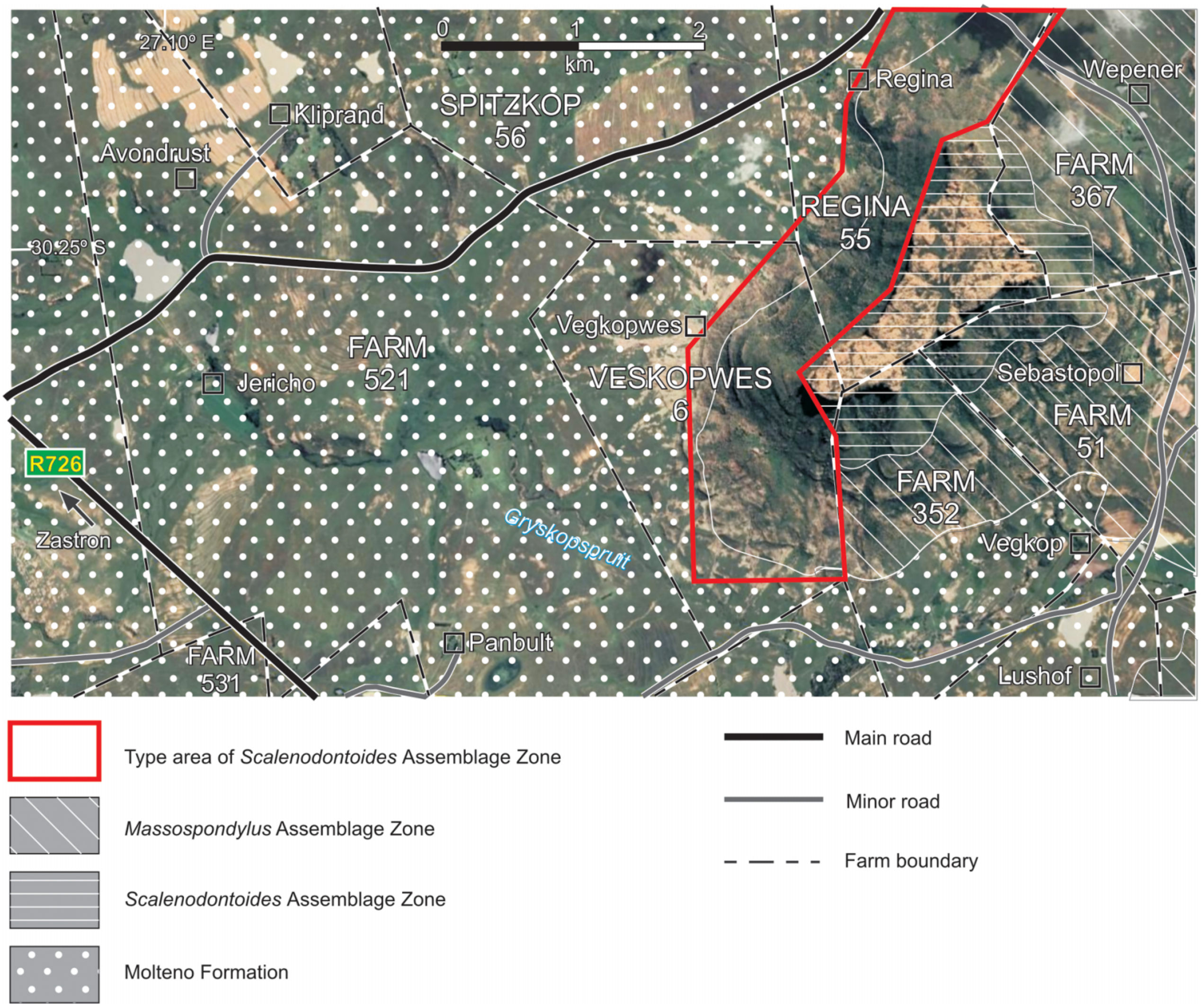

Figure 4. *Map of the Type locality of the* Scalenodontoides *Assemblage Zone on the farms Vegkopwes 6 and Regina 55 in the Zastron District, Free State Province.*

Excellence in Palaeosciences (CoE in Palaeosciences) are acknowledged for their generous financial support during this investigation (PAV grant: COE-2017, 2018; LS grant: COE-2016, 2017). Opinions expressed and conclusions arrived at, are those of the authors and are not necessarily to be attributed to the CoE. JNC and EMB were supported by the National Research Foundation NRF African Origins Platform (grants 98800, 118794 and 93544, 98825, respectively). LS was also supported by the Claude Leon Foundation.

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Editorial handling: R.M.H. Smith.