



Biostratigraphy of the *Lystrosaurus declivis* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa

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Abstract

The earliest Triassic (Induan) *Lystrosaurus* Assemblage Zone has long been recognised as a particularly significant biozone in palaeoecological and palaeoenvironmental studies as it contains a community assemblage that records the survival and recovery from the end-Permian mass extinction (EPME). Here renamed the *Lystrosaurus declivis* Assemblage Zone it represents the best record globally of the ecological changes in terrestrial community structure and stability during this time period. The assemblage is dominated by two species of small to medium-sized herbivorous dicynodonts *L. declivis* and *L. murrayi* that co-occur in equal abundance, along with a range of smaller and less common faunivorous and insectivorous taxa. The latter comprise cynodonts (*Thrinaxodon*, *Galesaurus*, and *Platycraniellus*), therocephalians (*Olivierosuchus*, *Regisaurus* and *Promoschorbynchus*), the diminutive parareptiles (*Saurodekteles*, *Sauropareion*, *Colleta*, *Phonodus* and *Procolophon*) and eureptilian arrivals possibly representing immigrant taxa (*Prolacerta*, *Heleosuchus* and *Noteosuchus*), among others. The attendant large carnivores were sabre-toothed *Moschorhinus* and the long-snouted archosauromorph *Proterosuchus*. In the aftermath of the mass extinction, new small temnospondyl taxa established their first occurrences i.e. *Broomistega*, *Lydekkerina*, and *Micropholis*, and have relatively high abundances compared to earlier temnospondyl records in the Karoo. Lithostratigraphically, the biozone for the most part spans the upper Palingkloof Member of the Balfour Formation and the overlying Katberg Formation in the western part of the basin, and the Normandien Formation in the east. The *Lystrosaurus declivis* Assemblage Zone of the main Karoo Basin hosts the type locality of the global Lootsbergian land-vertebrate faunachron. The biozone is one of the most widespread terrestrial faunal assemblages of western Gondwana with closely related species occurring in India and Antarctica. Similar, but much more distantly related taxa, occur in Induan-aged strata of Russia, China and Brazil.

Name

The *Lystrosaurus declivis* Assemblage Zone.

Proposer of name

Broom (1906) proposed the name '*Lystrosaurus* Beds' for the biozone, but it was redefined by Kitching (1970) who expanded

it to include the biostratigraphic range of *Procolophon*. Here, we propose the name *Lystrosaurus declivis* Assemblage Zone after the most common tetrapod species found, and limited to, the biozone.

Stratigraphic position

Biostratigraphic position

Overlies the *Daptocephalus* Assemblage Zone and underlies the *Cynognathus* Assemblage Zone.

Lithostratigraphic position

The biozone includes the upper Palingkloof Member of the Balfour Formation East of 24°E, and equivalent Harrismith Member of the Normandien Formation in the Northern Free State Province, as well as the entire Katberg Formation of the Tarkastad Subgroup, Karoo Supergroup (Groenewald and Kitching, 1995; Neveling, 2004; Smith and Botha-Brink, 2014).

A unit closely-spaced of multi-storied sandstone bodies lies within the upper third of the Katberg Formation in the distal parts of the Karoo Basin at various localities in the Xhariep District. It was termed the Swartberg member by Neveling (2004) after Swartberg Hill on the farm Bethel 763, southeast of the town Bethulie in the Xhariep District, and although not a formal member, it can be used to correlate between localities in the distal (and with its laterally-equivalent sandstone package in the proximal) sector of the basin (R Smith pers. obs.).

Above the Swartberg member the uppermost Katberg Formation fines upwards into the Burgersdorp Formation, which contains the overlying *Cynognathus* Assemblage Zone (Neveling, 2004). Neveling (2004) followed du Toit's (1917, 1918) initial proposal and placed the uppermost boundary of the Katberg Formation at the top of the uppermost, thick sandstone package, above which the red mudrock of the Burgersdorp Formation begins to dominate. The lowermost Burgersdorp Formation may also be determined biostratigraphically by the co-occurrence of *Procolophon* and trematosaurid and mastodontosaurid amphibians (Neveling, 2004).

Derivation of name

The name is derived from *Lystrosaurus declivis*, the most common vertebrate fossil species found within, and limited to, strata of this biozone.

Historical background

Broom first introduced the *Lystrosaurus* and *Procolophon* zones in 1906 and du Toit (1918) later remarked on the usefulness of *Lystrosaurus* for regional mapping purposes. Tripathi and Satsangi (1963) reported the presence of *Lystrosaurus* in the Panchet beds of India. Because these beds interdigitate with marine facies containing a well-established Triassic invertebrate fauna, *Lystrosaurus* became widely regarded as a Triassic taxon. Kitching (1970, 1977) expanded the Karoo biozone to include *Procolophon* because he maintained that it was found throughout the zone (although later studies have shown that *Procolophon* is limited to the upper two-thirds of the zone, Botha and Smith, 2006). Keyser (1979) proposed the name *Lystrosaurus-Thrinaxodon* Assemblage Zone, which was accepted by the South African Committee for Stratigraphy

(S.A.C.S.) in 1980. However, S.A.C.S. later reverted to the term *Lystrosaurus* Assemblage Zone and it was published as such in the S.A.C.S. Biostratigraphic Series No. 1 (Groenewald and Kitching, 1995). *Lystrosaurus* has since been found within the uppermost portion of the underlying Permian *Daptocephalus* Assemblage Zone (Smith, 1995; Smith and Ward, 2001; Botha and Smith, 2007) and thus, we revise the name to *Lystrosaurus declivis* Assemblage Zone to indicate the most abundant *Lystrosaurus* species that is limited to the biozone.

Palaeontology

Description of Assemblage Zone

An assemblage zone characterised by a low diversity of herbivorous vertebrates, the abundance of the dicynodont therapsid *Lystrosaurus declivis* in association with the dicynodont therapsid *Lystrosaurus murrayi*, the non-mammaliaform epicynodont therapsid *Thrinaxodon liorhinus*, the procolophonoid parareptile *Procolophon trigoniceps*, and the absence of the dicynodont therapsid *Daptocephalus leoniceps* (Figure 1).

Taphonomic notes on fossil occurrence

The vertebrate fossils of the *Lystrosaurus declivis* Assemblage Zone are primarily found in the mudrock sequences between channel sandstones. Fossils are found as articulated, semi-articulated or disarticulated, but still associated, skeletons often within brown-weathering calcareous nodules. In some planimetric exposures of channel bank facies of the Katberg Formation many partially articulated dorsal-up skeletons, some with mummified skin impressions can be found (Smith and Botha-Brink, 2011). A taphonomically significant occurrence in this biozone is the first appearance of monotaxic and multitaxic bonebeds in the Karoo succession. Juvenile *Lystrosaurus declivis* are the most common contributor to these floodplain hosted bonebeds that are interpreted as drought induced die-offs (Smith and Botha, 2005; Viglietti et al., 2013; Smith and Botha-Brink, 2014). Positively identified skeletons of the amphibian *Broomistega* (Fernandez, et al., 2013), the parareptile *Procolophon* (Kitching, 1977), the dicynodont *Lystrosaurus* (Modesto and Botha-Brink, 2010; Bordy et al., 2011; Botha-Brink, 2017) and the non-mammaliaform cynodont *Thrinaxodon* (Damiani et al., 2003; Smith and Botha-Brink, 2014) have been found within passively-filled underground burrow structures in the mudrocks of the uppermost Balfour and lower Katberg formations.

List of fossils

Abundant fossils of *Lystrosaurus declivis* are found from the lowermost boundary of the zone through to the upper portion, becoming scarce within the uppermost Katberg Formation (Figure 1A). This species has yet to be found at the uppermost boundary of the zone (Neveling, 2004). *Lystrosaurus murrayi* is also found in great abundance from the lower boundary and into the Katberg Formation, but positively identifiable material

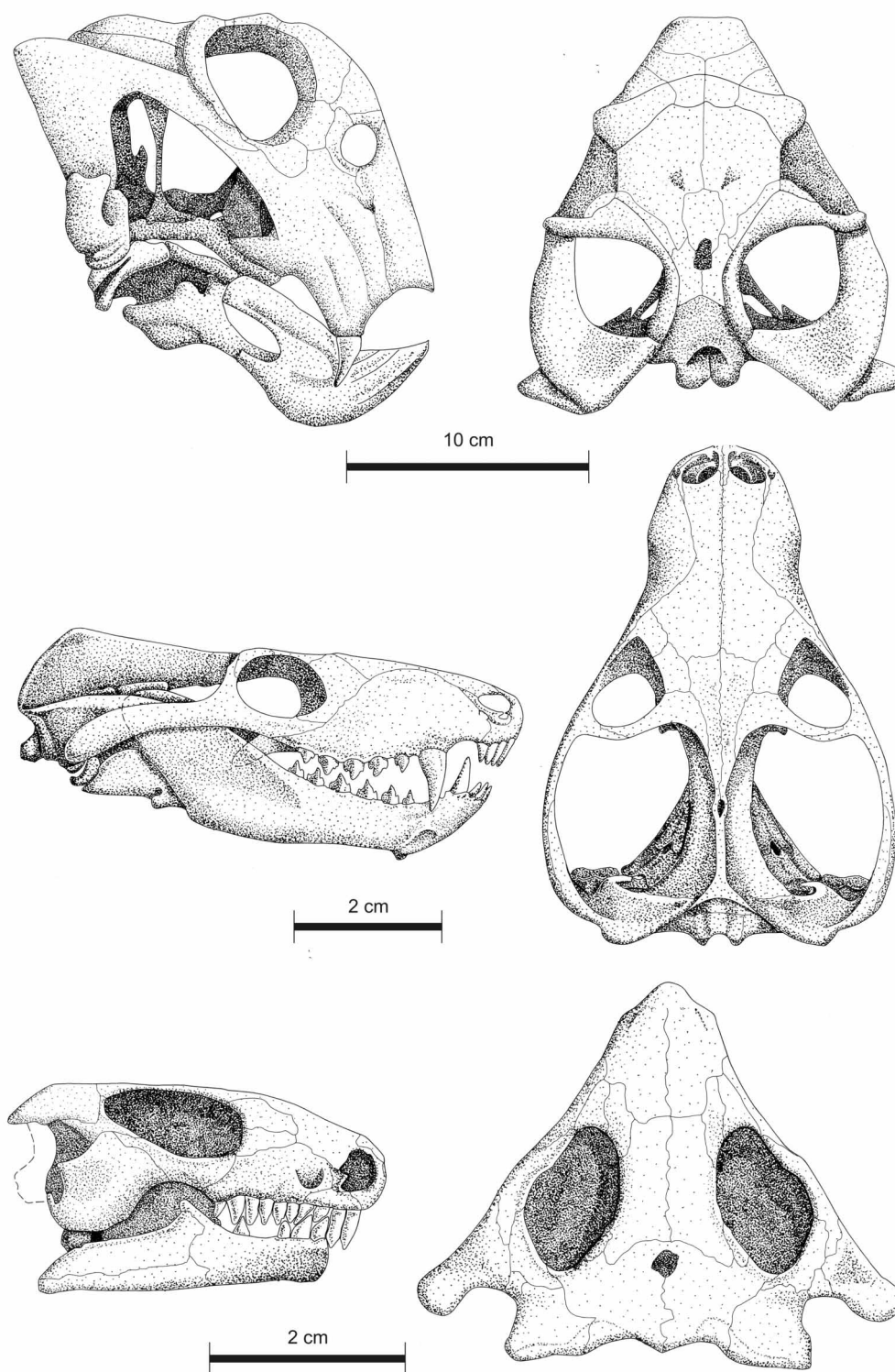


Figure 1. Lateral and dorsal views of the index taxa defining the *Lystrosaurus declivis* Assemblage Zone. (top) *Lystrosaurus declivis*, (centre) *Thrinaxodon liorhinus*, (bottom) *Procolophon trigoniceps*.

of this species has not been found above the Swartberg member (a regional member found in the Xhariep Municipal District [previously Bethulie and Rouxville districts], Neveling, 2004) in the uppermost Katberg Formation. These two species of *Lystrosaurus* are by far the most common taxa found in the

assemblage zone. *Thrinaxodon liorhinus* (Figure 1B) is commonly found in the Palingkloof Member and lowermost Katberg Formation, becoming scarce in the uppermost portion of the zone, although it has been found at the upper boundary (Neveling, 2004). *Procolophon trigoniceps* (Figure 1C) is

restricted to the upper two-thirds of the Katberg Formation and is found with increasing frequency from just below the Swartberg member to the upper boundary of the zone. The non-mammaliaform epicynodont *Galesaurus planiceps*, which is restricted to the Palingkloof Member and lowermost Katberg Formation, is also found in relative abundance. Although relatively rare, the archosauriform *Proterosuchus fergusi* is one of the first taxa to appear in the *Lystrosaurus declivis* Assemblage Zone and is thus helpful in locating the lower boundary of the zone. Fossils of the procolophonoid parareptiles "*Owenetta*" *kitchingorum* and *Saurodekteles rogersorum*, (note that these two taxa are soon to be synonymized into *Saurodekteles kitchingorum* resulting in the absence of *Owenetta* from the Triassic, Juan Cisneros pers. comm.) the dicynodont *Lystrosaurus curvatus*, Triassic records of the therocephalian

Moschorhinus kitchingi (a boundary-crossing taxon), and the non-mammaliaform epicynodont *Progalessaurus lootbergensis* are restricted to the Palingkloof Member (or equivalent units) and have yet to be found in the overlying Katberg Formation (Botha and Smith, 2007; Huttenlocker & Botha-Brink, 2013; Smith and Botha-Brink, 2014). A number of small temnospondyls make their first appearance near the base of this assemblage zone including *Micropholis stowi*, *Lydekkerina huxleyi* and *Broomistega putterilli*, and at the uppermost transition with the overlying *Cynognathus* assemblage (*Langbergia-Gargainia* Subzone), the medium to large temnospondyl *Kestrosaurus* and an indeterminate trematosaurid (Damiani et al., 2000) also appear.

Ranges of the vertebrate genera are depicted in Figure 2. Three new ichnofossils, *Dicynodontipus*, *Procolophonichnium*

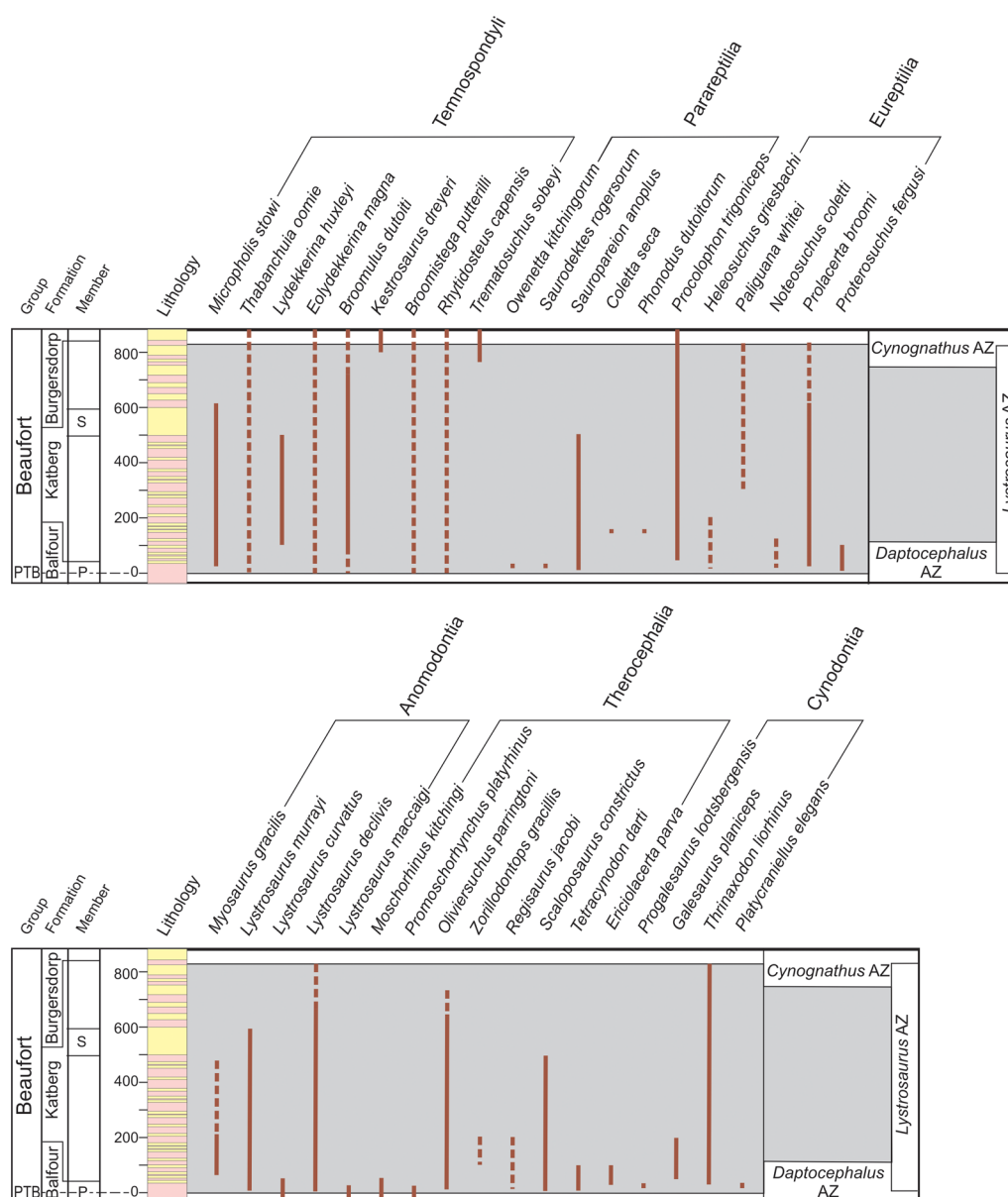


Figure 2. Composite stratigraphic section showing the biostratigraphic ranges of the vertebrate taxa found within the *Lystrosaurus declivis* Assemblage Zone. Lithological sections measured at Lootsberg Pass, Bethel and Perdelaagte. Scale in metres. P=Palingkloof, S=Swartberg, PTB=Permo-Triassic boundary.

and *Rhynchosauroides* (Marchetti et al., 2019) have been added to the existing *Thalassinoides* and *Histioderma* attributed to *Procolophon* and *Lystrosaurus* respectively.

According to the collection data provided by Smith et al. (2012) by far the most abundant taxon encountered in the LAZ is *Lystrosaurus* (73%) followed by *Procolophon* (17%), *Thrinaxodon* (3%) and *Lydekkerina* (2%). However, both *Procolophon* and *Lydekkerina* are known to occur as monotaxic bonebed accumulations, which likely contributes to their overrepresentation in the collections. Smith and Botha-Brink (2014) provide field data that suggests that the actual abundance of *Lystrosaurus* fossils is much higher. They record a narrow 20 m thick interval in the Lower Katberg Formation of their Bethulie section where *Lystrosaurus* fossils comprise more than 90% of the faunal content.

Vertebrates

Amphibia	<i>Micropholis stowi</i> <i>Thabanchuia oomie</i> <i>Lydekkerina buxleyi</i> <i>Eolydekkerina magna</i> <i>Broomulus dutoiti</i> <i>Kestrosaurus dreyeri</i> <i>Broomistega putterilli</i> <i>Rhytidosteus capensis</i> <i>Trematosauridae indet.</i>
Amniota	
Parareptilia	<i>'Owenetta' kitchingorum</i> <i>Saurodekteles rogersorum</i> <i>Sauropareion anoplus</i> <i>Coletta seca</i> <i>Phonodus dutoitorum</i> <i>Procolophon trigoniceps</i>
Eureptilia	
Lepidosauromorpha	<i>Paliguana whitei</i>
Archosauromorpha	<i>Heleosuchus griesbachi</i> <i>Noteosuchus colletti</i> <i>Prolacerta broomi</i> <i>Proterosuchus fergusi</i>
Synapsida	
Therapsida	
Anomodontia	<i>Myosaurus gracilis</i> <i>Lystrosaurus curvatus</i> <i>Lystrosaurus murrayi</i> <i>Lystrosaurus declivis</i> <i>Lystrosaurus maccaigi</i>
Therocephalia	<i>Ericiolacerta parva</i> <i>Moschorhinus kitchingi</i> <i>Olivierosuchus parringtoni</i> <i>Promoschorhynchus platyrhinus</i> <i>Regisaurus jacobi</i> <i>Scaloposaurus constrictus</i> <i>Tetracynodon darti</i>
Cynodontia	<i>Progalesaurus lootsbergensis</i> <i>Galesaurus planiceps</i> <i>Thrinaxodon liorhinus</i> <i>Platycraniellus elegans</i>

Invertebrates	Arthropoda	cf. <i>Gymnostreptus</i>
Plants		<i>Agathoxylon</i> <i>Glossopteris</i> <i>Trizygia speciosum</i> <i>Paracalamites</i>
Trace fossils	Invertebrate	<i>Katbergia</i> <i>Scoyenia</i> <i>Macanopsis</i> <i>Gyrolithes/Daimonelix</i> <i>Cylindricum</i> <i>Planolites</i> <i>Skolithos</i>
	Vertebrate	<i>Thalassinoides (Procolophon)</i> <i>Histioderma (Lystrosaurus)</i> <i>Dicynodontipus</i> <i>Procolophonichnium</i> <i>Rhynchosauroides</i>

Geological description

Thickness of biozone

Maximum thickness is at least 830 m in the southeastern Karoo Basin near Katberg Pass, becoming thinner in both westerly and northerly directions. The biozone varies in thickness from more than 830 m in the Groot Winterberg southwest of Queenstown and approximately 450 m in Lootsberg Pass south of Middelburg, to approximately 120 m at Oliviershoek Pass south of Harrismith and approximately 40 m in the Normandien Pass northeast of Harrismith (Figure 2). At its most westerly occurrence near Nieu Bethesda, Eastern Cape and at its most northerly occurrence at Verkykerskop in the Free State, the top of the biozone is eroded away, but the remnants indicate thicknesses of roughly 120 m and 40 m respectively.

Lithology

The lowermost portion of the *Lystrosaurus declivis* Assemblage Zone comprises the predominantly argillaceous Palingkloof Member of the Balfour Formation and is characterised by massively-bedded maroon and olive-grey siltstone interbedded with relatively few minor thin sandstone sheets with sharp, flat basal and upper contacts. The lower Palingkloof contains tabular sheet sands structured with horizontal to climbing ripple lamination and have distinctive sharp flat basal and upper contacts, the former commonly with sand-filled desiccation polygons and the latter preserving patches of claystone-veneered oscillation ripples. Horizons of rough-surfaced irregularly-shaped calcareous nodules and scattered small spherical glaeboles (possible pisoliths) with internal shrinkage cracks are ubiquitous to these massive mudrock beds. The distinguishing sedimentological features of this facies include the predominance of the dark reddish-brown coloured (2.5 YR 2.5/4) massively bedded silty mudstone. The upper portion of the Palingkloof Member is distinguished from the underlying section by a change in mudrock colour from dark

reddish-brown to a lighter maroon. This facies is characterised by several 1 to 5 m thick regions of alternating 1 to 3 cm thick mudstone-siltstone couplets. Irregularly-shaped calcareous nodules (that often contain fossil bone), scattered small spherical peloids with internal shrinkage cracks, and isolated *Katbergia* and tetrapod burrow casts occur within the siltstone beds.

This unit gradually coarsens upwards into the predominantly arenaceous Katberg Formation and reveals a progressive increase in vertically stacked tabular olive-grey medium-grained sandstone bodies, which are separated by upwardly thinning intervals of blocky weathering light olive grey siltstone and fissile dark red mudstone beds. The thicker channel sandstones commonly display elongate basal scours or gulleys that have eroded into the underlying mudrock and are often filled with lenses of reworked pedogenic nodule conglomerate. The sandstones contain irregular disconformity surfaces that are commonly lined with mudstone clast conglomerate whereas the basal conglomerates consist of mud pebbles, reworked fossil bone fragments and spheroidal pedogenic glauabules commonly showing internal septarian shrinkage cracks (Botha et al. 2020).

Depositional environment

The sequence of *Lystrosaurus declivis* Assemblage zone depositional facies from predominantly red mudrocks with thin sheet sandstones up into a progressively more arenaceous succession dominated by vertically-stacked multi-storey channel sandstones is interpreted as a rapid shift from the high sinuosity meandering channels of the *Daptocephalus* Assemblage Zone below, through low sinuosity anastomosed systems in the lower half of the zone, into a northward prograding braid-plain setting in the upper half along with concomitant climatic drying (Smith 1995, Smith and Botha-Brink 2014).

The silt and sand-filled desiccation cracks and the presence of silt granules in the red mudrocks are interpreted as the first indication of aeolian dust in the depocentre. A loessic contribution to the thick massive silty-mudstone is supported by their uniform massive texture with planar or gently undulating contacts that are commonly veneered with claystone indicative of relatively rapid, episodic sedimentation (Giles et al., 2013).

Weakly developed pedogenesis with textural Bca horizons showing claystone-lined shrink/swell planes and small spherical carbonate nodules are interpreted as immature loessic soils similar to the Triassic loessites described by Chan (1999) from the Ankareh Formation of north-central Utah.

The vertically accreted multi-storied conglomeratic sandstone bodies are similar to the sandy ephemeral stream channel fills described from the mid-Devonian of southern England by Tunbridge (1984). He interpreted them as in-channel deposits of wide, shallow low-sinuosity rivers with a highly fluctuating discharge regime. The presence of numerous spherical pea-sized calcareous pisoliths (or glauabules) with septarian shrinkage cracks in the clast-supported melange of red mudrock pebbles, rolled bone fragments and other pedogenic calcareous nodules indicate that they too are reworked from the alluvium into which the channel has incised. The pisoliths are similar to those described from Quaternary calcretes of western

Australia (Arakel, 1982) and the Indo-Gangetic alluvial plains of India (Khadkikar et al., 1998). In both instances they are formed by the repeated alternation between saturated and dry soil moisture conditions under a warm climate monsoonal rainfall regime. The appearance of similar septarian glauabules in the PTB stratigraphic record in the main Karoo Basin serves to strengthen the sedimentological facies interpretation for warm climatic conditions with highly seasonal rainfall in this part of western Gondwana in the earliest Triassic. Pace et al. (2009) interpreted the pisolitic conglomerates as remnants of completely degraded landscapes.

Boundaries

Lower boundary

Characterised by the first appearance of the dicynodonts *Lystrosaurus declivis* and *Lystrosaurus murrayi*, and the archosauriform *Proterosuchus fergusi*.

Upper boundary

The upper boundary of the *Lystrosaurus declivis* Assemblage Zone is drawn at the first occurrence of the fairly common trirachodontid cynodont *Langbergia* and the medium-sized archosauriform *Garjainia*, defining the base of the *Cynognathus* Assemblage Zone.

Lateral boundaries

Outcrops continuously around the Karoo Basin (Figure 3).

Subdivisions

There are no formal subdivisions within the biozone. However, *Lystrosaurus declivis* and *L. murrayi* become very abundant in the lowermost Katberg Formation, which has been referred to as the *Lystrosaurus* abundant zone (Botha and Smith, 2006), and *Procolophon* dominates the upper third of the Katberg Formation, which has resulted in this region sometimes being referred to as a *Procolophon* abundant zone (e.g. Broom, 1906; Neveling et al., 2004; Botha and Smith, 2006).

Regional aspects

Geographic distribution

The main outcrop of the *Lystrosaurus declivis* Assemblage Zone strata comprises a region of varying thickness that extends from just south of Middelburg in the southeast to Mthatha (previously Umtata) in the southwest in the Eastern Cape Province northward through the western Kwa-Zulu Natal Province and through the eastern Free State Province to Harrismith in the northeast (Figure 3).

Lateral variation

The relative abundance and diversity of the *Lystrosaurus declivis* assemblage is constant throughout the basin. The only



Figure 3. Distribution of the *Lystrosaurus declivis* Assemblage Zone (green) in the Beaufort Group (yellow). Type locality (see Figure 4) is indicated by open square.

discernible variation is in the maximum size of *L. declivis* that appears to gain larger maximum body sizes in the northern and eastern parts of the basin compared to further south.

Correlation

The *Lystrosaurus declivis* Assemblage Zone is equivalent to the Lootsbergian land-vertebrate faunachron of Lucas (1998). These vertebrate-defined units correlate chronostratigraphically with assemblages of the lower Fremouw Formation of Antarctica (Kitching et al., 1972), the Sanga do Cabral Formation, Paraná Basin of Brazil (based on the presence of *Procolophon*) (Barbarena et al., 1981; Souto-Rieiro and Holz, 1998; Abdala et al., 2002), and the Panchet Formation, Damodar Basin of India (Bandyopadhyay et al., 2002). The latter Panchet records also preserve reliable age controls based on marine-nonmarine interbeds.

Other age-equivalent assemblages may include LAZ-like vertebrates at higher taxonomic-levels, but present unique species endemic to those areas, and have yet to produce strong

overlap with the South African species from paleontological collecting. These include the Vokhmian and Rybinskian horizons of the Vetlugian Series in the South Urals Basin of Russia (Benton et al., 2004) and the lower Jiucaiyuan Formation, Junggar Basin of northwestern China (Cheng, 1993).

Lastly, other continental assemblages, as well as marine-nonmarine transitional assemblages, are known that include important invertebrate and macro- and micro-floral records, but lack stratigraphically informative vertebrates, making links to the Karoo Basin record more challenging. These include: the Kockatea Formation, Perth Basin, Blina Formation, Fitzroy Basin, Gosford and Terrigal formations, Sydney Basin, the Sagittarius Sandstone and Arcadia formations, Bowen Basin of Australia (Ochev and Shishkin, 1989; Michaelsen, 2002), and the Wordie Creek Formation of eastern Greenland (Lucas, 1998).

Age

The *Lystrosaurus declivis* Assemblage Zone is generally considered to be Early Triassic (Induan to early Olenekian)

based on global correlations with fossil plants and vertebrates (Lucas, 1998). Recent studies suggest that the upper Palingkloof Member is not older than 252.24 \pm 0.1 (Gastaldo et al., 2020) and may be as young as 251.7 \pm 0.3 (Botha et al., 2020). This likely places the base of the *Lystrosaurus declivis* Assemblage Zone within the basal Triassic as in the *Lystrosaurus murrayi*-dominated fauna of the Panchet beds in India (Tripathi and Satsangi, 1963).

Type locality

Groenewald and Kitching (1995) erected the holostratotype of the biozone along highway N9 through Lootsberg Pass and the adjacent area, between Graaff-Reinet and Middelburg, Eastern Cape Province. Approximately 450 m of the lower part of the zone is exposed in this area, but the uppermost Katberg Formation is not exposed here and importantly, relatively few fossils have been found in the road cutting and adjacent area. Thus, we introduce a new type locality for the *Lystrosaurus declivis* Assemblage Zone, a well-known locality that encompasses exposures on three adjoining farms, namely Bethel 763, Heldenmoed 677 and Donald 207 (commonly referred to

as Fairydale) in the Xhariep District 30 km northeast of the town Bethulie. We name the locality Bethel for brevity (GPS co-ordinates from the top of Swartberg Hill on Bethel 763 on 1:50 000 map 3026AD Tampusfontein: 30° 25'12.43"S 26° 15' 30.42"E, taken from Google Earth, 2018) and it is selected because of the abundance and diversity (at least 18 species) of tetrapod fossils that it has produced over the years, including the three index taxa and covers most of the zone from the base to the top of the Swartberg member (Figure 4).

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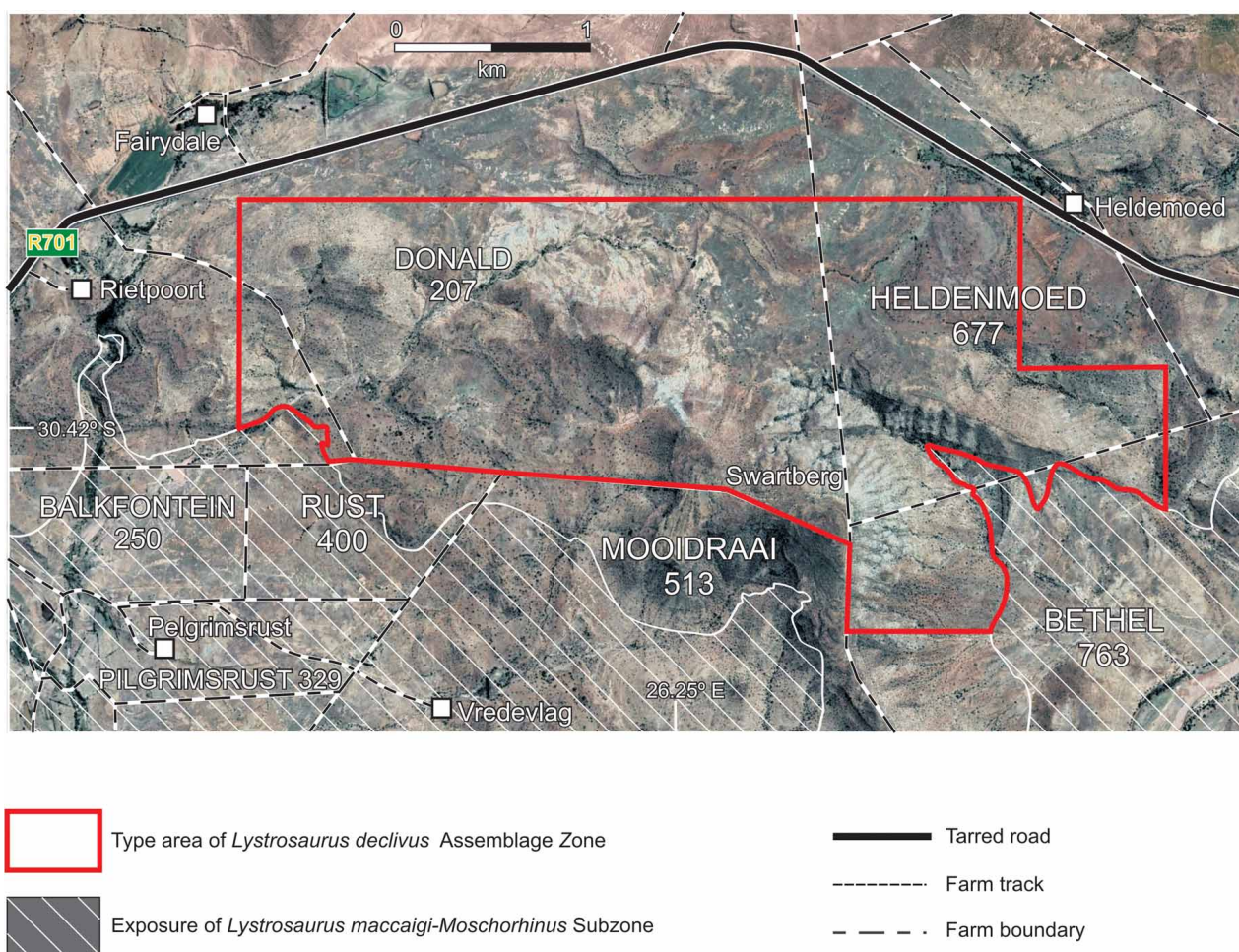


Figure 4. Map of the Type locality of the *Lystrosaurus declivis* Assemblage Zone on the farms Bethel, Heldenmoed and Donald in the Smithfield District, Eastern Cape, South Africa.

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