



# Biostratigraphy of the *Daptocephalus* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa

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## Abstract

The name *Daptocephalus* Assemblage Zone (DaAZ) is re-instated for vertebrate assemblages of the uppermost Permian strata (Balfour, upper Teekloof, and Normandien formations) of South Africa's main Karoo Basin (MKB). This involved taxonomic revision of the dicynodontoid "*Dicynodon*" *sensu lato*, reviving *Daptocephalus leoniceps*, and revising the stratigraphic ranges of co-occurring index taxa (*Theriongnathus microps*, *Procynosuchus delabarpeae*) of the *Dicynodon* Assemblage Zone (DiAZ) as it was known. This work has demonstrated the appearance of index taxa below the stratigraphically defined DiAZ. Moreover, the first appearance of *Lystrosaurus maccaigi* and *Moschorbinus kitchingi* in the upper reaches of the biozone calls for the establishment of a two-fold subdivision of the current DaAZ into lower (*Dicynodon-Theriongnathus*) and upper (*Lystrosaurus maccaigi-Moschorbinus*) subzones. The biostratigraphic utility of *Daptocephalus* and other South African dicynodontoids outside of the MKB is limited due to basinal endemism at the species level and varying temporal ranges of dicynodontoids globally. Accordingly, their use is recommended only for correlation within the Karoo Basin at this stage.

## Name

*Daptocephalus* Assemblage Zone.

## Proposer of name

First proposed by Kitching (1977) and revised by Viglietti et al. (2016).

## Stratigraphic position

### **Biostratigraphic position**

Overlies the *Cistecephalus* Assemblage Zone and underlies the *Lystrosaurus declivis* Assemblage Zone.

## **Lithostratigraphic position**

West of 24° east this biostratigraphic subdivision correlates to the upper part of the Teekloof Formation (Steenkampsvlakte and Javanerskop members) (Viglietti et al., 2017a). Between 24 and 25° east the biozone correlates to the Balfour Formation, extending from the uppermost Oudeberg Member through the Elandsberg to the lower Palingkloof Member. East of 25° east the biozone correlates to the Normandien Formation (Catuneanu et al., 1998).

## **Derivation of name**

Derived from a common large dicynodontoid *Daptocephalus leoniceps* which first appears in, and its stratigraphic range is confined to, this biozone. (Figure 1)

## Historical background

Owen (1845) first described *Dicynodon* from a set of fossil skulls collected by Andrew Geddes Bain during his work as a road engineer near the Fort Beaufort area of the Karoo Basin (Bain, 1845, 1856). These were also some of the earliest records of vertebrate fossils from the Karoo Basin of South Africa, and they were made the type specimens of *Dicynodon lacerticeps*. Later Van Hoepen (1934) recognized that the larger *Dicynodon* specimens were a new species and named these *Daptocephalus leoniceps*.

Kitching (1977) also treated *Daptocephalus* as valid and monotypic, later using this species to erect the terminal Permian *Daptocephalus* Range Zone for stratigraphic levels above the *Cistecephalus* Range Zone and below the *Lystrosaurus* Range Zone of Broom (1906). However, soon after, Cluver and Hotton (1981) proposed that *Daptocephalus leoniceps* is in fact a junior synonym of *Dicynodon lacerticeps* and subsequent studies by Brink (1986) and King (1988) generally supported this finding.

As a result, Kitching's '*Daptocephalus* Range Zone' was renamed the *Dicynodon* Assemblage Zone (DiAZ) by Keyser and Smith (1979) who introduced the assemblage zone concept to the Beaufort Group. Additionally, Keyser (1979) later adopted a scheme whereby two genera were used to define each assemblage which was ratified by SACS (1980) to conform to the International Sub-Commission on Stratigraphic Classification (Hedberg, 1976) regulations on stratigraphic nomenclature. Thus, the DiAZ became the *Dicynodon lacerticeps-Whaitsia* Assemblage Zone for a brief period, but updated recommendations by the ISSC (Salvador, 1994) meant Beaufort Group assemblage zones should revert to the use of a single genus in the name for the zone. Therefore, in the most recent publication on the status of the Karoo biostratigraphic zones (Rubidge et al., 1995; Kitching, 1995) the *Dicynodon-Whaitsia* Assemblage Zone reverted to the *Dicynodon* Assemblage Zone.

Subsequently, Kammerer et al. (2011) undertook a comprehensive taxonomic revision of "*Dicynodon*" sensu lato, reviving *Daptocephalus leoniceps*, and noted the latter might be a more appropriate index fossil for the DiAZ than *Dicynodon*. The previous definition of the DiAZ was also problematic because all three index species (*Dicynodon lacerticeps*, *Theriongnathus microps*, and *Procynosuchus delabarpeae*) are reported below the traditionally recognized base of the DiAZ. *Dicynodon* is considered to first appear in *Cistecephalus* Assemblage Zone (CAZ) strata (Angielczyk and Kurkin, 2003; Kammerer et al., 2011), as are *Theriongnathus* and *Procynosuchus* (Huttenlocker et al., 2011; Huttenlocker, 2014). The description of SAM-PK-K10138 as a new cynodont taxon (*Abdaladon diastematicus*; Kammerer, 2016a) removes *Procynosuchus* from the *Endothiodon* Assemblage Zone (previously the *Tropidostoma* Assemblage Zone; Day and Smith, this volume).

Given these ranges, the first co-occurrence of these species would be in rocks traditionally assigned to the CAZ, requiring a redefinition of the zone. A similar problem occurs at the top of the zone, where *Lystrosaurus maccaigi* first appears in Upper Permian rocks that are below the traditional lower boundary of

the *Lystrosaurus* Assemblage Zone (LAZ) just after the Permian-Triassic boundary (PTB) (Botha and Smith, 2007). Thus, it was proposed by Viglietti et al. (2016) that the *Daptocephalus* Assemblage Zone, with the original index fossil designated by Kitching (1977) be restored (Figure 1). In the light of taxonomic and stratigraphic range refinements, two subdivisions to the DaAZ are recommended.

## Palaeontology

### Description of Assemblage Zone

An assemblage zone characterised by the co-occurrence of the dicynodontoid *Daptocephalus leoniceps*, the therocephalian *Theriongnathus microps*, and the cynodont *Procynosuchus delabarpeae*. The presence of two distinct faunal assemblages warrants the formal distinction of two subzones. The lower *Daptocephalus* Assemblage Zone (DaAZ) comprises the *Dicynodon-Theriongnathus* Subzone (in co-occurrence with *Daptocephalus*) whereas the upper DaAZ is defined by the *Lystrosaurus maccaigi* – *Moschorhinus kitchingi* Subzone. The upper subzone is introduced to highlight the appearance of *L. maccaigi* below the overlying *Lystrosaurus declivis* Assemblage Zone boundary and its defining taxa are therefore *L. maccaigi*, *Daptocephalus* and *Moschorhinus*. Moreover, the appearance of *L. maccaigi* immediately precedes a significant a turnover event that resulted in the disappearance of *Theriongnathus*, *Procynosuchus*, and a significant drop in abundance and diversity of *Daptocephalus* Assemblage Zone fauna (Viglietti et al., 2016, 2018). These two subdivisions and their definitions will now be outlined.

### *Dicynodon* – *Theriongnathus* Subzone

#### Proposer of name

This name is here formally proposed for the first time.

#### Stratigraphic position

##### Biostratigraphic position

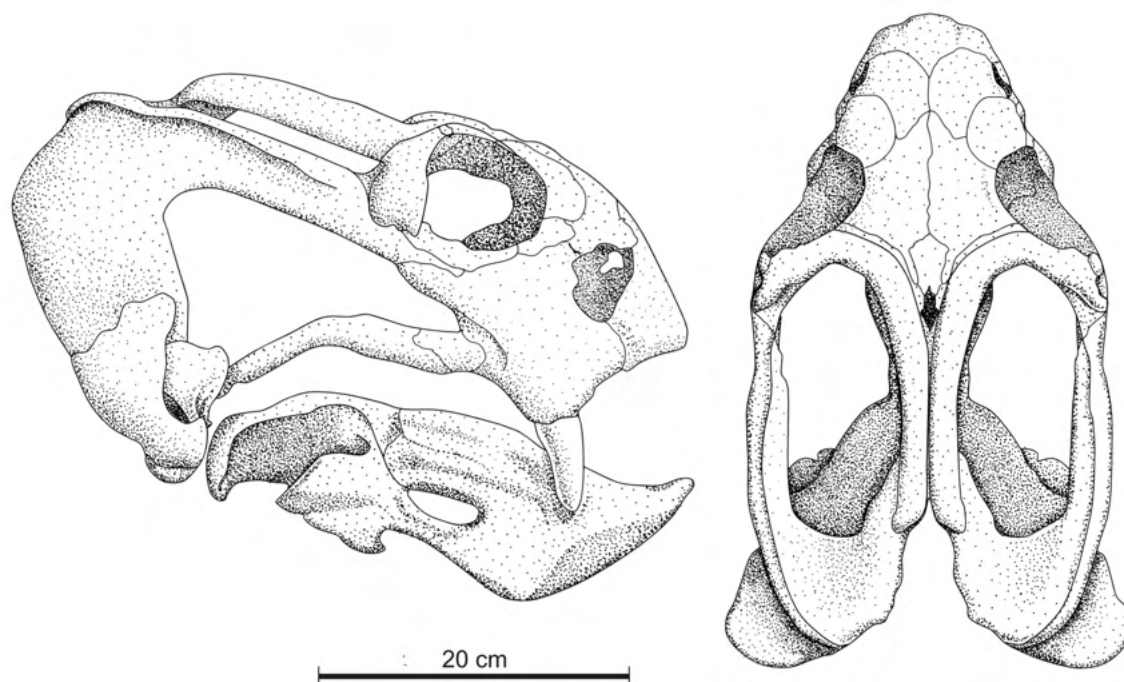
Overlies the *Cistecephalus* Assemblage Zone and underlies the *Lystrosaurus maccaigi-Moschorhinus* Subzone (upper *Daptocephalus* Assemblage Zone).

##### Lithostratigraphic position

West of 24° east this biostratigraphic subdivision correlates to the upper Teekloof Formation (Steenkampsvlakte and Javanerskop members) (Viglietti et al., 2017b). Between 24 and 25° east the biozone correlates to the Balfour Formation, extending from the uppermost Oudeberg Member into the Daggaboersnek and Ripplemead members (Viglietti et al., 2017a) (Figure 2).

#### Derivation of name

It is derived from two abundant vertebrate fossils in this stratigraphic interval of the *Daptocephalus* Assemblage Zone, which are *Dicynodon* and *Theriongnathus* (Figure 3).



**Figure 1.** Lateral and dorsal views of skull of the dicynodont *Daptocephalus leoniceps*, the main biozone defining fossil.

### Historical background

This interval once formed part of Broom's (1906) *Cistecephalus* Assemblage Zone. After extensive field observations and collecting, Kitching (1970, 1977) revised the *Cistecephalus* Range Zone and introduced the new *Daptocephalus* Range Zone to fill the biostratigraphic gap between the *Cistecephalus* and *Lystrosaurus* range zones. In his full description of the new biozone Kitching (1977) used the range of *Daptocephalus* as the index fossil for his original 'Daptocephalus Range Zone'. This biozone was subsequently redefined as the *Dicynodon* Assemblage Zone by Keyser and Smith (1979) because of the then accepted, and later published synonymy of *Daptocephalus leoniceps* with *Dicynodon lacerticeps* (Cluver and Hotton, 1981). This was formally accepted by SACS as the *Dicynodon-Theriognathus* Assemblage Zone (Keyser 1979) to be later shortened to *Dicynodon* Assemblage Zone (Kitching, 1995).

Recent fieldwork conducted by Viglietti (2016), and Karoo Collections Database investigations (Viglietti et al., 2016) has demonstrated distinct faunal communities present in the DaAZ that are stratigraphically separate. Thus, the lower DaAZ subzone, which comprises a faunal assemblage different to the upper DaAZ, is introduced as the *Dicynodon-Theriognathus* Subzone.

### Palaeontology

#### Description of subzone

The *Dicynodon-Theriognathus* Subzone is characterised by the stratigraphic co-occurrence of *Dicynodon* and *Theriognathus* with *Daptocephalus*.

#### Taponomic notes on fossil occurrences

Vertebrate fossils are encountered in the finer mudrock and siltstone deposits as isolated skulls, or articulated skeletons. Most (but not all) vertebrate fossils are encased in calcareous nodule material. Locally common, particularly in the Daggaboersnek and lower Ripplemead member (Tordiffe's 1978 Barberskrans Member) are plant fossils, stem and leaf impressions of *Glossopteris* and sphenophytes (Johnson 1976; Tordiffe, 1978; Johnson et al., 2006). Fossil fish are also abundant in the lower Ripplemead member in the Nieu Bethesda area, and these fish have been described in detail by Bender (2001, 2002).

#### List of fossils

Figure 4 delineates ranges of vertebrate genera, which are shown in the range chart in metre notation in the generalized and simplified lithological section measured at the type locality of the *Dicynodon-Theriognathus* Subzone (Viglietti, 2016). The list of fossil taxa that occur in the *Dicynodon-Theriognathus* Subzone was compiled using the most recent taxonomic assignments (Rossouw, 1970; Anderson, 1975; Gow, 1972; Bamford, 2000, 2004; Bender, 2000, 2001, 2002; Rubidge and Sidor, 2002; Sidor, 2003; Jalil and Janvier, 2005; Smith and Botha, 2005; Sidor and Rubidge, 2006; Cisneros et al., 2008; Fröbisch and Reisz, 2008; Huttenlocker and Abdala, 2015; Kammerer et al., 2011, 2015, 2016; Smith and Botha-Brink, 2014; Kammerer, 2015, 2016b, 2017; Viglietti et al., 2016, 2018; Marsicano et al., 2017).

Vertebrates		Cynodontia	<i>Cynosaurus suppostus</i>
Pisces	<i>Atherstonia scutata</i>		<i>Nanictosaurus kitchingi</i>
	<i>Atherstonia minor</i>		<i>Procyonosuchus delabarpeae</i>
	<i>Atherstonia seeleyi</i>	Invertebrates	
	<i>Bethesdaictys kitchingi</i>	Mollusca	<i>Palaeonodonta</i> sp.
	<i>Blourugia seeleyi</i>		
	<i>Elonictys whaitsi</i>	Plants Mosses	<i>Buthelezi</i> sp.
	<i>Kompasia delabarpi</i>	Equisetales	<i>Sphenophyllum</i> sp.
	<i>Namaictys digitata</i>		<i>Raniganjia</i> sp.
	<i>Pteronisculus meiringi</i>		<i>Phyllotheba</i> sp.
Amphibia	<i>Laccosaurus watstoni</i>		<i>Schizoneura</i> sp.
	<i>Rhinesuchus whaitsi</i>	Ferns	<i>Sphenopteris</i> sp.
Amniota		Cordaitales	<i>Noeggerathiopsis</i> sp.
Parareptilia	<i>Anthodon gregoryi</i>	Wood	<i>Australoxylon</i> sp.
	<i>Milleretta rubidgei</i>		<i>Prototawoxylon</i> sp.
	<i>Milleropsis pricei</i>	Trace fossils	
	<i>Millerosaurus nuffieldi</i>	Invertebrate	<i>Planolites</i> sp.
	<i>Millerosaurus ornatus</i>		<i>Diplichnites</i> sp.
	<i>Nanoparia pricei</i>		
	<i>Owenetta rubidgei</i>		
	<i>Pareiasaurus serridens</i>		
Eureptilia	<i>Youngina capensis</i>		
	<i>Saurosternon bainii</i>		
Synapsida			
Therapsida			
Biarmosuchia	<i>Burnetia mirabilis</i>		
Anomodontia	<i>Aulacephalodon baini</i>		
	<i>Basilodon woodwardi</i>		
	<i>Compsodon helmoedi</i>		
	<i>Daptocephalus leoniceps</i>		
	<i>Dicynodon lacerticeps</i>		
	<i>Dicynodontoides recurvidens</i>		
	<i>Digalodon rubidgei</i>		
	<i>Diictodon feliceps</i>		
	<i>Dinanomodon gilli</i>		
	<i>Emydops arctatus</i>		
	<i>Emydops oweni</i>		
	<i>Emydorhinus sciuroides</i>		
	<i>Kitchingamodon crassus</i>		
	<i>Oudenodon baini</i>		
	<i>Pristerodon mackayi</i>		
	<i>Rbachiocephalus magnus</i>		
	<i>Pelanomodon moschops</i>		
Gorgonopsia	<i>Aelurognathus tigriceps</i>		
	<i>Arctognathus curvimola</i>		
	<i>Clelandina rubidgei</i>		
	<i>Cynosaurus longiceps</i>		
	<i>Dinogorgon rubidgei</i>		
	<i>Gorgonops</i> sp.		
	<i>Lycenops</i> sp.		
	<i>Rubidgea atrox</i>		
Therocephalia	<i>Akidnognathus parvus</i>		
	<i>Cerdosuchoides burgheri</i>		
	<i>Ictidosuchoides longiceps</i>		
	<i>Ictidochampsia platyceps</i>		
	<i>Lycideops longiceps</i>		
	<i>Theriognathus microps</i>		

### Geological description

#### Thickness

The *Daptocephalus* Assemblage Zone is laterally variable in thickness. In the southern portion of the basin, the DaAZ is believed to reach a thickness of approximately 500 m, but this is not the total thickness of the Balfour Formation (see boundaries section). In the northern extent of the biozone, significant thinning of the section is documented (Kitching, 1977; Viglietti et al., 2016, 2017b) and the biozone is reduced to a thickness of approximately 90 m. West of 24° east, in the upper Teekloof Formation the DaAZ strata (Steenkampsvlakte and Javanerskop members) reach a maximum thickness of 235 m (Viglietti et al., 2017a). The current absence of *Lystrosaurus maccaigi* west of 24° east suggests that either the upper DaAZ has been eroded away or that strata equivalent to this portion of the assemblage zone were never deposited in this part of the basin. The thickness of the *Dicynodon-Theriognathus* Subzone is greatest in the southern part of the basin (Viglietti et al., 2017a) where it is at least 330 m thick in the Balfour Formation (Eastern Cape). In the northern parts of the basin, the total thickness of the *Dicynodon-Theriognathus* Subzone is greatly reduced to approximately 30 m in the Gariep Dam area in the southern Free State Province. Further north the *Dicynodon-Theriognathus* Subzone does not occur in the main Karoo Basin.

#### Lithology

Sandstones form a minor component of the lithology of the *Dicynodon-Theriognathus* Subzone (20 to 25%). In the Daggaboersnek Member, the maximum thickness for individual sandstones is 3 m and average thickness is 1.5 m. Sandstones are fine-grained, arkosic in composition and mainly comprise trough and planar crossbedding with ripple laminated units on sandstone tops. Mudstone and siltstone dominate the *Dicynodon-Theriognathus* Subzone (75 to 80%) with the average thickness of these units reaching 20 m. Thinly bedded, varve-like tabular green and minor red mudstone beds are also



encountered, interbedded with thin wave-rippled siltstone and sandstone beds. The top of the *Dicynodon-Theriongnathus* Subzone incorporates most of the arenaceous Ripplemead member.

#### Depositional history

Four depositional facies have been documented for the *Dicynodon-Theriongnathus* Subzone (Viglietti et al., 2018). The sandstone dominated units were either deposited in confined channels or unconfined crevasse splay deposits. The channel sandstones demonstrate fluctuating and waning energy discharge regimes which is likely the result of seasonal rainfall (Viglietti et al., 2018). Channel deposits comprise different architectural elements that show channel sinuosity was variable throughout the *Daptocephalus* Assemblage Zone (Viglietti et al., 2018). Lower sinuosity units tend to coincide with the appearance of subaerial unconformities that are likely linked to tectonic activity (Viglietti et al., 2017b, 2018). Mature palaeosols are rare in the *Dicynodon-*

*Theriongnathus* Subzone which implies that depositional rates were high in the floodplain facies deposits, comprising mainly mudstone and siltstone units. Lacustrine facies are confined to the *Dicynodon-Theriongnathus* Subzone and are most common in the Cradock and Bedford area in the Daggaboersnek Member (Viglietti, 2016; Viglietti et al., 2018). Lack of pedogenic nodules, and laterally extensive varve-like mudstone and sandstone laminations are indicators of lacustrine conditions (Reading, 1978; Boggs, 2006). In the *Dicynodon-Theriongnathus* Subzone, these facies contain plant and rare bivalve fossils.

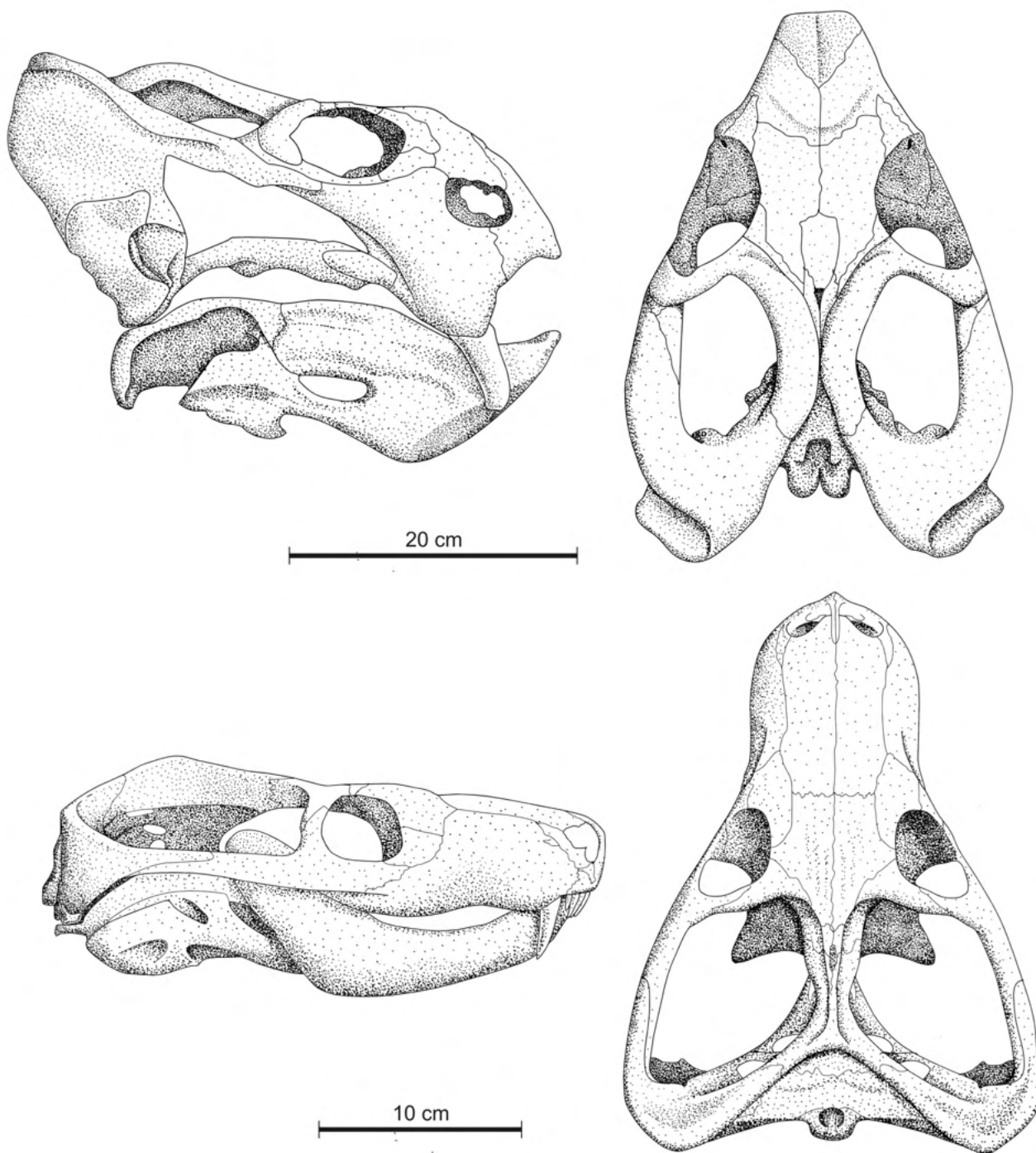
#### Boundaries

##### Lower boundary

The *Dicynodon-Theriongnathus* Subzone is characterized by the first appearance of *Daptocephalus leoniceps* in stratigraphic association with *Dicynodon lacerticeps* and *Theriongnathus microps*. The lower boundary has previously been difficult to



**Figure 2.** Distribution of the *Daptocephalus* Assemblage Zone (blue) within the Beaufort Group (yellow) with the lower *Dicynodon-Theriongnathus* Subzone (dotted) and the upper *Lystrosaurus maccaigi-Moschorhinus* Subzone (not dotted). Location of type localities for each subzone are indicated; *Dicynodon-Theriongnathus* Subzone (crossed square) and *Lystrosaurus maccaigi-Moschorhinus* Subzone (open square).



**Figure 3.** Skulls of the biozone defining fossils of the Dicycnodon-Theriognathus Subzone in lateral and dorsal views. *Dicycnodon lacerticeps* (top), *Theriognathus microps* (bottom).

define lithologically due to the original definitions of the underlying *Cistecephalus* Assemblage Zone (Kitching, 1970, 1977). At one point, parts of Kitching's *Endothiodon*, *Daptocephalus* and Kitching's (1995) *Dicycnodon* Assemblage Zones formed part of the *Cistecephalus* Assemblage Zone (Smith and Keyser, 1995).

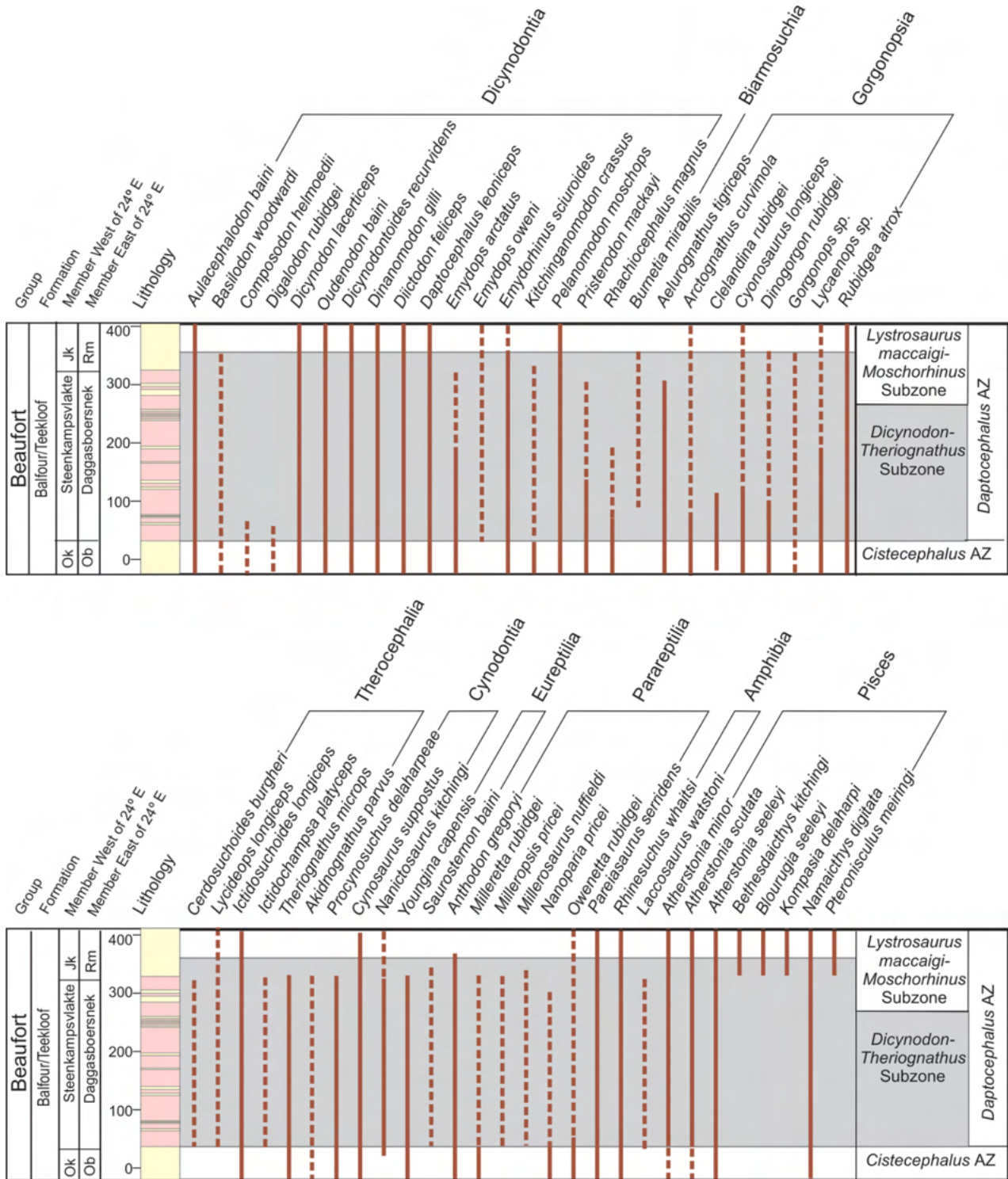
The top of Kitching's (1977) '*Cistecephalus* band' in the uppermost *Cistecephalus* Assemblage Zone of (Smith and Keyser

1995) was used to define the *Cistecephalus-Daptocephalus* Assemblage Zone boundary in the Graaff-Reinet area. This band lies within the lower Daggaboersnek Member (Balfour Formation), although its lateral and stratigraphic continuity has still not been clarified (Smith and Keyser, 1995). This band of fine silt- and mudstone can be observed on a small hillside in the lower Daggaboersnek Member on the Nieu Bethesda road immediately adjacent to the entrance to Wellwood Farm near

Graaff-Reinet (Kitching, 1977), and at the CAZ type locality (Steilkrans 96, now renamed Riverdene farm).

Viglietti et al., (2016) identified *Daptocephalus*, *Dicynodon*, *Theriognathus*, and *Procynosuchus* below this interval.

Accordingly, it is proposed that the lower boundary of the *Dicynodon-Theriognathus* Subzone extends below Kitching's (1977) 'Cistecephalus Band', but further fieldwork is required to confirm this.



**Figure 4.** Stratigraphic section with ranges of taxa of the Dicynodon-Theriognathus Subzone. The simplified lithological section is based on the vertical section logged at the Type locality of the Dicynodon-Theriognathus Subzone (Viglietti 2016, see Figure 5). Ok=Oukloof, Ob=Oudeberg, Jk=Javanerskop, Rm=Ripplemead. Scale in metres.



### *Upper boundary*

The upper boundary of the *Dicynodon-Therapsid* Subzone is characterised by the first appearance of *Lystrosaurus maccaigi* and *Moschorhinus kitchingi* in the uppermost Ripplemead member of the Balfour Formation.

### *Lateral boundaries*

The *Dicynodon-Therapsid* Subzone strata outcrop between 24 and 25° east (lower Balfour Formation) and west of 24° east (upper Teekloof Formation). Formation name distinctions have been made due to lateral change in lithology, and difficulty in tracing out distinct formations over hundreds of kilometers.

### *Subdivisions*

None.

### **Regional aspects**

#### *Geographic distribution*

The *Dicynodon-Therapsid* Subzone is confined to the southerly portion of the outcrop area of the DaAZ. It outcrops in the Nuweveld escarpment north of Beaufort West and south of Fraserburg. To the southeast, it is well exposed in the Winterberg and Sneeuwberg ranges near Cradock, Graaff-Reinet, and Nieu Bethesda. To the north, it thins rapidly in the southern Free State Province, and faunal assemblages suggest the subzone reaches the Jagersfontein area north of Gariep Dam (Viglietti et al., 2017a). However, all taxa reported from the Jagersfontein area are shared with the upper *Cistecephalus* Assemblage Zone (Groenewald et al., 2019), so further work is required to confirm this (Figure 2).

### **Lateral and vertical variation**

Lateral variation in thickness and lithology is documented for the *Dicynodon-Therapsid* Subzone. East of 24° east is an increase in lacustrine facies associations which are absent in the overlying *Lystrosaurus maccaigi-Therapsid* Subzone.

### **Correlation**

In southern Africa and globally, few definitive *Dicynodon-Therapsid* Subzone strata have been identified outside of the MKB. Currently Karoo-aged basins of Africa including the Luangwa (Zambia), Mid-Zambezi (Zambia and Zimbabwe) and Ruhuhu basins (Tanzania) contain tetrapod fossil assemblages that allows correlation with the *Tapinocephalus*, *Cistecephalus*, and *Lystrosaurus* Assemblage Zones. (Johnson et al., 1996; Sidor et al., 2014; Angielczyk et al., 2014a,b). However, recent fieldwork in the Luangwa Basin has yielded *Therapsid*, *Dicynodon*, and *Daptocephalus*, which if confirmed to be the same species as the MKB would allow for the first correlation to the *Dicynodon-Therapsid* Subzone outside of the MKB (B. Peacock., pers. observation, 2019).

### **Age**

Radiometric dates by Rubidge et al., (2013) of ~255.2 Ma place the Lower DaAZ in the Changhsingian of the late Permian Lopingian epoch.

### **Type locality**

SACS (1980) designated Platberg on Doornplaats farm (Farm 127) as the type locality for the original *Dicynodon* Assemblage Zone (Kitching, 1995). This type locality will be retained for the *Dicynodon-Therapsid* Subzone (Figure 5).

### ***Lystrosaurus maccaigi-Moschorhinus* Subzone**

#### **Proposer of name**

This name is here formally proposed for the first time.

#### **Stratigraphic position**

##### *Biostratigraphic*

Overlies the *Dicynodon-Therapsid* Subzone and underlies the *Lystrosaurus declivis* Assemblage Zone.

##### *Lithostratigraphic*

Unlike the underlying *Dicynodon-Therapsid* Subzone, the *L. maccaigi-Moschorhinus* Subzone does not occur west of 24° east in the Teekloof Formation (Viglietti et al., 2017a). However, it does occur between 24° and 25° east, correlating to the upper Balfour Formation including the uppermost Ripplemead, Elandsberg, and lowermost Palingkloof members. It has also been correlated to the Normandien Formation in the northeast of the basin (Catuneanu et al., 2005; Viglietti et al., 2017a) (Figure 2). In addition, the informal Escourt formation of Kwa-Zulu Natal Province has now been incorporated into the Normandien Formation, and the coal-bearing Emakwezini Formation of northern Kwa-Zulu Natal has also been considered Upper Permian in age (Bordy and Prevec, 2008).

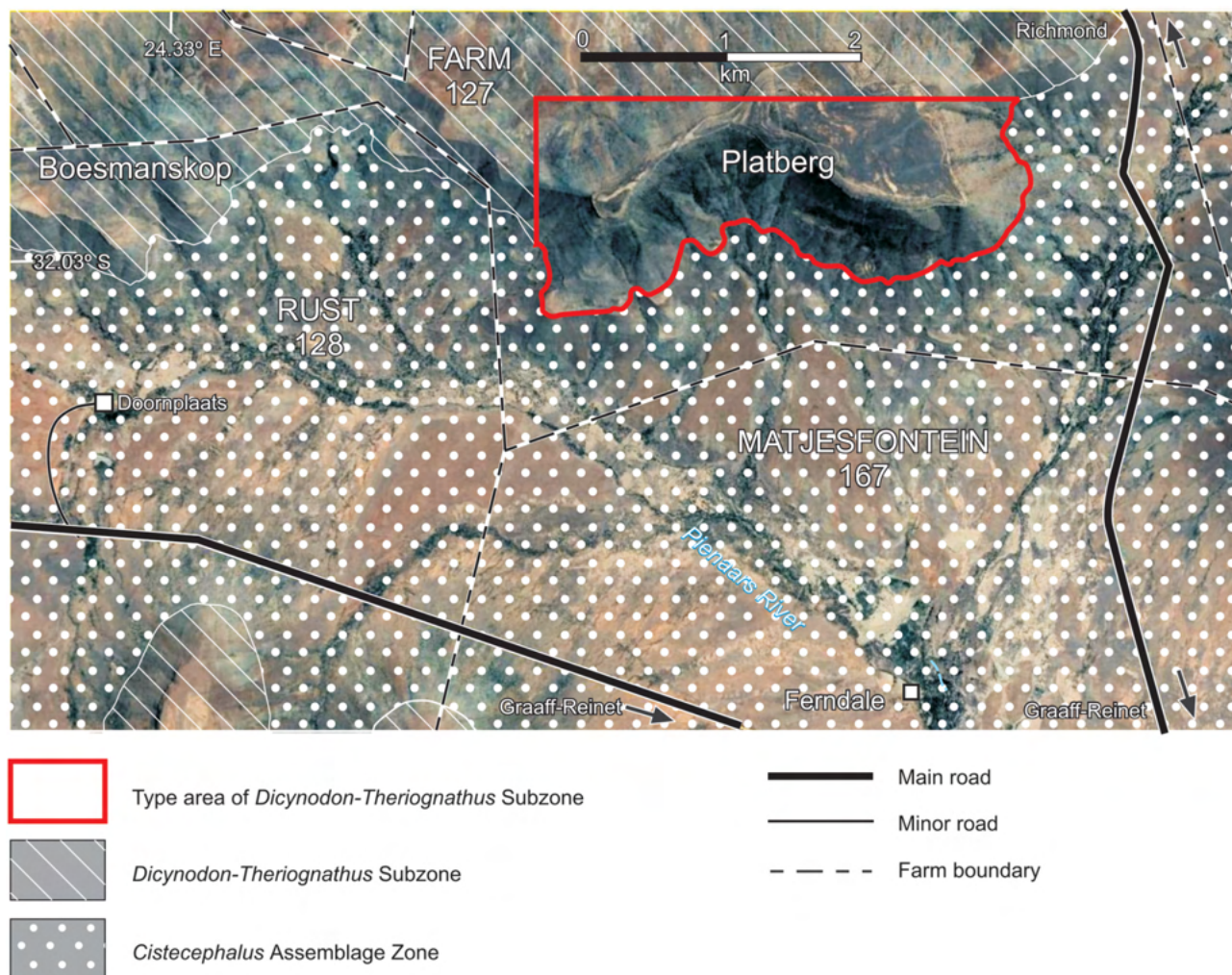
#### **Derivation of name**

The name is derived from two relatively abundant vertebrate fossil taxa that co-occur in the *L. maccaigi-Moschorhinus* Subzone, namely the dicynodont *Lystrosaurus maccaigi* and the therocephalian *Moschorhinus kitchingi* (Figure 6).

#### **Historical background**

*Lystrosaurus maccaigi* first appears in Upper Permian below the traditional lower boundary of the *Lystrosaurus* Assemblage Zone (LAZ) (Botha and Smith, 2007). Recent fieldwork conducted on by Viglietti (2016), and investigations into the Karoo Collections Database Viglietti et al. (2016, 2018) identified a distinct faunal community in the Upper Permian rocks that introduces *Moschorhinus kitchingi* as a co-occurring therocephalian. Therefore *L. maccaigi-Moschorhinus* Subzone is here proposed for the upper DaAZ.





**Figure 5.** Map of the Type locality of the Dicynodon-Theriognathus Subzone on Doornplaats farm (Farm 127), on the Murraysburg road, 30 km north of Graaff-Reinet, Eastern Cape Province.

### Palaeontology

#### Description of subzone

The *L. maccaigi-Moschorbinus* Subzone is characterized by the co-occurrence of *L. maccaigi* and *Moschorbinus kitchingi*.

#### Taphonomic notes on fossil occurrences

Well preserved vertebrate fossils occur in the mudrock-dominated overbank facies associations, and are usually found as isolated skulls, or articulated skeletons in association with mature pedogenic horizons and calcareous nodules. In the *L. maccaigi-Moschorbinus* Subzone large (cobble to boulder sized) brown-weathering nodules enclose many of the fossil bones (Viglietti et al., 2018). Fossils not encased in nodules are often fractured and compressed. Vertebrate fossils are also found in proximal channel, unconfined channel, and channelized facies associations (i.e. coarse siltstone, sandstone) mostly as fragmentary material in channel lag deposits, or isolated skeletal elements. Rarely, fossil plant beds comprising leaf, stem, wood,

fruiting body impressions, as well as insect impressions can be found in siltstone and fine sandstones in close association to confined channelized facies associations.

#### List of fossils

Figure 7 delineates ranges of vertebrate genera, which are shown in the range chart in meter notation in the generalized and simplified lithological section from the type locality of the *Lystrosaurus maccaigi-Moschorbinus* Subzone. The list of fossil taxa that occur in the *L. maccaigi-Moschorbinus* Subzone was compiled using the most recent taxonomic assignments: (Broom and Martins, 1913; Rossouw, 1970; Anderson, 1975; Bamford, 2000, 2004; Bender, 2000, 2001, 2002; Maisch, 2002; Jalil and Janvier, 2005; Smith and Botha, 2005; Botha and Smith, 2006, 2007; Smith et al., 2006; Fröbisch and Reisz, 2008; Kammerer et al., 2011, 2015, 2016; Smith and Botha-Brink, 2014; Kammerer, 2015, 2016b, 2017, 2019; Marsicano et al., 2017; Abdala et al., 2019).

		<b>Geological description</b>
Vertebrates		<i>Thickness</i>
Pisces	<i>Atherstonia scutata</i> <i>Atherstonia minor</i> <i>Atherstonia seeleyi</i> <i>Namaichthys digitata</i>	<p>The biozone reaches its maximum thickness in the south-central outcrop area near Graaff-Reinet and Cradock, where it attains a total thickness of ~120 m. In the northern parts of the basin, the total thickness of the DaAZ is greatly reduced (Kitching, 1970; Viglietti et al., 2017a) and the maximum thickness of the <i>L. maccaigi-Moschorbinus</i> Subzone is only 60 m in the Gariep Dam area of the southern Free State Province. In the northeastern portion of the basin the total thickness of the upper DaAZ is unknown, as the correlations to the south and west are currently poorly constrained (Groenewald, 1989, 1990; Catuneanu et al., 1998, 2005).</p>
Amphibia	<i>Rhinesuchus</i> sp. <i>Uranocentron senekalensis</i>	
Amniota		
Parareptilia	<i>Owenetta rubidgei</i> <i>Pareiasaurus serridens</i> <i>Spondylolestes rubidgei</i>	
Synapsida		
Therapsida		
Biarmosuchia	<i>Ictidorbinus martinsi</i>	
Anomodontia	<i>Aulacephalodon baini</i> <i>Daptocephalus leoniceps</i> <i>Dicynodon lacerticeps</i> <i>Dicynodontoides recurvidens</i> <i>Diictodon feliceps</i> <i>Dinanomodon gilli</i> <i>Emydops oweni</i> <i>Emydorbinus sciuroides</i> <i>Kwazulusaurus sbakai</i> <i>Lystrosaurus curvatus</i> <i>Lystrosaurus maccaigi</i> <i>Oudenodon baini</i> <i>Pelanomodon moschops</i> <i>Tbliptosaurus imperforatus</i>	
Gorgonopsia	<i>Arctognathus curvimola</i> <i>Cyonosaurus longiceps</i> <i>Lycaenops</i> sp. <i>Rubidgea atrox</i>	
Therocephalia	<i>Ictidosuchoides longiceps</i> <i>Lycideops longiceps</i> <i>Moschorbinus kitchingi</i> <i>Nanictidops kitchingi</i> <i>Promoschorbynchus platyrhinus</i> <i>Polycynodon elegans</i> <i>Scaloporbinus angulorugatus</i>	
Cynodontia	<i>Cynosaurus suppostus</i> <i>Nanictosaurus kitchingi</i> <i>Vetusodon elikbulu</i>	
Invertebrates		
Mollusca	<i>Palaeonodonta</i> sp.	
Plants		
Mosses	<i>Buthelezi</i> sp.	
Equisetales	<i>Sphenophyllum</i> sp. <i>Raniganjia</i> sp. <i>Phyllotheba</i> sp. <i>Schizoneura</i> sp.	
Ferns	<i>Sphenopteris</i> sp.	
Cordaitales	<i>Noeggerathiopsis</i> sp.	
Wood	<i>Australoxylon</i> sp. <i>Prototawoxylon</i> sp.	
Trace fossils		
Invertebrate	<i>Planolites</i> isp. <i>Diplichmites</i> isp.	
		<i>Lithology</i>
		<p>The base of the Upper DaAZ roughly coincides with the top of the sandstone-rich Ripplemead member, believed to form part of a third-order subaerial unconformity (Viglietti et al., 2017b). Sandstone bodies comprise planar and trough cross-bedded to ripple cross-laminated, greenish grey or pale olive sublitharenites. Mudstone makes up 75 to 80% of the total thickness of the upper DaAZ, with beds averaging 20 m. Red mudstone is locally common but increases in abundance to about 45% up-section into the basal Palingkloof Member (Johnson, 1976), however this is not an indication of palaeoenvironmental changes (Viglietti, 2016; Viglietti et al., 2018). Mudstone units are rich in mature palaeosols, pedogenic and diagenetic carbonate nodules. Large brown weathering (10R 2/2) nodules with green mudstone pellets, and pedogenic nodule conglomerates are also a conspicuous feature in the Upper DaAZ (Smith and Botha-Brink, 2014).</p>
		<i>Depositional history</i>
		<p>Three depositional facies have been documented for the <i>L. maccaigi-Moschorbinus</i> Subzone (Viglietti et al., 2018), which differentiates it from the underlying <i>Dicynodon-Theriongnathus</i> Subzone that has a unique lacustrine lithofacies component, particularly near Daggaboer south of Cradock. The sandstone dominated units were either deposited in confined channels or unconfined crevasse splay deposits. Channel deposits comprise different architectural elements that show channel sinuosity was variable throughout the <i>Daptocephalus</i> Assemblage Zone, however lower sinuosity architectural elements (i.e. downstream accretion and sandy bedforms) become more common towards the upper boundary of the <i>L. maccaigi-Moschorbinus</i> (Viglietti et al., 2018). Mature palaeosols and pedogenic nodule conglomerates are common in the upper DaAZ which implies depositional rates were lower and reworking frequent in the floodplain facies deposits, that comprise mainly the mudstone and siltstone units.</p>



**Boundaries***Lower boundary*

The *L. maccaigi-Moschorbinus* Subzone is characterised by the first appearance of *L. maccaigi* and *Moschorbinus* in the upper portion of the Balfour Formation's Ripplemead member.

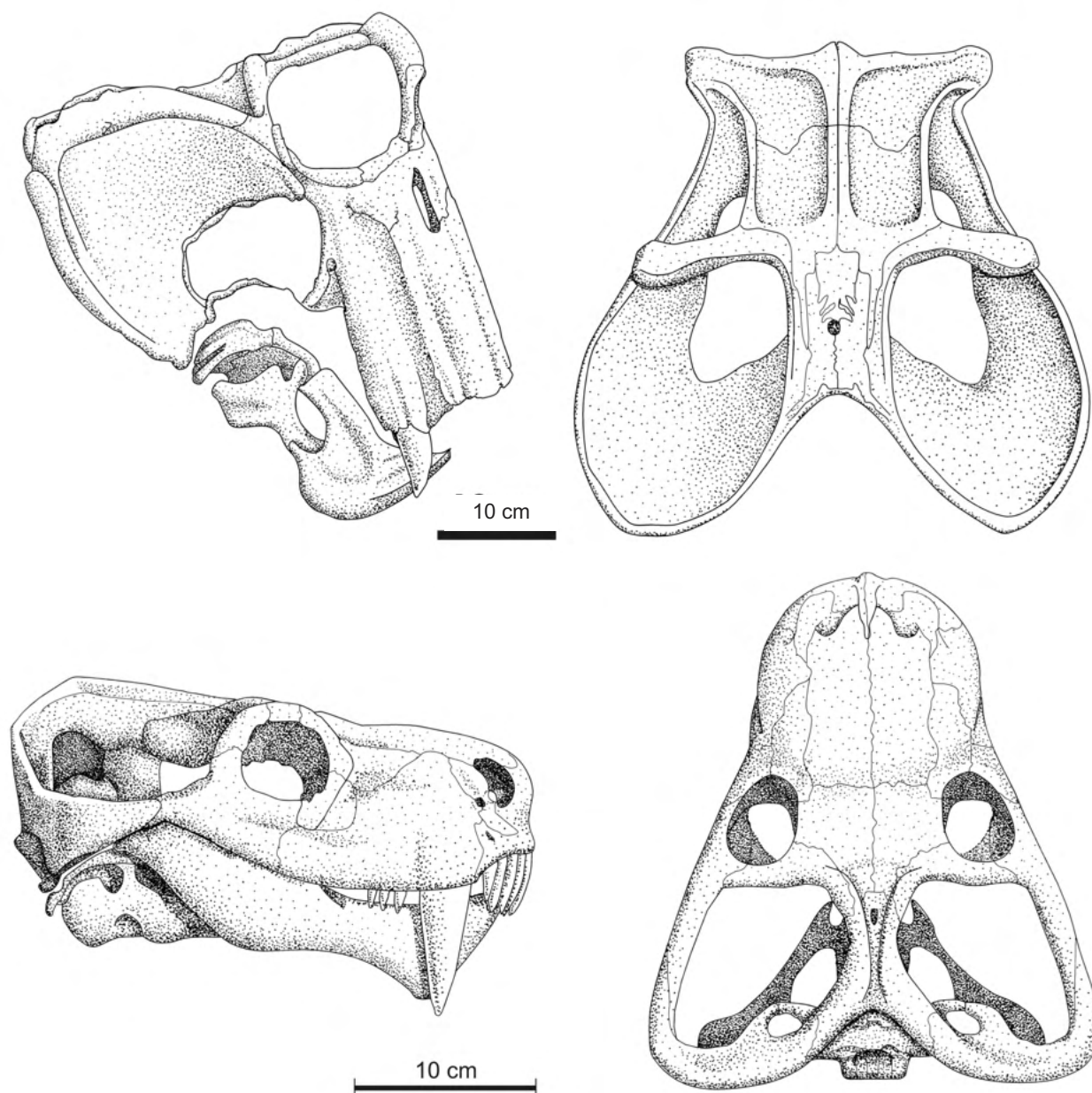
*Upper boundary*

The *L. maccaigi-Moschorbinus* Subzone terminates with the first appearance of *Lystrosaurus declivis*, and coincides with a significant extinction of Permian tetrapod taxa across the inferred Permo-Triassic Boundary in the Balfour Formation's

Palingkloof Member (Botha et al., 2020 but also see Gastaldo et al., 2020).

*Lateral boundaries*

*L. maccaigi-Moschorbinus* Subzone strata are exposed throughout the Karoo Basin however, the formations that correlate to this biostratigraphic subdivision are confined to between 24° and 25° east (upper Balfour Formation) and east of 25° east (Normandien and Escourt formations). Lithostratigraphic name distinctions have been made because of lateral change in lithology, and difficulty in tracing out distinct formations over hundreds of kilometres.



**Figure 6.** Biozone defining fossils of the *Lystrosaurus maccaigi-Moschorbinus* Subzone. The skulls of the *Lystrosaurus maccaigi* (top) and *Moschorhinus kitchingi* (bottom) in lateral and dorsal views.



*Subdivisions*

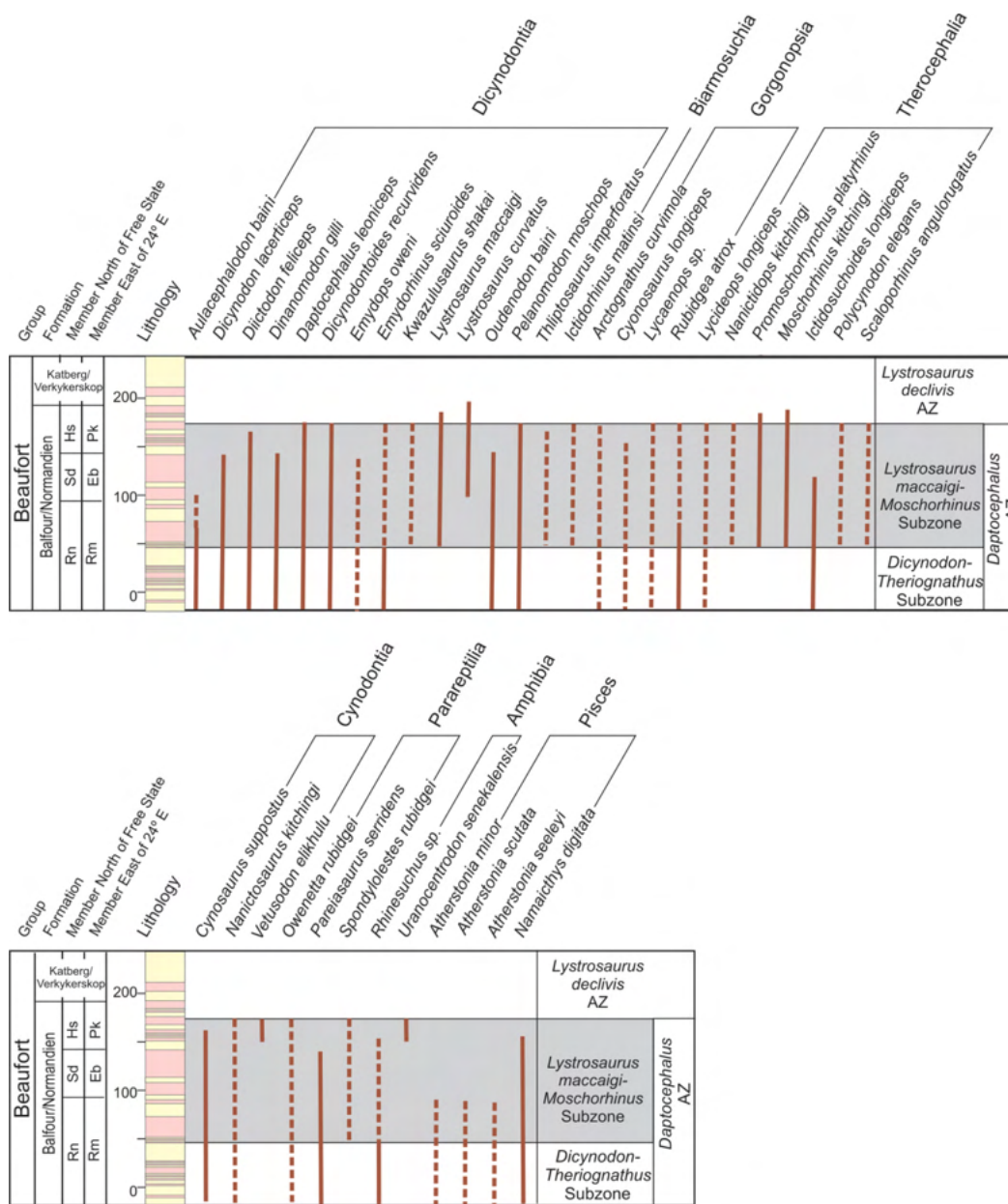
None.

**Regional aspects**

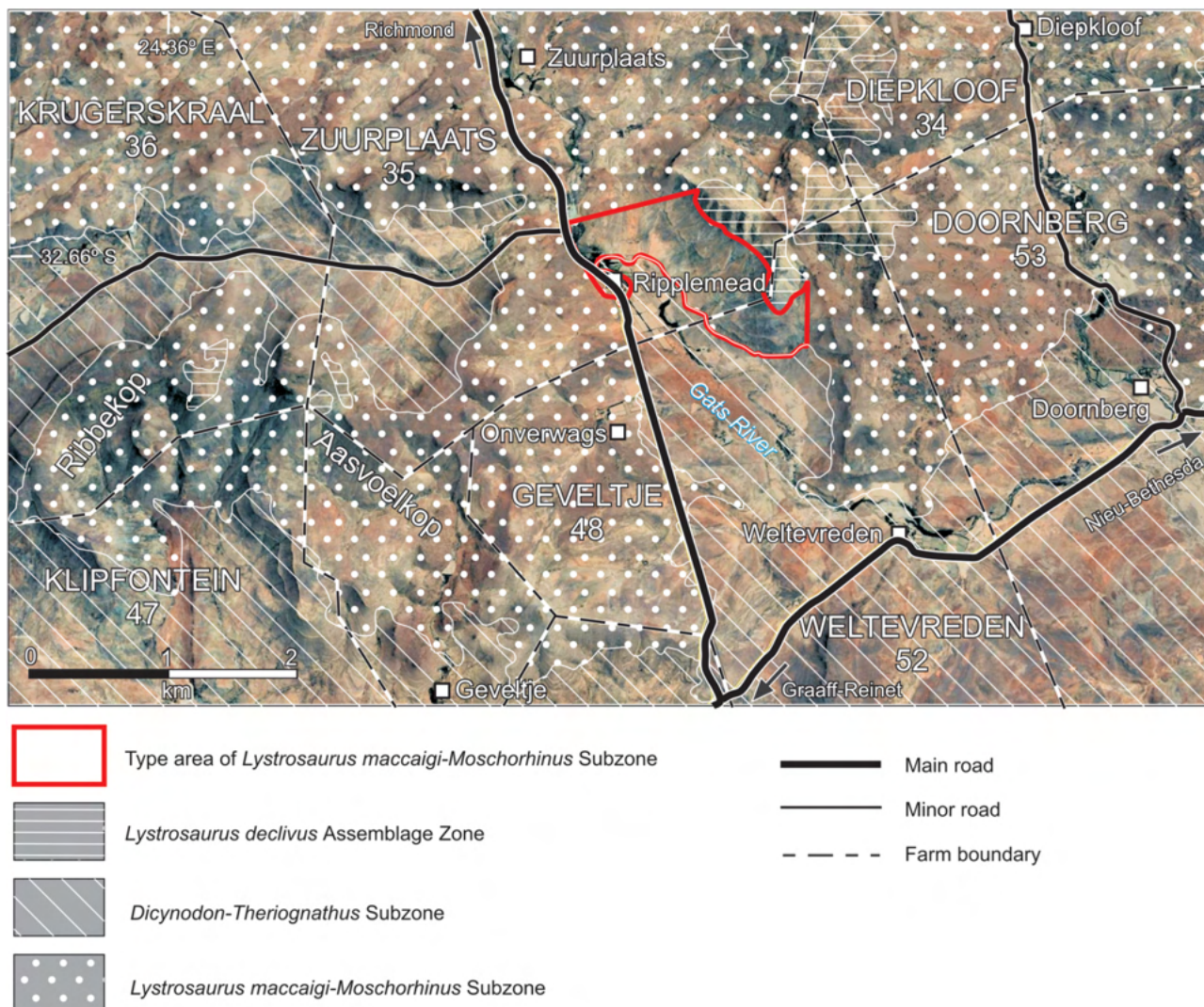
*Geographic distribution*

Good examples of *L. maccaigi-Moschorhinus* Subzone outcrops are in the Eastern Cape, Free State, and Kwa-Zulu Natal Provinces (Figure 2). Good exposures of the *L. maccaigi-Moschorhinus* Subzone are present west of Nieu Bethesda (Eastern Cape Province) along the Dassiesfontein Road, on the valley floor beneath Lootsberg Pass (south of Middelburg), and

on the Baviaansrivier road (north of Bedford). In the southern Free State Province, it can be observed along the N1 adjacent to Gariiep Dam (upper Balfour Formation). The upper DaAZ also outcrops around Harrismith in the eastern Free State Province and Kokstad in Kwa-Zulu Natal Province (Normandien Formation). The discovery of unique taxa in this region (e.g. *Kwazulusaurus skakai*, *Tbliptosaurus imperforatus*; Maisch, 2002; Kammerer, 2019) suggests the possibility of endemism, but more fieldwork is required to confirm this. The Estcourt Formation has a localised distribution between Estcourt and Impedle in Kwa-Zulu Natal Province, and is also considered coeval with the upper DaAZ, although it comprises plant and insect fossils, so this is difficult to confirm at this stage.



**Figure 7.** Stratigraphic ranges of the vertebrate taxa occurring in the *Lystrosaurus maccaigi-Moschorhinus* Subzone. The simplified lithological section is based on the vertical section logged at the Type locality of the *Lystrosaurus maccaigi-Moschorhinus* Subzone (Viglietti, 2016, see Figure 8). Rn (Rooinekke), Sn (Schoondraai), Hs (Harrismith), Rm (Ripplemead), Eb (Elandsberg), Pk (Palingkloof). Scale in metres.



**Figure 8.** Map of the Type locality of the *Lystrosaurus maccaigi-Moschorhinus* subzone on Ripplemead farm (Zuurplaats 35), 20 km north west of Nieu Bethesda, Eastern Cape Province.

#### Lateral and vertical variation

Lateral variation in thickness is documented for the *L. maccaigi-Moschorhinus* Subzone and the fauna shows no lateral biogeographic change. As little work has been conducted in the northeastern parts of the basin it is possible that localised assemblages and endemism may be found in future.

#### Correlation

A few places globally have fossil faunas that make it possible to make correlation to the *L. maccaigi-Moschorhinus* Subzone. Examples include the Guodikeng Formation in northwestern China (Metcalf et al., 2001) and the Sokolki fauna near Vyazniki and Gorokhovets on the Russian Platform (Newell et al., 2010). Similar faunal compositions have been described in China where the dicynodontoid *Jimusaria sinkianensis* co-occurs with *Lystrosaurus* much like in the upper DaAZ (Metcalf et al., 2001; Cao et al., 2008). Additionally, the Russian faunas

may be another coeval upper DaAZ deposit outside of the Karoo Basin, but the temporal distribution of Russian dicynodontoids (*Delectosaurus arefevi*, *Peramodon amalitzkii*, and *Vivaxosaurus trautscholdi*) may not be the same as *Dicynodon lacerticeps* or *Daptocephalus leoniceps*. In neighbouring Karoo-aged basins, the lack of *L. maccaigi* and *Moschorhinus* likely means there are no correlative strata in southern and east Africa.

#### Age

The upper *L. maccaigi-Moschorhinus* Subzone spans the upper Changhsingian of the latest Permian (~253 to 252 Ma) (Rubidge et al., 2013; Gastaldo et al., 2020).

#### Type locality

The type locality for the *L. maccaigi-Moschorhinus* Subzone is on Ripplemead farm (Zuurplaats 35) situated 20 km north west of Nieu Bethesda in the Eastern Cape Province (Figure 8).



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