



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

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Abstract

The *Cynognathus* Assemblage Zone is the youngest tetrapod biozone of the Beaufort Group (Tarkastad Subgroup, Karoo Supergroup). It is situated between the underlying *Lystrosaurus declivis* Assemblage Zone and the base of the overlying Molteno Formation (Stormberg Group) and corresponds to the entire Burgersdorp Formation. It is characterised by the presence throughout of the cynodont genus *Cynognathus*. The biozone reaches a maximum thickness of around 650 m in the southeast part of the basin and thins dramatically to the north, where it is only a maximum of 50 m thick. We here propose a three-fold subdivision into a lower *Langbergia-Garjainia* Subzone, a middle *Trirachodon-Kannemeyeria* Subzone and an upper *Cricodon-Ufudocyclops* Subzone. The basal contact is defined biostratigraphically by the first appearance of *Cynognathus crateronotus* and *Langbergia modisei*. The *Cynognathus* Assemblage Zone lacks a defined biostratigraphic upper limit, being unconformably terminated by the base of the overlying Molteno Formation, which lacks a terrestrial vertebrate fossil record other than trackways.

Name

The *Cynognathus* Assemblage Zone.

Stratigraphic position

Biostratigraphic position

This assemblage zone overlies the *Lystrosaurus* Assemblage Zone.

Proposer of name

The *Cynognathus* Zone was erected by Broom (1906a) and corresponds to Seeley's (1892) Zone of specialised theriodonts. Broom's (1906a) *Cynognathus* Zone nomenclature was accepted by Kitching (1970, 1972, 1977). Kitching (1995) first used the term *Cynognathus* Assemblage Zone.

Lithostratigraphic position

The *Cynognathus* Assemblage Zone is coincident with the Burgersdorp Formation.

Derivation of name

The *Cynognathus* Assemblage Zone is named after the cynodont genus *Cynognathus* (Figure 1). This genus is relatively common, especially in the middle part of its stratigraphic range, and is distinctive, even in the field. In South Africa it is represented by a single species, *C. crateronotus* (Seeley, 1895a, b; Wynd et al., 2018).

Historical background

Based on his trip to South Africa in 1889 the *Cynognathus* Assemblage Zone was first recognised by Harry Govier Seeley in 1892 as the Zone of specialised theriodonts (Seeley, 1892). Broom (1906a, 1907, 1909a) formulated a more precise biostratigraphic division of the fossiliferous horizons of the Beaufort Group and in his scheme Seeley's Zone of specialised theriodonts was renamed the *Cynognathus* Zone, and this was accepted by Kitching (1970, 1972, 1977).

Keyser and Smith (1978) introduced the terminology *Kannemeyeria* Assemblage Zone to replace the *Cynognathus* Zone. The dicynodont *Kannemeyeria* was preferred over *Cynognathus* as the zone's index fossil as the authors believed that *Cynognathus* was rare, and that it was impossible to accurately establish its biostratigraphic range. They furthermore argued that *Kannemeyeria* specimens were larger, more abundant and more easily recognisable in the field. Using a dicynodont genus was also in line with the practice for the biozonation of the rest of the Beaufort Group at that time. They did, however, note that complete skulls of *Kannemeyeria* were not common. The *Kannemeyeria* Assemblage Zone was refined to the *Kannemeyeria-Diademodon* Assemblage Zone by Keyser (1979) and this nomenclature was formally accepted by the South African Committee for Stratigraphy (SACS, 1980).

Kitching (1984) reassessed the biozonation of the Beaufort Group as accepted by the South African Committee For Stratigraphy (SACS, 1980) and proposed the name *Cynognathus-Diademodon* Assemblage Zone for the *Kannemeyeria-Diademodon* Assemblage Zone of SACS (1980). His reinstatement of *Cynognathus* as the zone's index fossil was based on his belief that the genus occurred throughout the biozone, and that it was abundant in collections worldwide. *Diademodon* was preferred over *Kannemeyeria* as an associated index fossil because it was the most abundant genus in the biozone (Kitching, 1977). To bring this biozone in line with internationally recognised nomenclature, Kitching (1995) reassigned the assemblage zone to the historically important genus *Cynognathus*, creating the *Cynognathus* Assemblage Zone.

Early workers who collected in the *Cynognathus* Assemblage Zone included Thomas Bain, Alfred (Gogga) Brown and Daniel Kannemeyer. Published accounts of their discoveries are given in Seeley (1888, 1889, 1892, 1894, 1895a and b, 1904, 1907, 1908a and b) and Broom (1903, 1905, 1906a, b, c and d, 1913a and b). Brown in particular made an enormous contribution to the knowledge of the fauna and flora of the biozone, and his collecting trips and localities are recorded in his twenty-one volume unpublished journal. He is credited with numerous discoveries including the amphibian *Batrachosubus browni*

(Broom, 1903), the captorhinid (parareptile) *Thelegnathus browni* (Broom, 1905), the archosauriform *Erythrosuchus africanus* (Broom 1906b), the enigmatic *Palaeodon browni* (Broom, 1906c), the rhynchosauroids *Howesia browni* (Broom, 1905, 1906d) and *Mesosuchus browni* (Watson, 1912), as well as numerous fish (Broom, 1909b) and plant fossils (Anderson and Anderson, 1985). In his later life Brown employed Albert William Higgins to collect for him, to whom is credited the discovery of the archosauriform *Euparkeria capensis* (Broom, 1913a and b; Ewer, 1965).

In 1889 Bain introduced Seeley to Brown and Kannemeyer. Kannemeyer, a medical doctor who lived in Burgersdorp, is remembered for the numerous skulls of *Kannemeyeria* (Weithofer, 1888) he collected from this area. From his trip to South Africa and the meeting with Kannemeyer and Brown, Seeley (1904, 1907, 1908a and b) described a number of *Cynognathus* Assemblage Zone vertebrate taxa.

Watson (1942) was the first to suggest a possible subdivision of the *Cynognathus* Assemblage Zone, based on the biostratigraphic ranges of *Kannemeyeria* and *Erythrosuchus* as they were then understood. He subdivided the zone into a lower zone (A), in which *Kannemeyeria* and *Erythrosuchus* occurred together, and an upper zone (B), in which *Kannemeyeria* was absent and *Erythrosuchus* was extremely rare. This biostratigraphic range for *Kannemeyeria* was corroborated by Kitching (1977) and Cooper (1982), but refuted by Keyser and Smith (1978) who believed that *Kannemeyeria* occurred throughout the biozone. Cooper (1982) felt that *Kannemeyeria* was restricted to the lower half of the Burgersdorp Formation, and further suggested that the upper part of the *Cynognathus* Assemblage Zone, above the biostratigraphic range of *Kannemeyeria*, would eventually yield an advanced fauna, equivalent to his *Tetragonias* Zone fauna. He also considered the cynodont genera *Cynognathus* and *Diademodon* to occur throughout the range of the *Cynognathus* Assemblage Zone. It should be noted that these trends were for the *Cynognathus* Assemblage Zone as known at the time, and before the recognition of the lowermost and uppermost subzone faunas (Kitching, 1977; Keyser and Smith, 1978; Cooper, 1982).

The early studies of the *Cynognathus* Assemblage Zone were limited to the Eastern Cape, southeastern Free State and Lesotho (Watson, 1914; Kitching, 1963; Smith, 1990) and prior to the 1990s these were the only areas in which the biozone was believed to occur. Kitching (1977, p.26) in fact explicitly states that "although the Beaufort beds have been carefully examined in a number of areas in the Wepener, Thaba Nchu, Ladybrand, Senekal, Bethlehem and Harrismith districts for the purpose of determining the extent of the *Cynognathus* Zone northwards in the Orange Free State, no fossil reptiles or sediments were found that could be assigned to the zone. At present it seems that there was no continuous deposition of the *Cynognathus* Zone to the north of Wepener".

Du Toit (1918) was the first to consider the uppermost sedimentary rocks of the Tarkastad Subgroup in the northeastern Free State to be a continuation of part of the Burgersdorp Formation in the southern Karoo Basin. This idea was expanded by Van Eeden (1937), who believed the Burgersdorp Formation to be present in the vicinity of Bethlehem and Kestell in

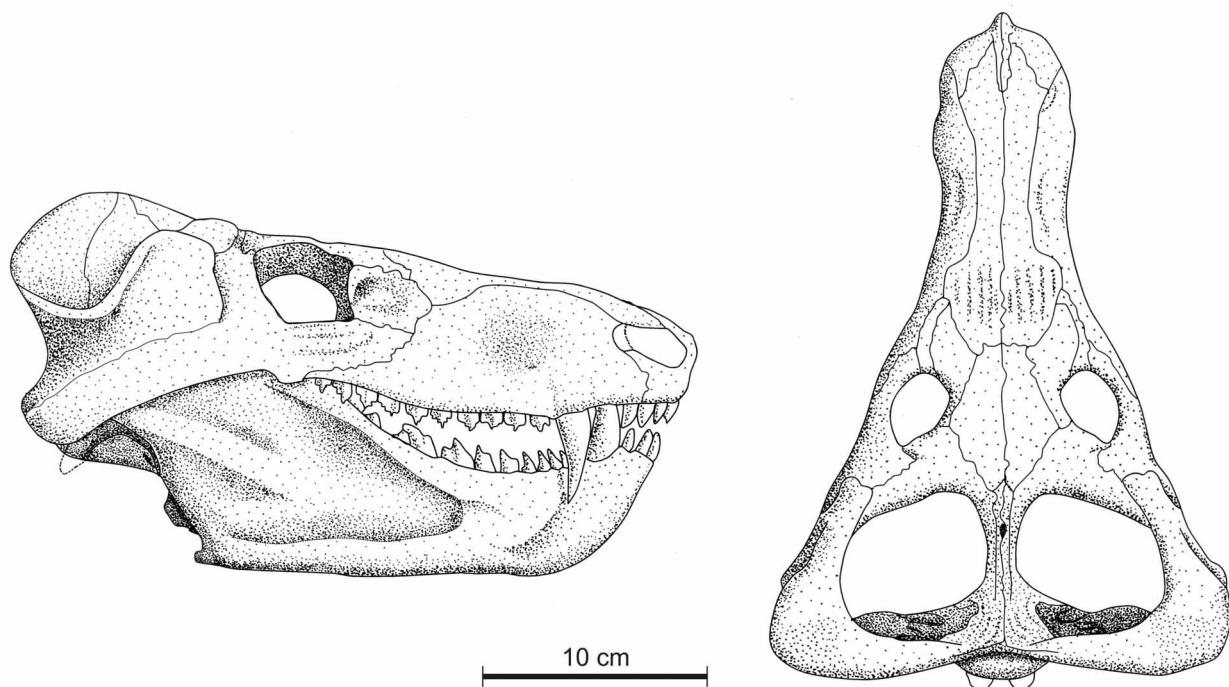


Figure 1. Illustration of the index taxon of the Cynognathus Assemblage Zone, *Cynognathus crateronotus*, in lateral and dorsal views.

the north of the basin. Groenewald (1984, 1989, 1990, 1996) accepted du Toit's claims, but argued that there was sufficient lithological difference between the deposits in the south and north of the basin to warrant separate formational distinction, and proposed the name Driekoppen Formation for the northern equivalents of the Burgersdorp Formation. Only the Burgersdorp Formation is however currently formally accepted (SACS, 1980; Johnson and Hiller, 1990), and the northern sequence is now considered sufficiently similar to the Burgersdorp Formation in the south to warrant its inclusion as a northern, distal facies (Hancox, 1998; Neveling, 2004).

Welman et al. (1991) provided what they believed to be the first palaeontological evidence to corroborate the proposed time equivalency of the southern and northern Burgersdorp Formation exposures, when they reported the presence of *Cynognathus* Assemblage Zone fossils from the northeastern and northwestern Free State. Their faunal list for the northern Burgersdorp Formation sites included the capitosaurid temnospondyl *Parotosuchus*, the archosaur *Erythrosuchus*, the cynodonts *Cynognathus* and *Trirachodon*, and the therocephalian *Bauria*, and they concluded that this represented a typical *Cynognathus* Assemblage Zone fauna. Re-assessment of this material has however shown that the archosaur material is assignable to the erythrosuchid *Garfjainia* (Gower et al., 2014) and that the temnospondyl material assigned by Welman et al. (1991) to *Parotosuchus* is in fact *Kestrosaurus* (Shishkin et al., 2004), the most common faunal element of the northern *Cynognathus* Assemblage Zone exposures. Abdala et al. (2006) further re-assigned the material assigned to *Trirachodon* to a new genus *Langbergia*. Unfortunately, the material assigned to *Bauria*, which was described by King (1996), was not included

in the Abdala et al. (2014) re-assessment of the taxonomy of the South African Bauriidae, but it is likely that this material is actually assignable to *Microgomphodon*.

Subsequent to the work of Welman et al. (1991) the northern Burgersdorp Formation exposures have been the focus of additional sedimentological and stratigraphic studies by Azzie (1994), Hancox et al. (1995), Hancox (1998, 2000), Groenewald et al. (2001) and Neveling (2002). Accounts of new fossil material include those of Shishkin and Welman (1994), King (1996), Damiani (1999, 2001a), Gow (1999), Groenewald et al. (2001), Damiani and Jeannot (2002), Bender and Hancox (2003, 2004), Shishkin et al. (2004), Abdala et al. (2007), Yates et al. (2012), Gaetano et al. (2012), Gower et al. (2014) and Jenkins (2018).

In the early 1990s collecting in the southernmost reaches of the Burgersdorp Formation began to show that a new, distinct fauna was present in the uppermost part of the Formation as well (Hancox and Rubidge, 1994). Material from this level has subsequently been described by Hancox and Rubidge (1996), Hancox (1998), Hancox et al. (2000), Hancox et al. (2013) and Kammerer et al. (2019).

Based on the new collecting in the Burgersdorp Formation in the north and south of the basin, Hancox et al. (1995) published a brief paper proposing an informal threefold subdivision of the *Cynognathus* Assemblage Zone based on the spatial and temporal distribution of mastodonsaurid temnospondyls and associated vertebrates. The original ideas behind this subdivision grew out of the description of a northern *Cynognathus* Assemblage Zone fauna by Welman et al. (1991), and the early findings of Hancox and Rubidge (1994) and Shishkin et al. (1995). This tripartite subdivision has found widespread acceptance in the literature (e.g. Hopson and

Kitching, 2001; Rubidge 2005; Abdala and Smith 2009; Fröbisch 2009; Martinelli et al., 2009; Abdala and Ribeiro, 2010; Nesbitt et al., 2013; Peeook et al., 2013; Angielczyk et al., 2014; Sidor et al. 2014a and b; Rubidge et al., 2016; Wynd et al., 2018; Hendrickx et al., 2019) and whilst various authors have utilised the informal subdivision in their correlations, no formal subdivision of the *Cynognathus* Assemblage Zone has been published.

Field-based research and taxonomic revisions of various South African fauna over the past two decades has vastly increased understanding of the rocks and fossils of the Burgersdorp Formation, to the extent that a formal biostratigraphic subdivision of the *Cynognathus* Assemblage Zone is now possible. The fauna of the redefined *Cynognathus* Assemblage Zone represents the later stages of recovery from the end-Permian mass extinction in the main Karoo Basin (Roopnarine et al. 2018).

Palaeontology

Description of the Assemblage Zone

An assemblage zone characterised by the occurrence of the cynodont genus *Cynognathus*. The *Cynognathus* Assemblage Zone is here subdivided into three subzones, a lower *Langbergia-Garjainia* Subzone, a middle *Trirachodon-Kannemeyeria* Subzone (equivalent to the entire *Cynognathus* Assemblage Zone as described by Kitching, 1995) and an upper *Cricodon-Ufudocyclops* Subzone (Figure 2).

The list of fossil taxa is derived from reliably identified specimens. Taxonomic and stratigraphic information is derived from work by the authors and from the following sources: Hutchinson (1973, 1975, 1978), Jubb and Gardiner (1975), Griffith (1978), and Bender and Hancox (2003, 2004) for the actinopterygians; Duffin (2001) for the chondrichthyans; Shishkin and Welman (1994), Warren (1998), Damiani (1999,

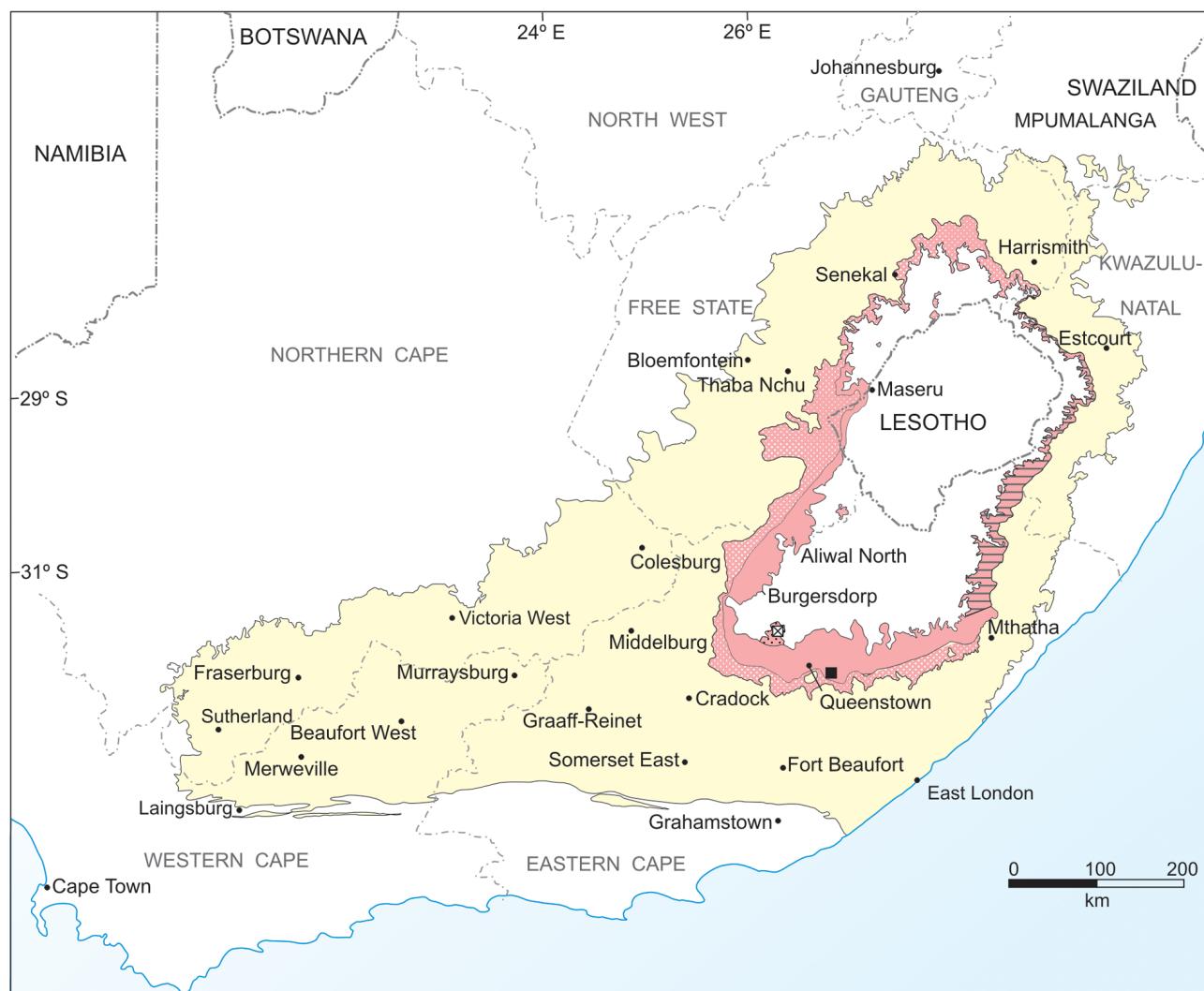


Figure 2. Distribution of the *Cynognathus* Assemblage Zone (brown) in the Beaufort Group, (yellow) showing the distribution of the *Langbergia-Garjainia* Subzone (white dotted), *Trirachodon-Kannemeyeria* Subzone (not dotted) and the *Cricodon-Ufudocyclops* Subzone (black dotted). Positions of type localities for the *Langbergia-Garjainia* Subzone (empty square); *Trirachodon-Kannemeyeria* Subzone (solid black square), and *Cricodon-Ufudocyclops* Subzone (crossed square) are indicated. Stratotype section is at Nonesis Nek Pass (see Figure 7).

2001a, b), Damiani and Jeannot (2002), Morales and Shishkin (2002), Damiani and Rubidge (2003), Damiani and Hancox (2003), Damiani and Kitching (2003), Damiani (2004a,b), Shishkin et al. (2004) and Damiani (2008) for the temnospondyls; Gow (1999) and Jenkins (2018) for *Palaeodon*; Dilkes (1995, 1998) and Butler et al. (2015) for the rhynchosaurids; Gower (2003) and Gower et al. (2014) for the erythrosuchids; Abdala et al. (2014) for the bauriids; Renaut (2000), Hancox et al. (2013) and Kammerer et al. (2019) for the dicynodonts; and Seeley (1895a), Grine et al. (1979), Bradu and Grine (1979), Abdala et al. (2005, 2006), Sidor and Hopson (2018) and Hendrickx et al. (2019) for the cynodonts. Plant taxa are from Anderson and Anderson (1985) and fossil wood from Bamford (1999, 2004).

***Langbergia-Garjainia* Subzone**

Proposer of name

This subzone is proposed for the first time in this work.

Stratigraphic position

Biostratigraphic position

The *Langbergia-Garjainia* Subzone occurs above the *Lystrosaurus declivis* Assemblage Zone and underlies the *Trirachodon-Kannemeyeria* Subzone of the *Cynognathus* Assemblage Zone.

Lithostratigraphic position

Occupies the lowermost part of the Burgersdorp Formation, which is roughly 100 m in the thickest part of the section.

Derivation of name

The name is derived from the distinctive and fairly common trirachodontid cynodont *Langbergia modisei* and the medium-sized erythrosuchid archosauriform *Garjainia madiba*, which co-occur only in the rocks of this subzone (Figure 3).

Historical background

The interpretation advanced by du Toit (1918) and Van Eeden (1937) on the lateral extent of the Burgersdorp Formation long implied the presence of the *Cynognathus* Assemblage Zone as far north as the towns of Bethlehem and Kestell in the northern Free State. Yet it was not until Welman et al. (1991) reported fossils assignable to this biozone from the northeastern and northwestern Free State Province that there was any palaeontological evidence to corroborate the northward extension of the *Cynognathus* Assemblage Zone.

Hancox et al. (1995) and Shishkin et al. (1995) pointed out that the fossil fauna recovered from the northern Free State Province was dominated by the capitosauroid temnospondyl *Kestrosaurus*, and utilised this genus as the basis for a lower subdivision of the *Cynognathus* Assemblage Zone. Neveling (2002, 2004) and Neveling et al. (2005) demonstrated the

southern limit of this fauna could be extended as far as the towns of Tarkastad and Queenstown. This new biozone was previously referred to as the “lower zone”, “lowermost subzone” (Hancox et al., 1995; Shishkin et al., 1995), “subzone A fauna” (Hancox and Rubidge 1997; Hancox 1998), the “*Kestrosaurus* grouping” (Shishkin 2000), the “*Kestrosaurus* Assemblage Zone” (Neveling 2002, 2004) and *Cynognathus* A biozone (Rubidge, 2005).

Palaeontology

Description of subzone

A concurrent range zone characterised by the presence of the cynodonts *Langbergia modisei* and the erythrosuchid archosauriform *Garjainia madiba*. To date no dicynodonts are known from the subzone, making this the only stratigraphic interval in the Beaufort Group lacking dicynodont fossils. No fossil wood has been collected to date and the only direct evidence of plant fossils is a single small sphenophyte cast (Hancox, 1998).

Taphonomic notes on fossil occurrences

The overwhelming majority (>95%) of fossils assigned to this subzone has been recovered from the north-western exposures of the Burgersdorp Formation, between the towns of Senekal and Bethlehem. Here vertebrate material has been collected from dark reddish brown (10R 3/4) horizontally laminated to massive, lacustrine mudstones and siltstones, light grey (5Y 7/1), fine to medium-grained channel sandstones and their associated intraformational lag conglomerates, and in dark reddish-brown (10R 3/4) overbank mudstones and siltstones, and intercalated thin (>1 m) sandstones. The most common taphonomic mode in the lower lacustrine mudstones and siltstones is as well-preserved, complete, though totally disarticulated elements. Isolated elements may also be recovered from channel sandstones. A rich (in terms of both number and diversity) microfauna has been collected from the intraformational lag conglomerates, with almost all of the fossil material being fragmentary. Bone elements tend to be incomplete, being represented by the most robust bones such as mandibular remains, isolated teeth, amphibian post glenoid areas, pterygoids and tabulars, and various long bone heads, phalanges and vertebrae. Coprolites are extremely abundant.

Bone is rare in the overbank deposits of the uppermost Burgersdorp Formation of the distal sector, but includes amphibian, archosauriform, procolophonid and cynodont material. Most of the fossils from this sequence occur as isolated, disarticulated specimens with thick haematic coatings. In places, cracks in the fossil material are filled with calcite. A similar taphonomic signature is exhibited by fossil material collected from the lowermost Burgersdorp Formation in the southern Free State and Eastern Cape provinces.

List of fossils

See Figure 4 for ranges of the vertebrate genera.

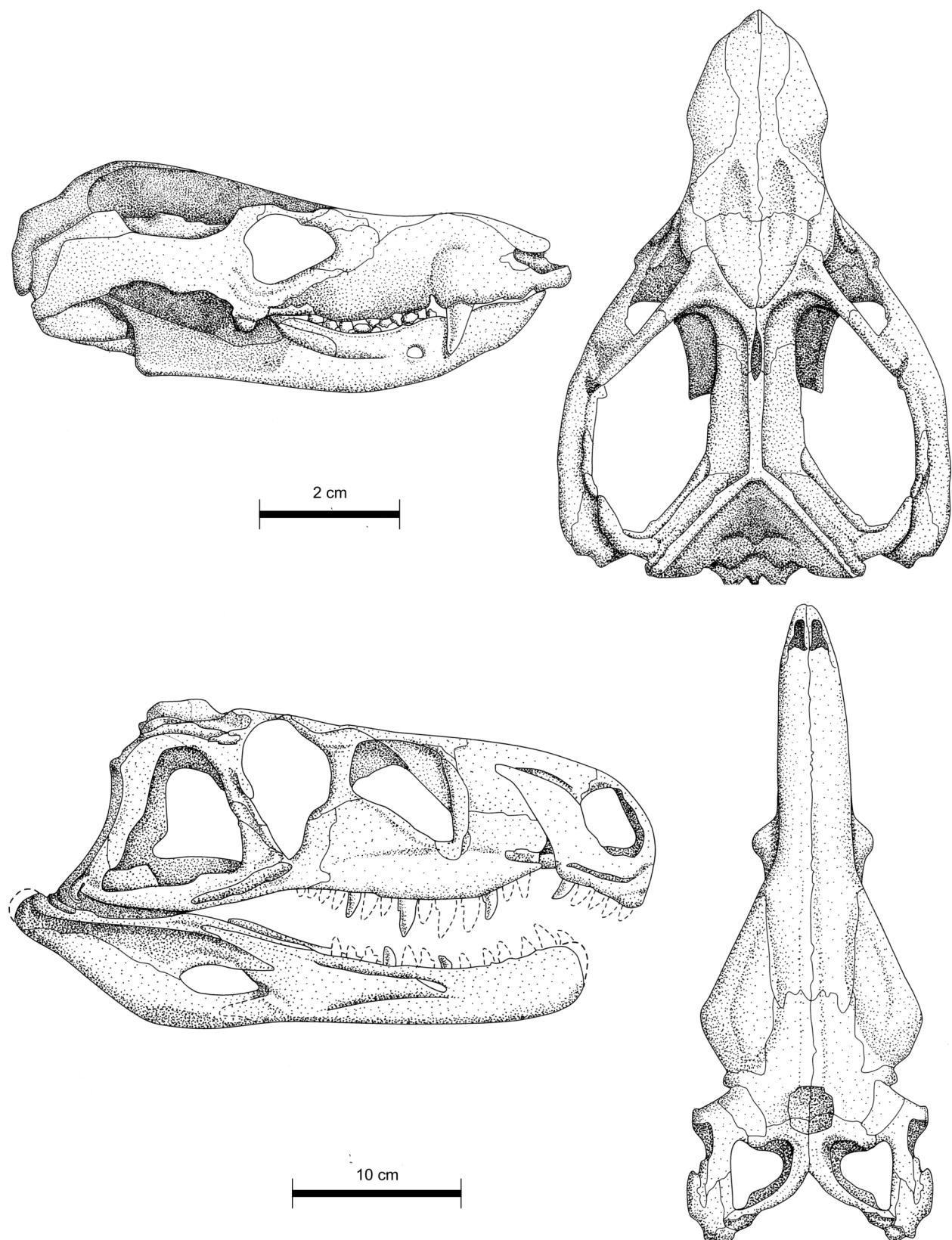


Figure 3. Illustration of the index taxa of the Langbergia-Garjainia Subzone in dorsal and lateral view. (top) *Langbergia modisei* (bottom) *Garjainia prima*.

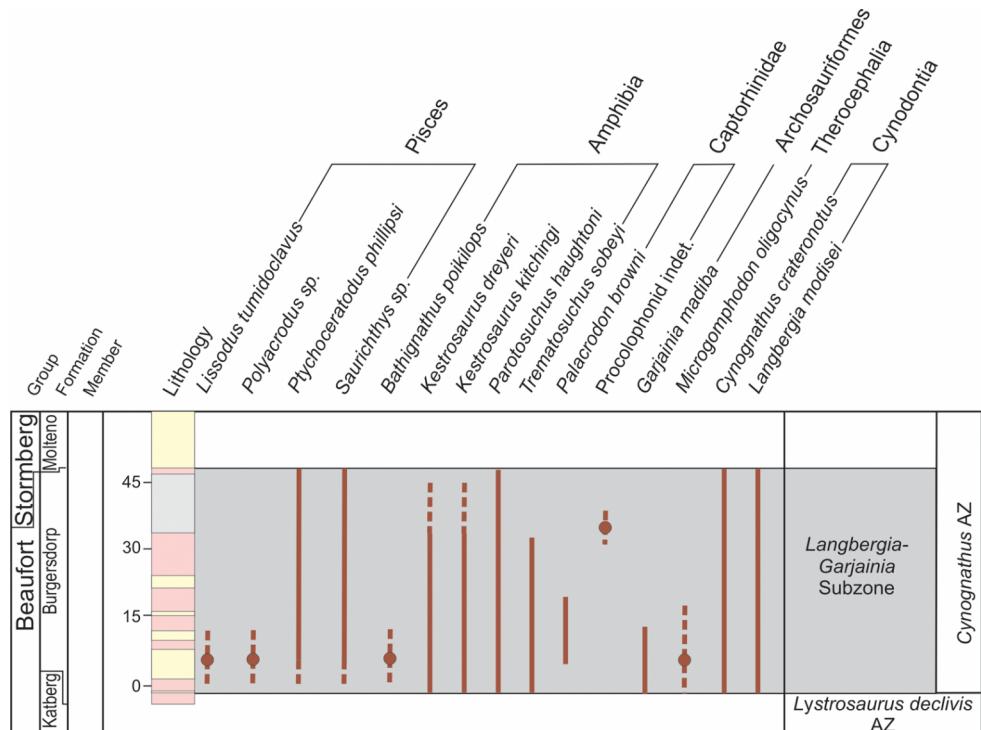


Figure 4. Stratigraphic ranges of vertebrate taxa occurring in the Langbergia-Garjainia Subzone. Lithology of grey interval of stratigraphic section is uncertain due to poor outcrop.

Vertebrates			
Pisces	<i>Lissodus tumidoclavus</i>		
	<i>Polyacrodus</i> sp.		
	<i>Ptychoceratodus phillipsi</i>		
	<i>Saurichthys</i> sp.		
Amphibia	<i>Bathignathus poikilops</i>		
	<i>Kestrosaurus dreyeri</i>		
	<i>Kestrosaurus kitchingi</i>		
	<i>Parotosuchus haughtoni</i>		
	<i>Trematosuchus sobeyi</i>		
Amniota			
Parareptilia	<i>Procolophonid</i> indet.		
Eureptilia	<i>Palaeodon brownii</i>		
Archosauriformes	<i>Garjainia madiba</i>		
Synapsida			
Therapsida			
Therocephalia	<i>Microgomphodon oligocynus</i>		
Cynodontia	<i>Cynognathus crateronotus</i>		
	<i>Langbergia modisei</i>		
Trace fossils			
Vertebrate	Trirachodontid burrow casts		
Invertebrate	<i>Diplichnites</i> sp.		
	Crayfish burrows		
	<i>Lockeia</i> sp.		
	<i>Planolites</i> sp.		
Coprolites	<i>Alococopros triassicus</i>		
	<i>Eucoprus cylindratus</i>		
	<i>Heteropalacopros</i> sp.		
	<i>Hyronocopros ambipola</i>		

Geological description

Thickness

The *Langbergia-Garjainia* Subzone reaches a maximum thickness of 100 m between Aliwal North and Thaba Nchu (Rutherford, 2009; Rutherford et al., 2015), thinning northwards to around 50 m in the Paul Roux area. The fossil record is currently too sparse to establish the biozone thickness south of Aliwal North.

Lithology

In the fossiliferous exposures of the north-western Free State the stratigraphic succession may be subdivided into a lower, horizontally-laminated to massive, fines-dominated unit, a more sandstone-rich middle sequence, and an upper, fines-dominated sequence, which in places also preserves isolated thick lenticular sandstones. The lower fines unit is between 10 to 20 m thick, and is dominated by dark reddish brown (10R 3/4) mudstone and siltstone, which is generally laminated to semi-massive in nature and lacks pedogenic overprinting. At places lag horizons of reworked ferromanganese glaebules occur, which often contain multi-taxa bone assemblages. The middle sandstone unit, up to 6 m thick, is dominated by light grey (5Y 7/1), fine-grained sandstone, internally structured by trough and planar cross-stratified and ripple laminated sandstones. The sandstone unit may preserve bone bearing intraformational clast conglomerates. The upper sequence comprises up to 40 m of dark reddish-brown (10R 3/4) fines and intercalated thin

(>1 m) sandstones, which are more grayish brown (5YR 3/2) towards the top of the sequence. Mudstone units show evidence of colour mottling, as well as stacking of weakly developed vertic structures, with fine blue siltstone infill. Apart from rare occurrences of bone at the base of thin sandstones, the upper mudstone dominated succession preserves only sporadic bones (and coprolites) that usually have thick encrustations of haematite and calcite.

In the south the lithology is dominated by massive greyish red (5R 4/2, 10R 4/2) and pale reddish brown (10 5/4) fines with subordinate greenish grey (5GY 6/1) and light grey (N7) sandstone, arranged in upwards-fining packages up to 7 m thick. Calcareous nodules, desiccation features and bioturbation characterise the thin and laterally constrained pedogenic horizons. Stacked, fine-grained sandstone sheets, commonly occur near the top of this subzone in the south.

Towards the south, rocks of the *Langbergia-Garjainia* biozone are conformably overlain by middle Burgersdorp Formation strata, whereas in the north between Senekal and Paul Roux they are unconformably overlain by the Indwe Member of the Molteno Formation.

Depositional history

The lack of pedogenic modification, the homogeneous nature of the fines, and the abundance of well-preserved amphibian and archosaur remains in the northern exposures suggests that the rocks of the lowermost part of *Langbergia-Garjainia* Subzone were deposited in extensive lacustrine systems (Groenewald, 1989; Welman et al., 1991; Hancox, 1998). The middle sandstone dominated unit represents both low energy meandering channels and lacustrine deltas. Secondary rounding of clay pebbles, coprolites and fossil bone in the bioclast lags implies the reworking of earlier deposits, and the rounding of floodplain material and the abrasion of skeletal material in channel. The uppermost fines dominated succession exhibits colour mottling and preserves numerous large rhizocretions, root infills and desiccation cracks. These are thought to represent fairly rapid overbank floodplain aggradation, punctuated by periods of incipient soil development. Where present, the sandstones in the upper sequence have a width to depth ratio of 1:15 to 1:20, are lenticular in nature, and are internally structured by horizontal and trough cross-stratification. Hancox (1998) proposed that this was deposited by a high-sinuosity channel system with fluctuating discharge based on the lenticular nature and fining-upward fill of the channel sandstones, characterised by fine grained horizontal and trough cross-stratification. Neveling (2002, 2004) proposed a similar fluvial environment, subject to ephemeral flow patterns, for the outcrops of this subzone in the southern Free State and Eastern Cape provinces.

Boundaries

Lower boundary

The base of the *Langbergia-Garjainia* Subzone is defined as the first appearance datum of the cynodont genus *Cynognathus*, the

same as for the *Cynognathus* Assemblage Zone more broadly. It also coincides with the first occurrence of both *Langbergia modisei* and *Garjainia madiba*.

Upper boundary

The upper boundary of the *Langbergia-Garjainia* Subzone is defined by the first occurrence of the trirachodontid cynodont *Trirachodon berryi* and the dicynodont genus *Kannemeyeria simocephalus*.

Lateral boundaries

No lateral cut-offs or pinch-outs occur.

Subdivisions

No subdivision of the *Langbergia-Garjainia* Subzone is proposed.

Regional aspects

Geographic distribution

Spatially, the *Langbergia-Garjainia* Subzone extends from the town of Queenstown in the south (Neveling 2002) to a line between the towns of Senekal and Harrismith in the north (Figure 2). The subzone has been traced as far east as Bergville. To date its extent further south in KwaZulu-Natal is unknown. The *Langbergia-Garjainia* Subzone is best exposed in the Aliwal North, Thaba Nchu, Senekal and Paul Roux districts.

Lateral and vertical variation

As mentioned above, the overwhelming majority (>95%) of fossils assigned to this subzone have been recovered between the towns of Senekal and Bethlehem in the northwestern Free State Province. Limited exposure may explain the decrease in fossil discoveries further east to Bergville, but to the south a clear and rapid decrease in fossil abundance is evident, with a limited number of specimens recovered from exposures near Rouxville, and numbers decreasing even more towards Tarkastad. Even in the Senekal and Bethlehem localities, complete fossil vertebrate specimens are not abundant, but are fairly evenly distributed in the lower portion of the succession where fossil amphibians predominate. Where developed in the middle sandstone unit, fossil material is common in the intraformational conglomerates. Fossils become scarcer in the upper part of the northern succession.

Correlation

The fossil fauna from the *Langbergia-Garjainia* Subzone can be correlated to the *Parotosuchus* Fauna of Russia via the co-occurrence of the erythrosuchid genus *Garjainia* and the temnospondyl genus *Parotosuchus*.

Age

Based on correlation with ammonite-containing rocks from the Cis-Caspian depression and western Kazakhstan, the *Parotosuchus* Fauna is dated as Early Triassic (late Olenekian; Shishkin et al., 2000). Based on the correlation proposed above an Early Triassic age has been accepted by most authors for the *Langbergia-Garjainia* Subzone (Hancox et al., 1995; Shishkin et al., 1995; Hancox and Rubidge 1997; Hancox 1998; Shishkin et al., 2000; Neveling, 2004; Shishkin et al., 2004; Rubidge, 2005; Gower et al., 2014).

Type locality

Extensive donga exposures on the farm Driefontein 11 in the Bethlehem District, Free State Province, is the stratotype locality for the *Langbergia-Garjainia* Subzone (Figure 5).

Trirachodon-Kannemeyeria Subzone

Proposer of name

This subzone is first proposed in this work.

Stratigraphic position

Biostratigraphic

The *Trirachodon-Kannemeyeria* Subzone occurs above the *Langbergia-Garjainia* Subzone and underlies the *Cricodon-Ufudocyclops* Subzone.

Lithostratigraphic

Occupies the middle part of the Burgersdorp Formation.

Derivation of name

This subzone is named after the distinctive and fairly common trirachodontid cynodont *Trirachodon berryi* and the distinctive dicynodont *Kannemeyeria simocephalus* that co-occur only in the strata defined by this subzone (Figure 6).

Historical background

The *Trirachodon-Kannemeyeria* Subzone as described here corresponds to the *Cynognathus* Assemblage Zone as described in Kitching (1995), and to Seeley's (1892) zone of specialised theriodonts, Broom's (1906a, 1909a) *Cynognathus* Beds, Kitching's (1970, 1977) *Cynognathus* Zone, the *Kannemeyeria* Assemblage Zone of Keyser and Smith (1978), the *Kannemeyeria-Diademodon* Assemblage Zone of Keyser (1979) and the *Cynognathus-Diademodon* Assemblage Zone of Kitching (1984).

It would also correspond to what has previously been referred to as the "middle subzone" (Hancox et al., 1995; Shishkin et al., 1995), "subzone B fauna" (Hancox and Rubidge 1997; Hancox 1998), the "Xenotosuchus grouping" (Shishkin 2000), and the *Cynognathus* B biozone (Rubidge, 2005).

Palaeontology

Description of subzone

The *Trirachodon-Kannemeyeria* Subzone is characterised by the occurrence of the cynodonts *Trirachodon berryi*, *Cricodon kannemeyerii*, *Cynognathus crateronotus* and *Diademodon tetragonus*, the dicynodont *Kannemeyeria simocephalus*, the temnospondyl *Xenotosuchus africanus* (Morales and Shishkin, 2002, Damiani, 2008) and to a lesser degree the erythrosuchid *Erythrosuchus africanus*. Actinopterygian fish are abundant near Rouxville, at the Bekkerskraal locality (Broom, 1909b, Hutchinson, 1973, Jubb and Gardiner, 1975). Plant fossils are rare but are known from two major localities in the vicinity of Aliwal North and Burgersdorp (Anderson and Anderson, 1985).

Taphonomic notes on fossil occurrences

Complete articulated skeletons are rare. Disarticulated, but well preserved, dispersed and isolated tetrapod fossils occur in mudstone/siltstone overbank deposits, frequently associated with calcareous concretions. Complete skulls of tetrapods also occur in fine-to medium-grained sandstone lenses. Fragmentary non-mammalian synapsid and amphibian remains frequently occur in localised "bone beds" within the mudstones, and also in conglomerates at the base of lenticular sandstones (Kitching, 1963).

List of fossils

See Figure 7 for ranges of the vertebrate genera.

Vertebrates

Pisces	<i>Atopocephala watsoni</i> <i>Ceratodus capensis</i> <i>Ceratodus ornatus</i> <i>Cleithrolepida extoni</i> <i>Coelacanthus africanus</i> <i>Elonichthys browni</i> <i>Helichthys browni</i> <i>Helichthys elegans</i> <i>Meidiichthys browni</i> <i>Ptychoceratodus phillipsi</i> <i>Saurichthys</i> sp. <i>Batrachosuchus browni</i> <i>Jammerbergia formops</i> <i>Laidleria gracillis</i> <i>Microposaurus casei</i> <i>Vanastega plurimidens</i> <i>Xenotosuchus africanus</i>
Amphibia	
Amniota	
Parareptilia	<i>Myocephalus crassidens</i> <i>Palaeodon browni</i> <i>Teratophyon spinigenis</i> <i>Theledectes perforates</i> <i>Thelephon contritus</i> <i>Thelerpeton oppressus</i>

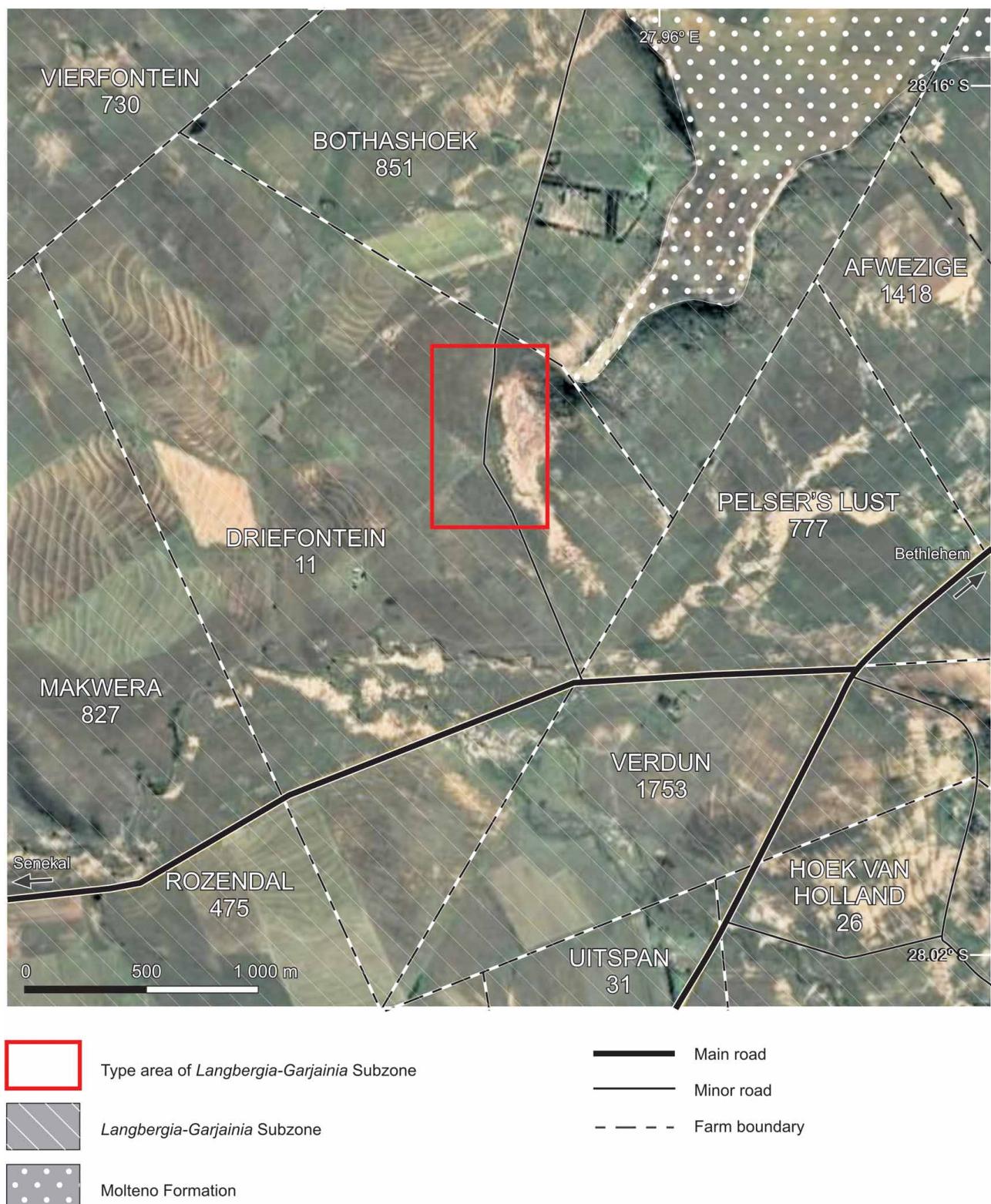


Figure 5. Map showing the Type locality of the Langbergia-Garjainia Subzone.

Eureptilia	
Archosauromorpha	<i>Eohydrosaurus wolvaardti</i> <i>Howesia browni</i> <i>Mesosuchus browni</i> <i>Erythrosuchus africanus</i> <i>Euparkeria capensis</i>
Synapsida	
Therapsida	
Anomodontia	<i>Kannemeyeria simocephalus</i> <i>Kombuisia frerensis</i>
Therocephalia	<i>Bauria cynops</i> <i>Melinodon simus</i> <i>Sesamodon browni</i> <i>Watsoniella breviceps</i>
Cynodontia	<i>Bolotridon frerensis</i> <i>Cricodon kannemeyeri</i> <i>Cynognathus crateronotus</i> <i>Diademodon tetragonus</i> <i>Lumkuia fuzzii</i> <i>Trirachodon berryi</i>
Trace fossils	
Vertebrate	Burrow casts
Invertebrate	Tetrapod coprolites <i>Cruiziana</i> sp. Arthropod trails
Invertebrates Mollusca	<i>Unio karooensis</i>
Plants	<i>Asterotheca</i> sp. <i>Burgersia papillophylla</i> <i>Calamites aliwalensis</i> <i>Cladophlebis</i> sp. <i>Dadoxylon</i> sp. <i>Dicroidium hughesii</i> <i>Dilatata kitchingii</i> <i>Ginkgoites dutoiti</i> <i>Lepidopteris brownie</i> <i>Lepidopteris madagascariensis</i> <i>Nilsonia reservolensis</i> <i>Pseudostenitis brownie</i> <i>Sewardiostrobus laxus</i> <i>Sphenobaiera browniana</i> <i>Sphenobaiera stormbergensis</i> Rhizoliths and rhizocretions

Geological description

Thickness

The thickness of the *Trirachodon-Kannemeyeria* Subzone varies from 500 m in the south between Queenstown and Lady Frere, to around 150 m between Burgersdorp and Aliwal North, and around 70 m in the vicinity of Thaba 'Nchu (Rutherford 2009, Rutherford et. al., 2015).

Lithology

For the most part, the strata of the middle part of the Burgersdorp Formation are characterised by fining upward

cycles of arenitic sandstone, overlain by thick sequences of fines. The sandstones of the Burgersdorp Formation are predominantly fine to medium grained and yellowish grey (5Y 7/2), light brownish grey (5Y 6/1), greenish grey (5GR 6/1), light olive grey (5Y 6/1) or greyish red purple (5RP 4/2) in colour. They tend to weather to dusky yellow (5Y 6/4), olive grey (5Y 3/2) or very dusky purple (5P 4/2). Fragmentary reptilian and amphibian fossil remains, as well as casts and imprints of fossil plant stems and leaves are, in many places, preserved in the sandstones. The finer fraction consists predominantly of greyish red (5R 4/2 to 10R 4/2) and greyish red purple mudstones (5RP 4/2), light bluish grey (5B 7/1), greenish grey (5G 6/1) and light olive grey (5Y 5/2) siltstones, and light bluish grey (5B 7/1) fine to very fine-grained sandstones. Well preserved, though non-abundant, remains of fossil reptiles and amphibians, as well as coprolites, rhizocretions, root casts and silicified wood are preserved in the finer grained rocks. Brown-weathering calcareous concretions encasing complete vertebrate skeletons are present within sandstones towards the middle part of the succession. Clay-pebble conglomerates containing fossilised bone are not uncommon in the biozone. Fines to sandstone ratios of \pm 4:1, and channel width to depth ratios of between 18 to 20 are common. The channel complex deposits are internally composed of channel and point bar elements, and characteristically display a classic fining upward sequence.

Depositional history

The sedimentary strata of the Burgersdorp Formation that preserve a *Trirachodon-Kannemeyeria* Subzone fauna were previously interpreted as being deposited by meandering, high sinuosity rivers, with fine grained sediment accumulating in an inland basin, receiving detritus from the south, southwest and southeast (Hiller and Stavrakis, 1984; Johnson and Hiller, 1990; Kitching, 1995; Groenewald, 1996; Hancox, 1998; Bordy and Krummeck, 2016; Bordy et al., 2019). The recognition of: thick and thin, lenticular, bedload and mixed-load dominated channel fill elements; low angle lateral accretion surfaces; point bars with interspersed mudstone couplets; a high suspended load/bedload ratio; and the presence of thick suspended load floodplain deposits with interspersed sandstone splays led Hancox (1998) to propose a mixed load, high sinuosity meandering fluvial system with frequent periods of overbank flooding and levee breach. The high variance and low vector strengths of the palaeocurrent data is further evidence for deposition by a high sinuosity meandering system rather than a low sinuosity system (Hancox, 1998; Bordy et al., 2019).

Boundaries

Lower boundary

The base of the *Trirachodon-Kannemeyeria* Subzone is defined as the first appearance of *Trirachodon berryi* and *Kannemeyeria simocephalus*, which are considered to occur at the same level.

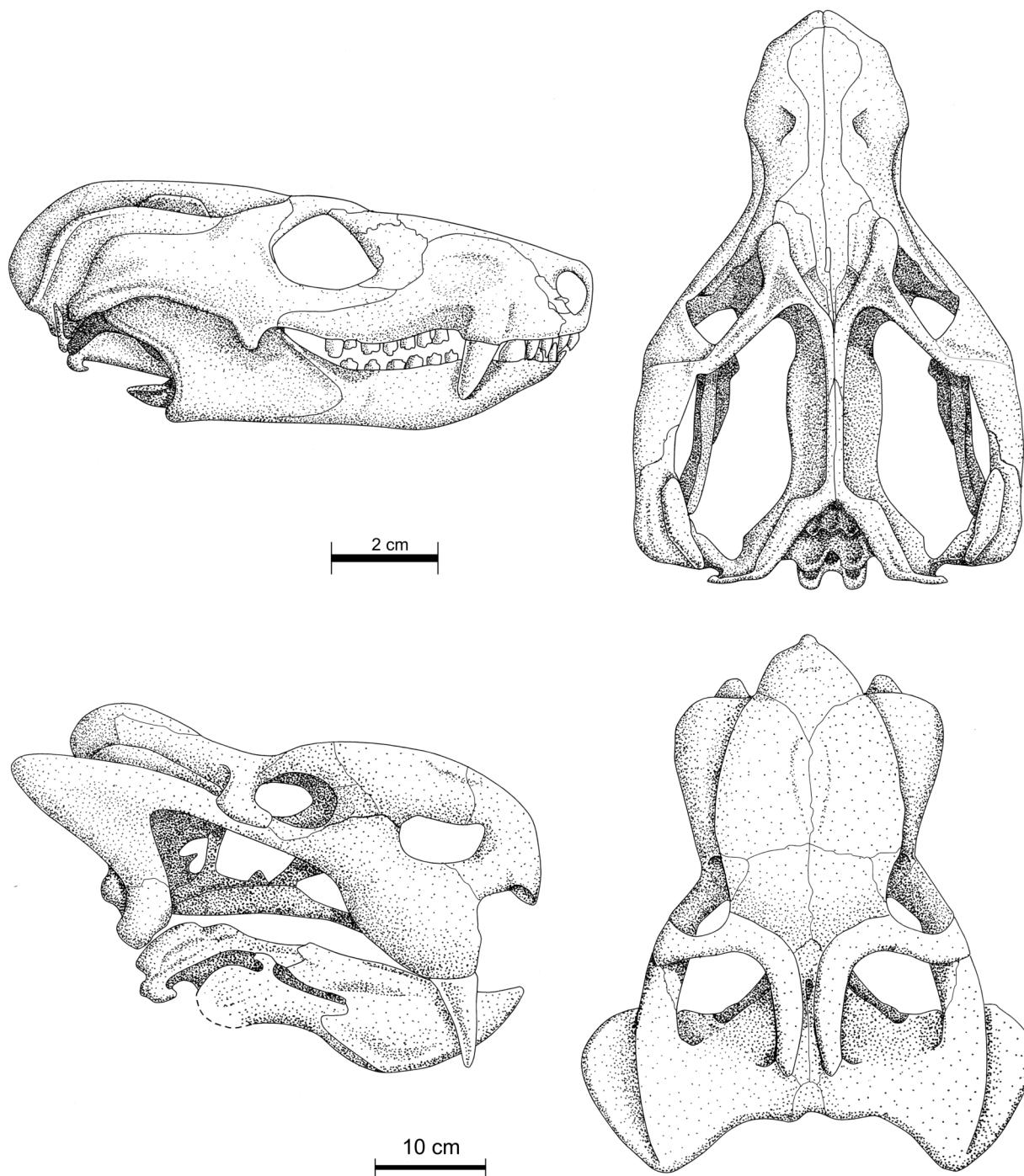


Figure 6. Illustration of the index taxa of the Trirachodon-Kannemeyeria Subzone in dorsal and lateral view. (top) *Trirachodon berryii*; (bottom) *Kannemeyeria simocephalus*.

Upper boundary

The top of this subzone is defined by the first appearance the dicynodont *Ufudocyclops mukanelai* and the cynodont *Cricodon metabolus*.

Lateral boundaries

The *Trirachodon-Kannemeyeria* Subzone has its greatest thickness in the southern part of the basin, and thins northward. In the south of the basin between Molteno and Zastron it is overlain by the Bamboesberg Member of the Molteno Formation, and from Zastron northwards by the overlying Indwe Member of the Molteno Formation.

Subdivisions

No subdivision of the *Trirachodon-Kannemeyeria* Subzone is proposed.

Regional aspects

Geographic distribution

Rocks containing a *Trirachodon-Kannemeyeria* fauna equate to the middle part of the Burgersdorp Formation (Hancox 1998; Neveling 2002) and outcrop from Cala and Queenstown in the south as far as Thaba 'Nchu in the north (Figure 2). From the Lady Frere and Queenstown districts the biozone has been traced as far east as the Engcobo district. In KwaZulu-Natal the biozone becomes progressively narrower as it thins in a northeasterly direction. In the far south of the basin these rocks are disconformably overlain by strata of the upper Burgersdorp

Formation whereas, progressing north of the town of Molteno, rocks containing a *Trirachodon-Kannemeyeria* fauna are disconformably overlain first by the Bamboesberg Member of the Molteno Formation, and north of Zastra, by the Indwe Member of the Molteno Formation.

Lateral and vertical variation

Complete specimens are not abundant but are fairly evenly distributed in the lower portion of the succession. They become scarcer in the upper part of the succession as well as showing a decrease in the variety of fossil forms, with fossil amphibian remains being relatively common. Paleontologically there is also a change towards a greater amount of preserved plant material, and an increase in the number of recovered specimens of *Kannemeyeria* in the upper part of the subzone (Hancox, 1998).

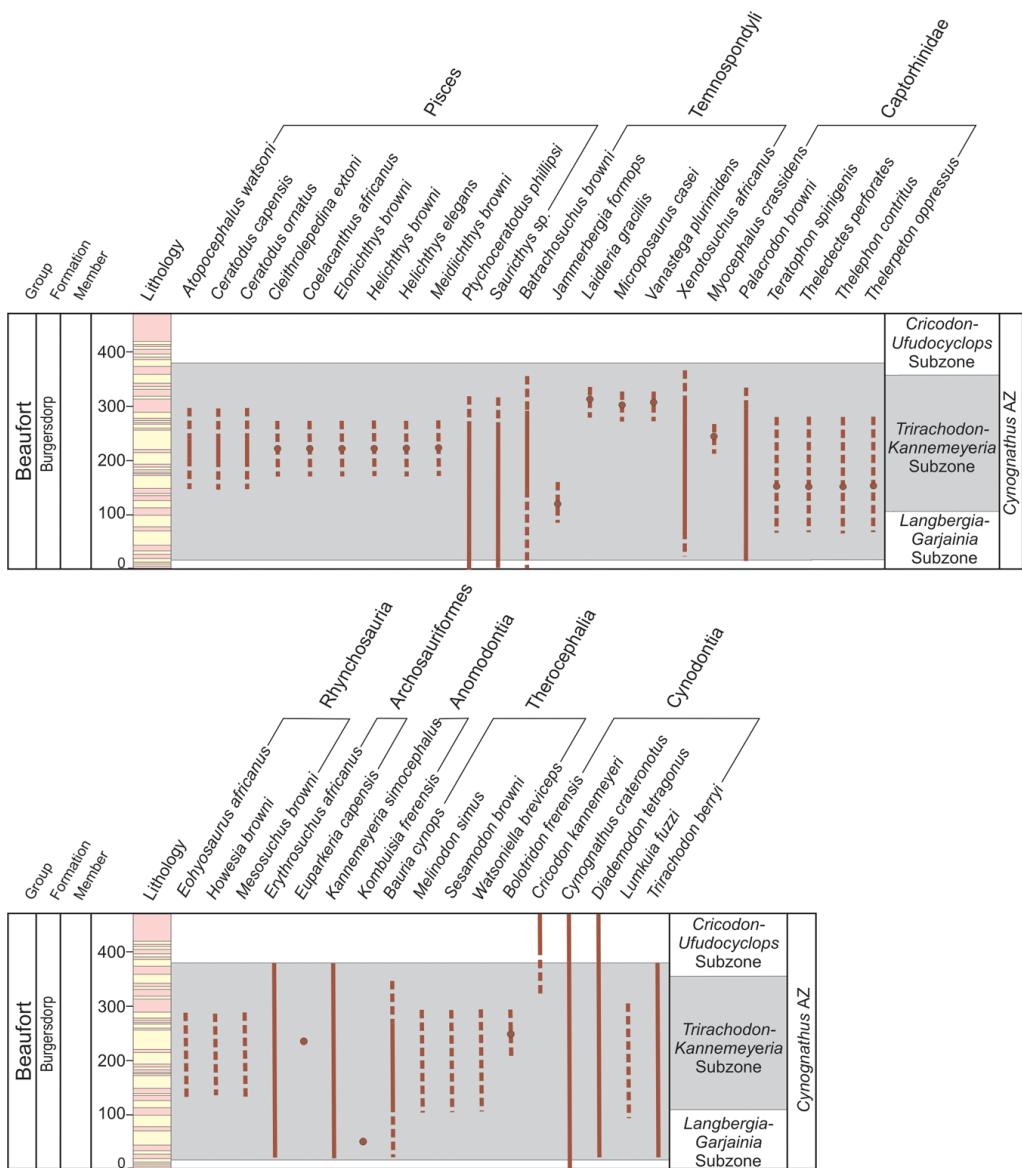


Figure 7. Stratigraphic ranges of vertebrate taxa occurring in the *Trirachodon-Kannemeyeria* Subzone.

Correlation

The *Trirachodon-Kannemeyeria* Subzone may be correlated to the Lower Omingonde Formation of Namibia (Keyser, 1973), the lower horizon of the Ntawere Formation of Zambia (Cruickshank 1965, 1986, Peecook et al., 2013, 2018, Wynd et al., 2018) the uppermost Kingori/lower Lifua members of Tanzania (Cruickshank 1965, 1986, Smith et al., 2018), the upper member of the Fremouw Formation of Antarctica (Sidor et al., 2008), the Lower Ermaying Formation of China (Li and Cheng, 1995) and the *Eryosuchus* Fauna of Russia.

South America, and particularly Argentina and southernmost Brazil, has an extensive record of non-marine Triassic sedimentary successions. Faunal links between terrestrial Triassic assemblages from South America and South Africa are however rare (Abdala and Smith 2009), and until recently were based only on the common presence of the cynodonts *Cynognathus crateronotus* (Bonaparte 1969, 1982; Abdala 1996) and *Diademodon tetragonus* (Martinelli et al., 2009) from the Río Seco de la Quebrada Formation (Stipanicic et al., 2007) of the Puesto Viejo Group of Argentina.

Age

No radiometric dates exist for the *Trirachodon-Kannemeyeria* Subzone strata and the ages are derived directly from correlation of fossil faunas with better-dated Gondwanan successions in Africa, South America and north China. Various age estimates have been given, but in general they are assigned a Middle Triassic (early Anisian) age (Keyser, 1973; Grine et al., 1979; Hammer, 1990; Hancox, 1998, 2000; Rubidge, 2005; Butler et al., 2015; Liu et al., 2017; but see also Ottone et al., 2014).

Type locality

The South African Committee for Stratigraphy (SACS, 1980) designated the Nonensis Nek area on the main road between Queenstown and Lady Frere as the stratotype locality for the *Kannemeyeria-Diademodon* Assemblage Zone and this is retained here for the *Trirachodon-Kannemeyeria* Subzone (Figure 8).

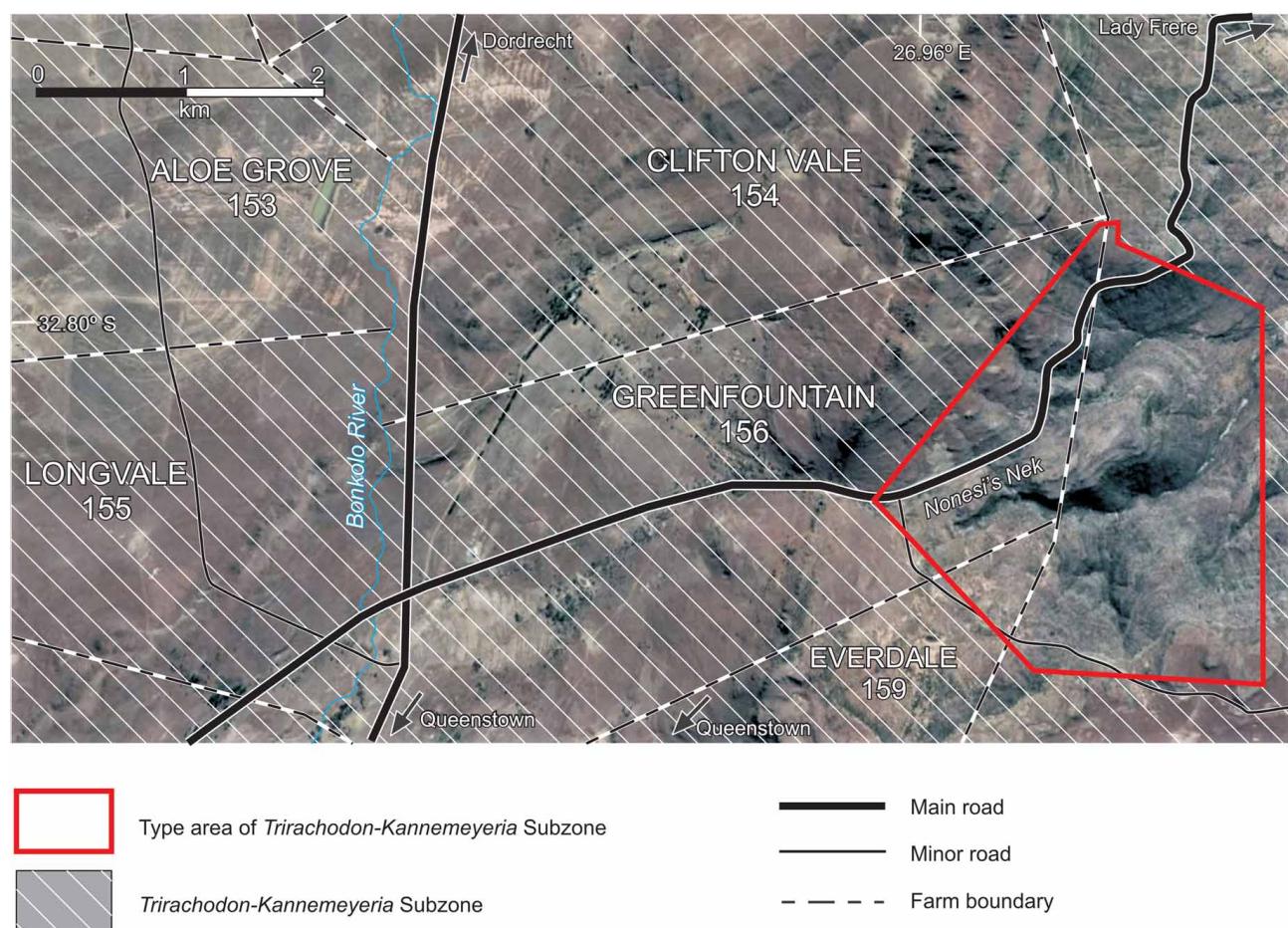


Figure 8. Map showing the Type locality of the *Trirachodon-Kannemeyeria* Subzone.

Cricodon-Ufudocyclops Subzone***Proposer of name***

This subzone is proposed in this paper.

Stratigraphic position***Biostratigraphic***

The *Cricodon-Ufudocyclops* Subzone occurs above the *Trirachodon-Kannemeyeria* Subzone. It is in turn disconformably overlain by the Bamboesberg Member of the Molteno Formation.

Lithostratigraphic

Occupies the uppermost part of the Burgersdorp Formation, which is roughly 150 m thick.

Derivation of name

This subzone is named after the distinctive and fairly common trirachodontid cynodont *Cricodon metabolus* and the distinctive dicynodont *Ufudocyclops mukanelai* that co-occur only in the strata defined by this subzone (Figure 9).

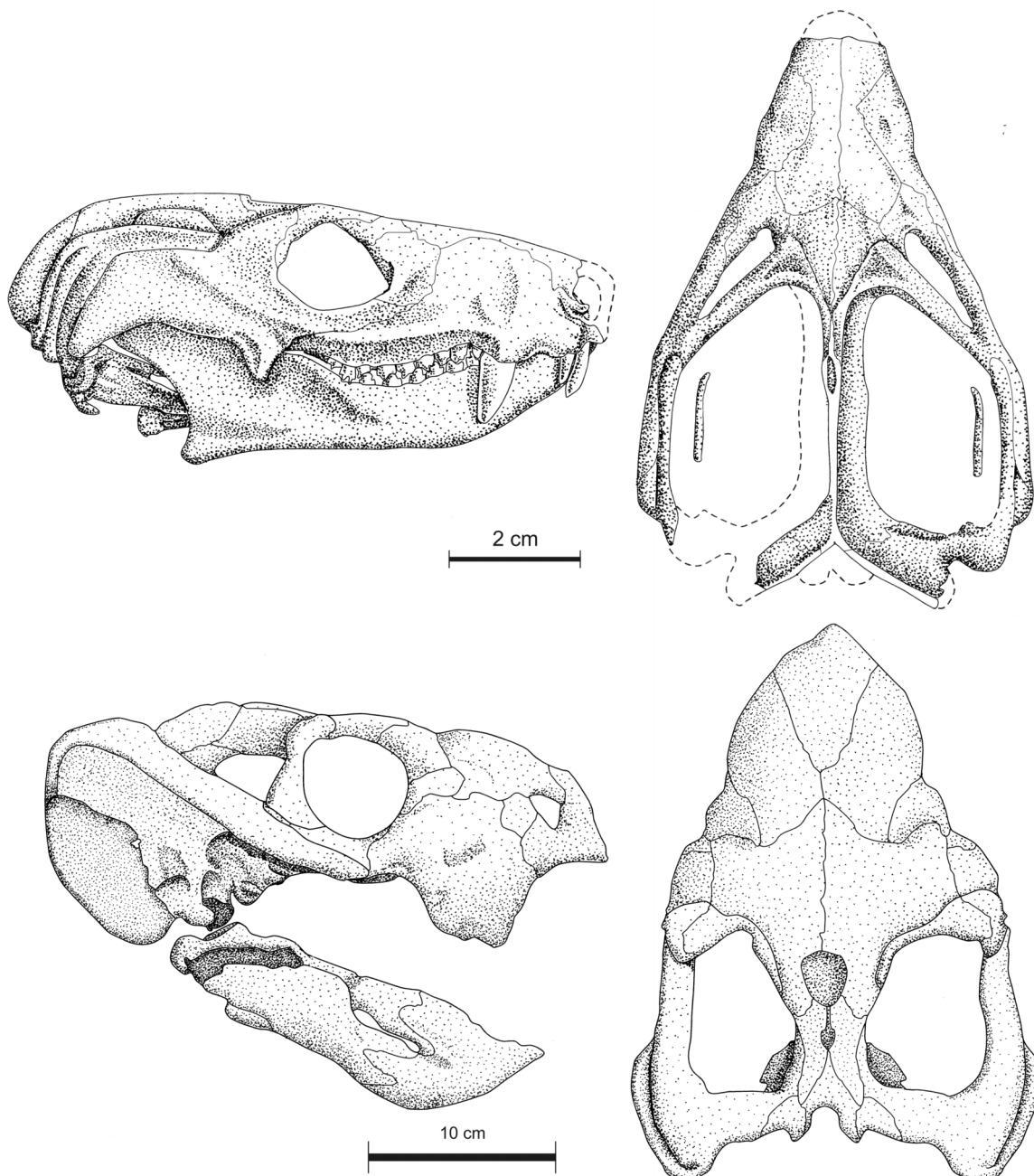


Figure 9. Illustration of the index taxa of the *Cricodon-Ufudocyclops* Subzone in dorsal and lateral view. (top) *Cricodon metabolus*; (bottom) *Ufudocyclops mukanelai*.

Historical background

The biozone was discovered by Graeme Morgan in the mid-1990s, with most of the descriptive work being that of Hancox (1998). Additional palaeontological descriptions are provided in Damiani and Hancox (2003), Abdala et al. (2005), Hancox et al. (2013) and Kammerer et al. (2019).

The *Cricodon-Ufudocyclops* Subzone corresponds to what has previously been referred to as the upper zone and uppermost faunal assemblage (Hancox et al., 1995), the “uppermost subzone” (Shishkin et al., 1995; Hancox and Rubidge 1996), subzone C (Hancox and Rubidge 1997; Hancox et al., 2000), the upper *Cynognathus* grouping (Shishkin et al., 2000), the *Cynognathus* C Biozone (Rubidge, 2005) and the *Cricodon* subdivision (Rubidge et al., 2016).

Palaeontology

Description of subzone

The *Cricodon-Ufudocyclops* Subzone is characterised by a dominance of cynodont fossils, particularly the index taxon *Cricodon metabolus*. It is a concurrent range zone characterised by the presence of *Cricodon metabolus* and the dicynodont *Ufudocyclops mukanelai*.

Taphonomic notes on fossil occurrences

Articulated skeletons are very rare. Disarticulated, but well preserved, dispersed and isolated tetrapod fossils occur in laminated mudstone/siltstone units. Complete skulls of tetrapods also occur in fine-to-medium grained sandstones and this mode of preservation is by far the most common in the subzone. Fragmentary therapsid and temnospondyl amphibian remains also occur in localised palaeosol horizons. No archosauriformes or fish are yet known from the subzone.

List of fossils

See Figure 10 for ranges of the vertebrate genera.

Vertebrates

Amphibia	<i>Paracyclotosaurus morganorum</i>
Amniota	
Synapsida	
Therapsida	
Anomodontia	<i>Ufudocyclops mukanelai</i>
	<i>Shansiodon</i> sp.
Cynodontia	<i>Cricodon metabolus</i>
	<i>Cynognathus crateronotus</i>
	<i>Diademodon tetragonus</i>

Trace fossils

<i>Skolithos</i> sp.
<i>Planolites</i> sp.
Worm burrows

Plants

<i>Calamites</i> sp.
<i>Dicroidium</i> sp.
<i>Podocarpoxylon</i> sp.
<i>Sphenobaiera</i> sp.

Geological description

Thickness

The biozone reaches a maximum thickness of 150 m in the Sterkstroom area of the Eastern Cape (Hancox, 1998).

Lithology

For the most part the strata of the upper part of the Burgersdorp Formation are characterised by fining upward cycles of sandstone, overlain by thick sequences of fines. The upper part of the Burgersdorp Formation has a higher percentage of sandstone than either the middle or lower sections, and the channel geometries are significantly deeper than in the underlying middle Burgersdorp Formation. The sandstone bodies also lack interspersed mudstone couplets within the point bar elements (Hancox, 1998). The sandstones of the upper Burgersdorp Formation are predominantly fine to medium grained and yellowish grey (5Y 7/2), light brownish grey (5Y 6/1), greenish grey (5GR 6/1), light olive grey (5Y 6/1) or greyish red purple (5RP 4/2) in colour. They tend to weather to dusky yellow (5Y 6/4), olive grey (5Y 3/2) or very dusky purple (5P 4/2). They are internally structured predominantly by horizontal and large scale trough cross-stratification.

Fragmentary and complete reptilian and amphibian fossil remains, as well as casts and imprints of fossil plant stems and leaves, are in many places preserved in the sandstones. The finer fraction consists predominantly of greyish red (5R 4/2 to 10R 4/2) and greyish red purple mudstones (5RP 4/2), light bluish grey (5B 7/1), greenish grey (5G 6/1) and light olive grey (5Y 5/2) siltstones, and light bluish grey (5B 7/1) fine to very fine-grained sandstones. Complete fossil tetrapod material may be preserved in places in the overbank fines, which in places are also pedogenically modified.

Depositional history

The gross fining upward sequence, sand body geometry, internal architecture (including point bar elements without mudstone drapes) and facies relationships of the channel sandstones in the upper Burgersdorp Formation resemble the classic high sinuosity, meandering stream model (Hancox, 1998). The abundance of upper flow regime horizontal stratification and large scale trough cross-stratification, with large mudstone intraclasts and high cut-banks are evidence for formation of the deposits in a mixed load large sized meandering river system with considerable bank relief and channel depth. The presence of abundant bank stabilising vegetation is directly evidenced by impressions of large fossil pteridosperm axes, casts of the sphenophyte *Calamites* and silicified wood (Hancox, 1998).

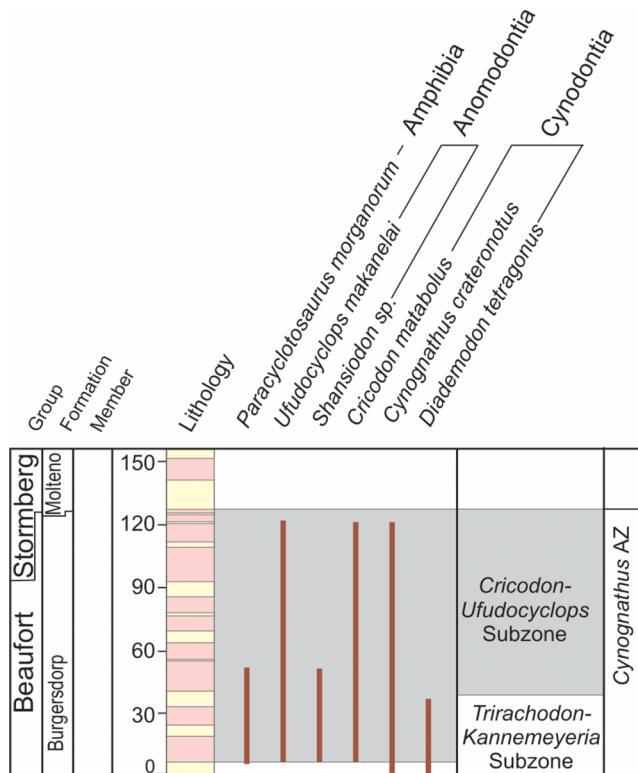


Figure 10. Stratigraphic ranges of vertebrate taxa occurring in the Cricodon-Ufudocyclops Subzone.

Boundaries

Lower boundary

The base of the *Cricodon-Ufudocyclops* Subzone is defined as the first appearance of *Cricodon metabolus* and *Ufudocyclops mukanelai*.

Upper boundary

The top of this subzone is undefined biostratigraphically because vertebrate fossils are lacking in the overlying Bamboesberg Member of the Molteno Formation.

Lateral boundaries

The *Cricodon-Ufudocyclops* Subzone occurs only in the southern part of the basin and is thickest in the Sterkstroom area. It thins northward and is overlain by the Bamboesberg Member of the Molteno Formation.

Subdivisions

No subdivision of the *Cricodon-Ufudocyclops* Subzone is proposed.

Regional aspects

Geographic distribution

Sedimentary rocks assigned to this subzone are best exposed in the Sterkstroom to Molteno districts and spatially, the *Cricodon-*

Ufudocyclops Subzone is restricted to this strip in the Bamboesberg Mountains of the Eastern Cape.

Lateral and vertical variation

Complete specimens are not abundant but are fairly evenly distributed in the succession. Cynodonts dominate the fauna. Fossils become scarcer in the upper part of the succession towards the contact with the Molteno Formation (Hancox, 1998).

Correlation

The fossil fauna of the *Cricodon-Ufudocyclops* Subzone may be correlated to parts of the upper Omingonde Formation of Namibia (Keyser 1973), the upper horizon of the Ntawere Formation of northeastern Zambia (Sidor and Hopson, 2018) and the Lifua beds of Tanzania (Wynd et al., 2018). The occurrence of *Paracylotosaurus* would allow for a genus level link to the Yerrapalli Formation of India (Damiani and Hancox, 2003), Wiannamatta Group of Australia (Watson 1958), and the occurrence of *Shansiodon* to the Upper Ermaying Formation (*Sinokannemeyeria* Fauna) of China (Li and Chen, 1995, Hancox, 1998, Hancox et al., 2013).

Age

No radiometric dates exist for the *Cricodon-Ufudocyclops* Subzone and the age arguments are derived directly from faunal correlation of the subzone. Based on these correlations the

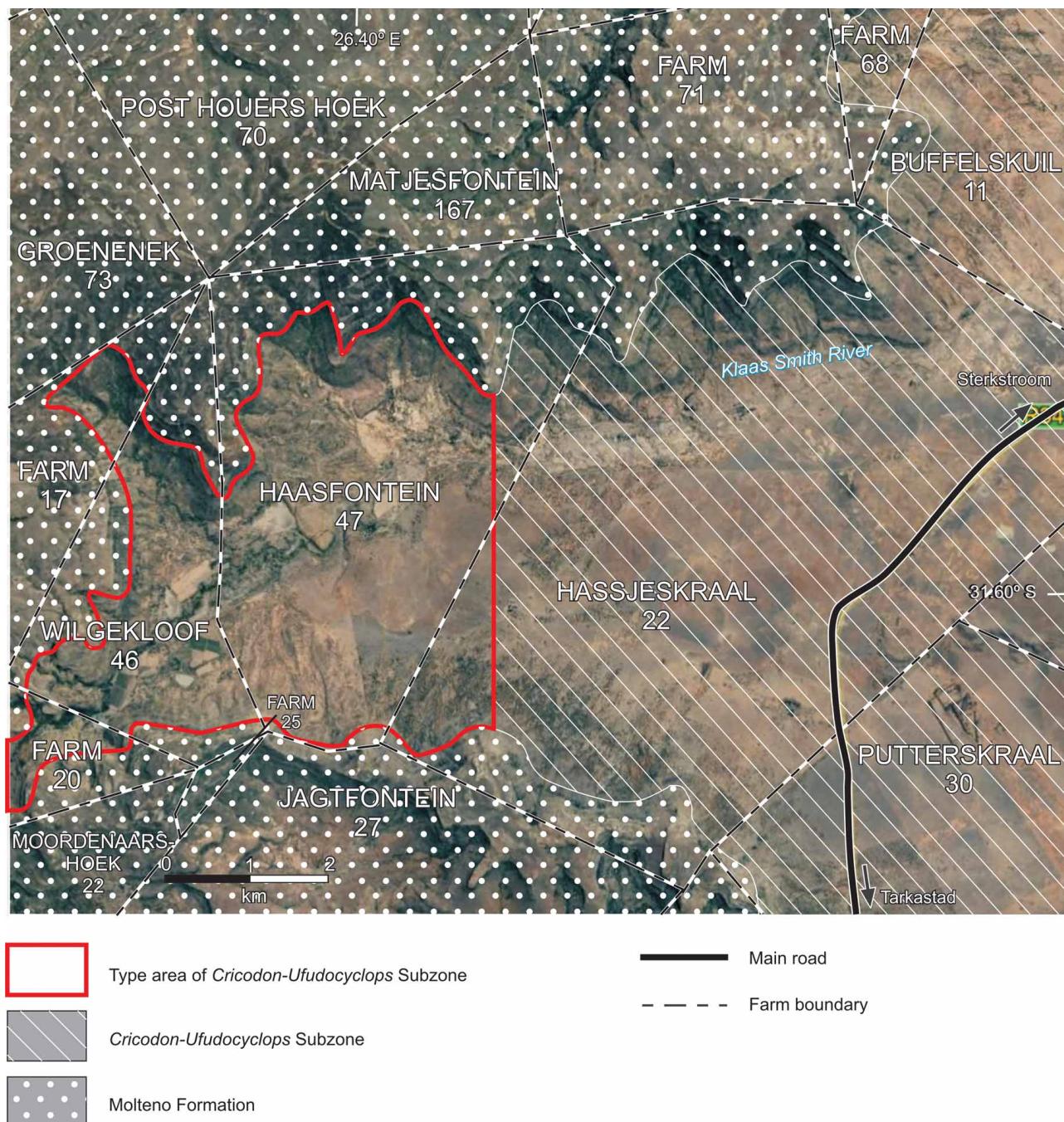


Figure 11. Map showing the Type locality of the *Cricodon-Ufudocyclops* Subzone.

Cricodon-Ufudocyclops Subzone may be considered as Middle Triassic (late Anisian or early Ladinian). Liu et al. (2017) have recently published a high resolution chemical abrasion–thermal ionization mass spectrometry (CA-TIMS) date of 243.53 Ma (late Anisian) for a volcanic ash interbedded with vertebrate fossils from the Ermaying Formation (*Sinokannemeyeria* Fauna) of China. The co-occurrence of *Shansiodon* in these two faunas may suggest that the *Cricodon-Ufudocyclops* Subzone is of a similar age. It should however be noted that Ottone et al. (2014) obtained a SHRIMP 238U/206Pb age of 235.8 ± 2.0 Ma, for a rhyolitic ignimbrite interdigitated between the Quebrada de los

Fósiles and Río Seco de la Quebrada formations (Puesto Viejo Group) in Argentina, which contains *Cynognathus* and *Diademodon*, and hence the uppermost parts of the *Cricodon-Ufudocyclops* Subzone may even reach into the Carnian (Late Triassic).

Type locality

We here designate exposures on the farm Avilion in the Sterkstroom District as the stratotype locality for the *Cricodon-Ufudocyclops* Subzone (Figure 11).

Acknowledgements

The senior author would like to record the important mentoring role of Professor James Kitching in igniting the spark of passion for the geology and palaeontology of the *Cynognathus* Assemblage Zone. The late Graeme Morgan is specifically acknowledged for the original discovery of the fossil fauna of the *Cricodon-Ufudoclyops* Subzone. We would also like to thank all the farmers who allowed access to their lands, for their permissions, and for the hospitality shown. Numerous colleagues who have helped collect in the biozone, particularly at the Driefontein site. You are too numerous to name individually, but we would like to thank you all collectively. Dr Eva Schneiderhan is thanked for her help collecting in the field and for her creation of the original type locality maps. We would like to acknowledge The African Origins platform of the National Research Foundation of South Africa (NRF), the Palaeontological Scientific Trust (PAST), and the DSIR/NRF Centre of Excellence for Palaeosciences for financial assistance. This work also benefitted greatly from a critical review by Professor Chris Sidor.

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