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Re-assessing the age of the type locality of *Nythosaurus larvatus* (Therapsida, Cynodontia) and implications on the evolutionary dynamics of cynodonts

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A B S T R A C T

Nythosaurus larvatus was one of the first cynodonts named and, for a long time, the only therapsid for which the endocranial cast was described. The holotype and only skull of this species is thus a landmark in the history of therapsid palaeontology. It is believed to have come from Commissie Drift 303 (Free State Province, South Africa), a locality that has been traditionally dated to the *Lystrosaurus declivis* Assemblage Zone. However, this age was mostly based on the synonymy between *Nythosaurus larvatus* and *Thrinaxodon liorhinus*, the former being the only fossil indisputably reported from this locality and the latter being an index taxon for the *Lystrosaurus declivis* Assemblage Zone. A recent revision of *Nythosaurus larvatus* also questioned the age of Commissie Drift. Here, we report the result of our fieldwork to re-assess the age of this locality. We find that the stratigraphy conforms to the lower Burgersdorp Formation and that the fossil tetrapod fauna does not match the *Lystrosaurus declivis* Assemblage Zone. The overall scarcity of fossil bones, absence of plants and dicynodonts, and relative dominance of amphibian remains all point to an assignation to the *Langbergia–Garjainia* Subzone of the *Cynognathus* Assemblage Zone, which is consistent with the stratigraphy. The discovery of new material attributable to cf. *Nythosaurus* bolsters the notion that this taxon is from the late Olenekian. *Nythosaurus larvatus* can safely be considered a valid taxon, and may in fact occur elsewhere in this subzone.

1. Introduction

Non-mammalian Cynodontia are the most direct ancestors of mammals among non-mammalian Therapsida (Abdala et al., 2020; Abdala, 2021). Understanding their evolution is key to deciphering the origin of modern mammalian biodiversity. The rich fossil record of the South African Karoo chronicles the transition from the basal-most cynodonts to the earliest mammals in great detail (Abdala et al., 2023; Norton et al., 2023). The first half of the Triassic, represented by the *Lystrosaurus declivis* and *Cynognathus* Assemblage Zones (AZs) in the Karoo Basin, is a pivotal interval of time that staged the extinction of archaic, non-eucynodont taxa and the evolutionary radiation of the Eucynodontia (Probainognathia and Cynognathia) that replaced them (Abdala et al., 2020; Abdala, 2021). Despite this, some rare cynodont taxa from this interval preserved a rather conservative body plan, evocative of Late Permian taxa (Pusch et al., 2021, 2022, 2024). Additionally, the recent works on *Lumkuia*, *Nythosaurus*, *Bolotridon*, *Progalesaurus*, and *Cistecynodon* highlight the so far underestimated uniqueness of the cynodont fauna of that time interval (Pusch et al., 2021, 2022, 2024; Benoit et al., 2022; Benoit, 2023). These taxa highlight the pivotal role that the fossil record of southern African Early Triassic cynodonts may play in better understanding the evolutionary dynamics at the root of the mammalian clade, as some taxa, and perhaps even a whole evolutionary radiation of cynodonts, may have gone unrecognised so far (Abdala et al., 2020; Abdala, 2021; Pusch et al., 2022, 2024).

Among these cynodonts, *Nythosaurus larvatus* (known only by its holotypic skull, NHMUK PV R1715) is of particular interest. It was originally described by Owen in 1876, which makes it one of the first cynodont taxa to be named; and for a long time, it was the only basal synapsid for which the brain endocast was illustrated and studied (Owen, 1876; Watson, 1913; Edinger, 1975; Hopson, 1979; MacLean, 1990). *Nythosaurus larvatus* was quickly considered synonymous with *Galesaurus planiceps* (Seeley, 1889), then *Thrinaxodon liorhinus* (Van Heerden, 1972, 1988) or considered a nomen dubium (Hopson and Kitching, 1972; Brink, 1988), but Pusch et al. (2022) recently resurrected the taxon based on a detailed redescription of NHMUK PV R1715 using μCT.

The type specimen is currently believed to have come from Commissie Drift 303 (sometimes spelled Kommissie Drift, Commissie Drift, Commissee Drift, or Kommissiedrift), a farm in the Smithfield District (Free State Province) (Broom, 1905, 1932; Kitching, 1977; Pusch et al., 2022). The specimen was presented to the NHMUK by W.G.

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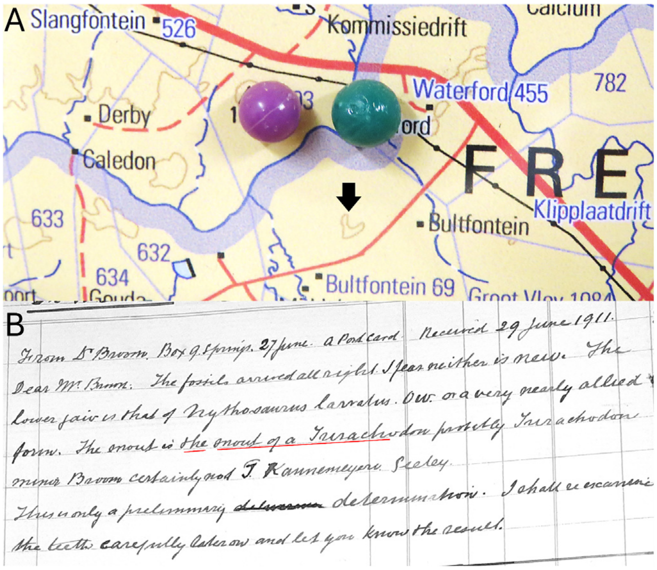
Atherstone of the Albany Museum in 1872, and accessioned into the NHMUK catalogue as *Galesaurus planiceps* (https://data.nhm.ac.uk/object/2cc6f0ba-6ba5-442c-b24e-9f88cd5cdfd0). The specimen was recognised as a new taxon and described as *Nythosaurus larvatus* by Owen (1876), but subsequently synonymised with *Galesaurus* by Seeley (1889). Seeley (1894) would later erect *Thrinaxodon liorhinus* for another specimen originally identified as *Galesaurus* (see, *e.g.*, Owen, 1887). Broom (1910, 1911) recognised NHMUK PV R1715 to be distinct from *Galesaurus*, and instead more similar to Seeley's *Thrinaxodon*. Broom (1910) synonymised *Thrinaxodon* with *Nythosaurus*, recognising that the latter had priority, and attributed the varied number of postcanines between NHMUK PV R1715 and other specimens of *Thrinaxodon* to be due to the individuals exhibiting different stages of tooth replacement. Broom (1932) would later recognise *Nythosaurus* to be distinct from *Thrinaxodon*, a view that was echoed by Parrington (1936), who also provided a list of characters to differentiate between the two taxa.

When he first proposed the *Lystrosaurus* and *Procolophon* beds, Broom (1906, 1915) listed "*Nythosaurus*" as coming from the "*Procolophon* zone"—*Procolophon trigoniceps* being the third index taxon for the current *Lystrosaurus declivis* AZ (Botha and Smith, 2020). It is extremely likely that despite writing *Nythosaurus*, Broom (1910, 1911, 1912, 1915) was in fact referring to both *Nythosaurus* and *Thrinaxodon* as he recognised that *Nythosaurus* had priority over *Thrinaxodon*. As a result from this convoluted history, it has been assumed that the holotype of *Nythosaurus larvatus* must have come from some outcrops of the Katberg Formation (Seeley, 1894; Broom, 1905, 1906, 1911, 1915, 1932). An Induan age for NHMUK PV R1715 is thus generally accepted (Pusch et al., 2022).

However, Pusch et al. (2021, 2022) have recently resurrected the taxon *Nythosaurus larvatus* and demonstrated that non-eucynodont cynodont taxa survived in the *Cynognathus* AZ. In fact, possible non-eucynodont cynodont-like teeth have been reported as late as the Cretaceous (Lasseron, 2019). All of the above make associations of "galesaurid-grade" taxa with the *Lystrosaurus declivis* AZ *de facto* obsolete. Moreover, as noted by Pusch et al. (2022), the geology at Commissie Drift 303 has not been addressed recently. Given the dramatic improvements in knowledge of the biostratigraphy of Karoo-aged deposits in southern Africa since the discovery of NHMUK PV R1715 (Smith et al., 2020), it is fair to question some of the assumptions made on the age of *Nythosaurus larvatus*.

On his wall-sized compilation of 1:250,000 topocadastral maps made in 1972 (see Benoit et al., 2024a), James Kitching placed two colour-coded pins on Commissie Drift 303: a green pin to represent his "*Lystrosaurus* zone" (roughly equivalent to today's *Lystrosaurus declivis* AZ and *Lystrosaurus maccaigi*–*Moschorhinus* Subzone of the *Daptocephalus* Assemblage Zone, Botha and Smith, 2020) and a purple one for his "*Daptocephalus* zone" (roughly equivalent to today's *Daptocephalus* AZ) (Fig. 1A). Neveling (2004) and Pusch et al. (2022) mention that there are exposures of the *Lystrosaurus declivis* and *Cynognathus* AZs in the area around Commissie Drift 303. On the 1:250,000 geological map of Aliwal North, the area is assigned to the Tarkastad Subgroup which encompasses the *Lystrosaurus declivis* and *Cynognathus* AZs. A provenance from the *Cynognathus* AZ is thus possible too. In a letter to the amateur palaeontologist Alfred Brown (Fig. 1B), Robert Broom identified a specimen from the Burgersdorp Formation as *Nythosaurus larvatus* (Brown's unpublished notebook Volume 15 page 424). This is most likely the same specimen Broom (1912) would later name *Nythosaurus browni*, now synonymised with *Cynognathus crateronotus* (Van Heerden, 1974). This shows that Broom considered that the range of *Nythosaurus larvatus* could have extended into the *Cynognathus* AZ. Noteworthily, the preservation style of specimen NHMUK PV R1715 (*i.e.*, haematitic nodule preserving a small cynodont skull and lower jaw in occlusion as an imprint on the surface of the nodule and exposing the brain endocast) has been described as "unusual" for the Katberg Formation (Pusch et al., 2022), but resembles that of SAM-PK-K11655 recently described from the Burgersdorp Formation at Lemoenfontein 44 (*i.e.*, the brittle bone is removed with the haematitic coating during erosion, exposing the brain endocast and cast of the bones; Wolvaardt et al., 2023).



From Dr Broom. Box 9. Springs. 27 June. a Post Card Received 29 June 1911.
Dear Mr Brown: The fossils arrived all right. I fear neither is new. The
lower jaw is that of Nythosaurus larvatus. Ow. or a very nearly allied
form. The snout is the snout of a Trirachodon probably Trirachodon
minor Broom certainly not T. Kannemeyeri Seeley.
This is only a preliminary ~~[illegible]~~ determination. I shall re examine
the teeth carefully later on and let you know the result.

Fig. 1. Unpublished historical documents referring to *Nythosaurus larvatus*. A, Excerpt of Kitching's (1972) wall-map showing the green ("*Lystrosaurus* zone") and purple ("*Daptocephalus* zone") pins. B, Excerpt from A. Brown's notes stating: "From Dr Broom. Box 9. Springs. 27 June. A postcard received 29 June 1911. Dear Mr Brown: The fossils arrived all right. I fear neither is new. The lower jaw is that of *Nythosaurus Larvatus* Ow. or a very nearly allied form. The snout is the snout of a *Trirachodon* probably *Trirachodon minor* Broom certainly not *T. Kannemeyeri* Seeley. This is only a preliminary determination. I shall re examine the teeth carefully later on and let you know the result."

As such, the possible age for the *Nythosaurus larvatus* holotype spans from the *Daptocephalus* to *Cynognathus* AZs, from as old as the latest Permian (255.2 Ma) to as young as the late Middle Triassic (243.53 Ma), or even early Late Triassic (235.8 Ma) (Hancox et al., 2020, but see Lucas and Hancox, 2022). Such an error margin of up to twenty million years is a pity given the historical and scientific importance of this specimen. Consequently, the stratigraphy and fossil fauna of Commissie Drift 303 are re-assessed based on new fieldwork data.

2. Material and methods

We explored Commissie Drift 303 (topocadastral map 3026BC, Koukraal; Mohokare Local Municipality; GPS: S30° 16,838′ E26° 38,113′) for a week in search of index fossils. Fieldwork involved surface collecting. The localities of all fossils were logged using GPS. Fragile fossils were consolidated with Paraloid B72. Mechanical preparation using airscribes was performed at the Evolutionary Studies Institute (ESI) of the University of the Witwatersrand, Johannesburg. Collecting was carried out under the South African Heritage Resources Agency (SAHRA) collection permit no. 3938 (CaseID: 21835). A stratigraphical section was logged using a Jacob's Staff fitted with an Abney level to record sedimentological features, log fossil stratigraphical positions, and identify the rock formations exposed at Commissie Drift 303 as accurately as possible.

Institutional abbreviations: BP: Evolutionary Studies Institute (formerly Bernard Price Institute), University of the Witwatersrand, Johannesburg, South Africa; NHMUK: Natural History Museum, London, United Kingdom; SAM: Iziko: South African Museum of Natural History, Cape Town, South Africa.

3. Results

3.1. Geology and stratigraphy

The geology at Commissie Drift 303 is best exposed on the only hill of the farm. The relatively small patches of outcrops are located at the base of the hill, by the N6 road (Fig. 2), conforming to the description of the site provided by Kitching (1977).

Owen (1876) described the type locality of *Nythosaurus larvatus* as being a 'Tafelberg' (a flat-topped hill in Afrikaans), but the hill on Commissie Drift 303 is more conical than flat (Fig. 2). Furthermore, Broom (1905) and subsequent authors (*e.g.*, Kitching, 1977) described the site as “East side of Commissee Drift, Caledon River”. However, Commissie Drift 303 is divided by the N6 road into two subplots, one to the north and another to the south. The outcrops are all located in the middle of the southern subplot, approximately where Kitching's purple pin is placed on his wall map (Fig. 1A). As such, the indication “East side of Commissee Drift, Caledon River”, makes little geographical sense. Maps from the early 1900s (available on the Digital Collection of the University of Cape Town; https://ibali.uct.ac.za/s/jacobson-africana/item/96949; https://ibali.uct.ac.za/s/jacobson-africana/item/97260) show that the boundaries of Commissie Drift 303 have not changed and that the farm did not extend East of the Caledon River. Interestingly, Kitching seemingly tried to align the geography with Broom's description of the locality by using two pins on his map, one on the hill (purple pin) and another (green pin) on the easternmost point of the farm (Fig. 1A, note that the latter is a “*Lystrosaurus* zone” pin that likely marks what he thought may be the locality where *Nythosaurus* was discovered). We visited the easternmost point of the farm and can confirm beyond any possible doubt that there are no outcrops there. If NHMUK PV R1715 was indeed found on Commissie Drift 303, it must have come from the foot of the conical hill.

Alternatively, it is possible that *Nythosaurus* may be from the neighbouring farm, Bultfontein 69, on the eastern bank of the Caledon River. This farm has a conspicuous flat-topped hill and exposes the same rocks as Commissie Drift 303 (Fig. 2B; GPS: S30° 17,835′ E26° 38,651′). This would perfectly reconcile the geography with Broom, Kitching, and Owen's descriptions of the type locality of *Nythosaurus larvatus*. This is plausible if the place referred to as “Commissee Drift” was, in fact, the drift road across the river rather than the farm itself.

The results presented below were collected at Commissie Drift 303 because it provided access to a more complete stratigraphical section and more extensive outcrops. The flat top hill on Bultfontein 69 only exposes a subset of the rocks available on Commissie Drift 303 (*i.e.*, the upper part of Horizon 1 and the Eldorado marker of Neveling, 2004, see below).

The exposures at Commissie Drift 303 match the lower Burgersdorp Formation in the proximal part of the basin (Fig. 3A, Neveling, 2004; Neveling et al., 2005). The lowest 25 m mostly includes very soft red–purple mudrock (Burgersdorp Horizon 1 in Neveling, 2004). The few identifiable fossils found in this horizon include one partial cynodont skull, a large theriodont canine (possibly *Cynognathus*), a temnospondyl cranial fragment, and three *in situ* tetrapod burrows, one of which contained a disarticulated partial archosauromorph skeleton (Fig. 3B–G).

This horizon is topped by a 5 m thick sandstone cap, which corresponds to the Eldorado marker (Fig. 3A). At the base of the sandstone, a thin pebble-lag delivered isolated amphibian bones (Fig. 3G). Above the Eldorado marker, about 80 m of blue–grey siltstone alternated with three fine-grained layers of grey sandstone (corresponding to the Burgersdorp Horizon 3 and Andriesberg member of Neveling, 2004) completes the sedimentary sequence (Fig. 3A). No fossils were recovered in these arenaceous layers. The hill is topped by a thick sill of dolerite.

3.2. Palaeontology

No fossil plants, procolophonids, or dicynodonts were found. Two large amphibian skull fragments were recovered from Horizon 1 (Fig. 3D, G). They can be referred to temnospondyls based on their large size and the fact that this is the only group of amphibians so far recovered in the Main Karoo Basin (Smith et al., 2020). The reticulate polygonal pattern on the bones is consistent with stereospondyls (Rinehart and Lucas, 2013). The largest fragment noticeably displays a cast of the internal surface of the cranial bones which resembles the preservation style of NHMUK PV R1715 (Fig. 3C).

The post-crania recovered in an *in situ* burrow at the base of Horizon 1 includes a well-preserved vertebra (Fig. 3E). This vertebra has an elongate centrum with the posterior articular surface positioned ventral to the level of the anterior one, identical to the ‘parallelogram-shaped’ centra that are typical of archosauromorph presacral vertebrae (Ezcurra et al., 2014; Ezcurra, 2016). The diapophysis and parapophysis are closely appressed and positioned on the anteroventral surface of the centrum, and the latter is about three times as long as high. These characters are typically present in the cervical vertebrae of most non-archosauriform archosauromorphs such as *Prolacerta* (BP/1/2675) from the *Lystrosaurus declivis* AZ, but differ markedly from the much shorter cervicals of rhynchosaurs and archosauriforms (Ezcurra, 2016), including *Garjaina*, the only named archosauromorph from the lower Burgersdorp Formation (Gower et al., 2014). However, the neural spine of this vertebra is approximately as tall as wide, which contrasts with the much shorter neural spine in *Prolacerta* (BP/1/2675). Other small-sized archosauromorphs have been found in the lower Burgersdorp Formation, but no cervical has been reported yet (Hancox et al., 2023). This is the first time that an early archosauromorph has been recovered in a burrow cast (although the disarticulated nature of the remains supports a post-mortem deposition rather than the animal dying *in situ*).

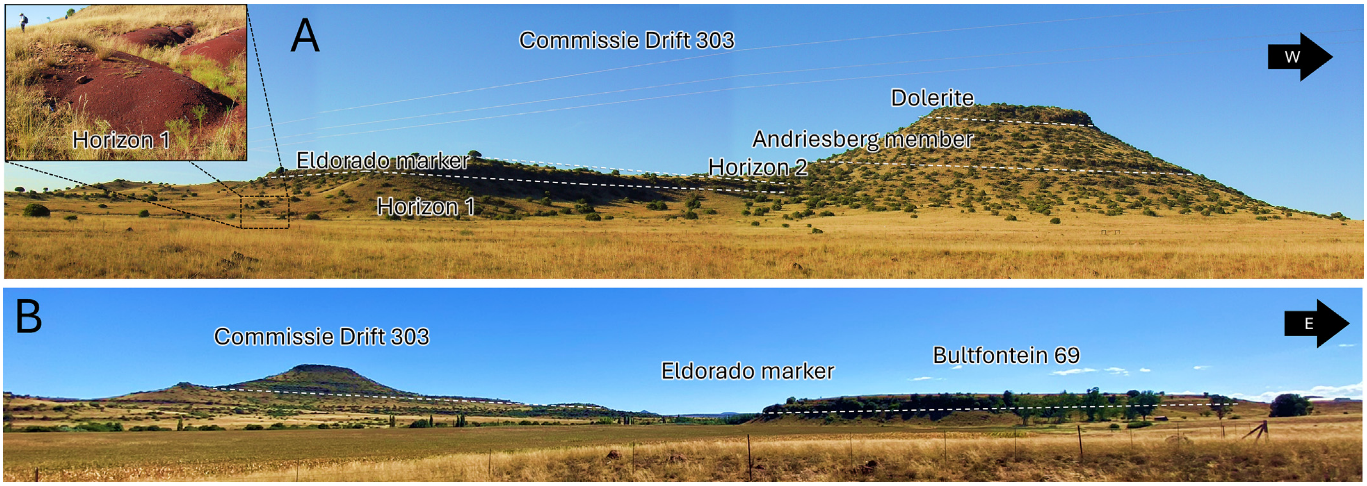


Fig. 2. Views of Commissie Drift 303. A, View from the N6 Road, with a magnification of Horizon 1. B, View from Bultfontein 69 showing the flat-topped hill to the right.

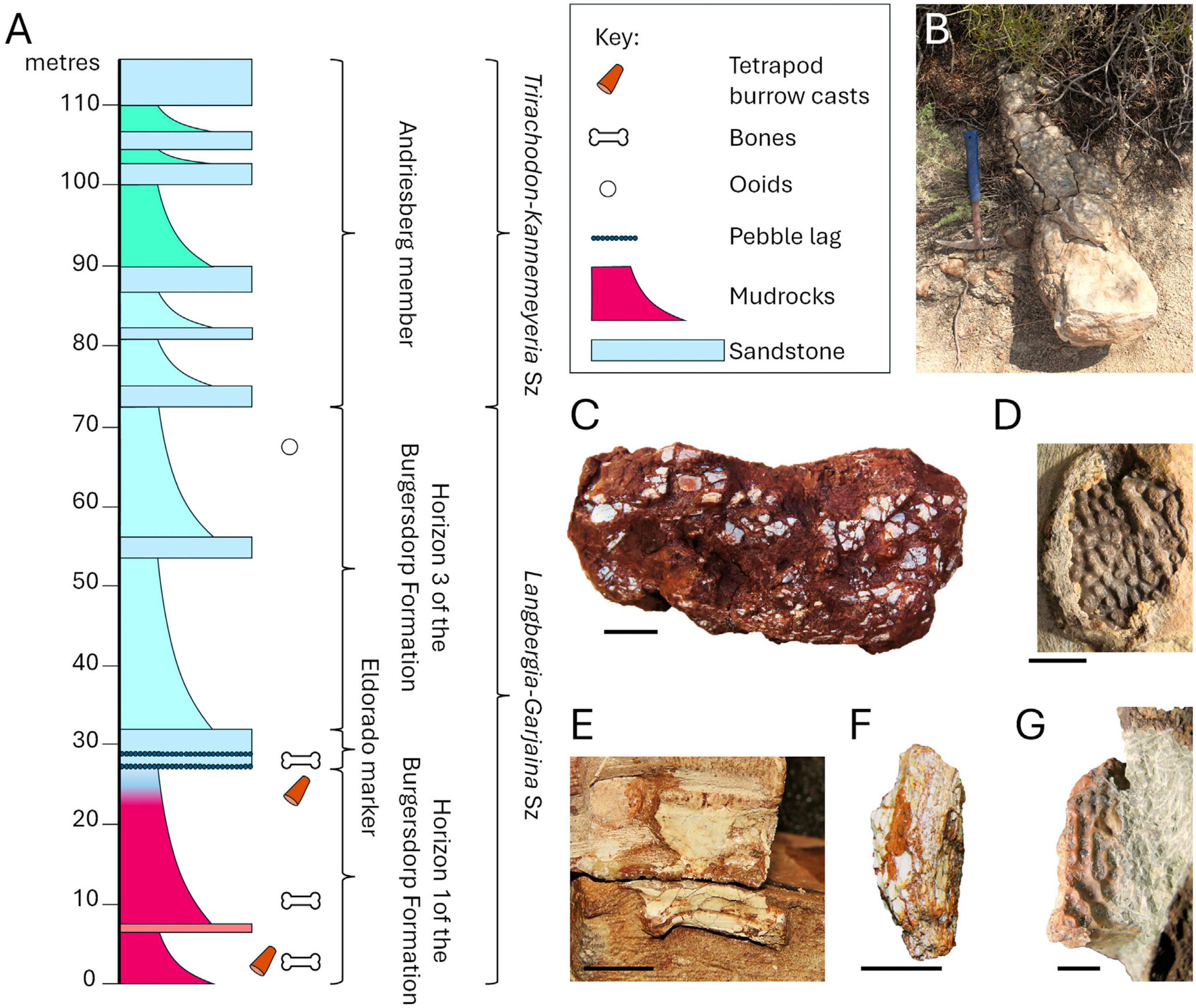


Fig. 3. Geology and palaeontology at Commissie Drift 303. A, Stratigraphical section. B, Tetrapod burrow cast *in situ*. C, Cf. *Nythosaurus* skull in lateral view (BP/1/9366). D, Cranial fragment of a temnospondyl indet. (BP/1/9368). E, Vertebra of an archosauromorph indet. in lateral view, anterior to the left (BP/1/9370). F, Fragment of a maxillary bone of a large theriodont, maybe *Cynognathus* (BP/1/9369); G, Cranial fragment of a temnospondyl indet. (BP/1/9367). Scale bars = 1 cm.

All three burrows discovered at Commissie Drift 303 show a bean-shaped cross section (Fig. 3B) similar to those traditionally attributed to the cynodont *Langbergia*, although the typical bifurcating morphology of the burrow is not preserved (Groenewald et al., 2001; Krapovickas et al., 2013; Bordy et al., 2019). No osteological remains attributable to this taxon were found, however.

One large canine fragment accompanied with casts of incisors or replacement teeth may be referrable to the largest carnivorous theriodont of the lower Burgersdorp Formation, *Cynognathus* (Figs. 3F, 4A).

The most diagnostic fossil found at Commissie Drift 303, besides NHMUK PV R1715, is a new partial cynodont skull (Figs. 3C, 4B). The highly fragmented skull preserves a lower and partial upper jaw. It is here referred to cf. *Nythosaurus* as it shares with the holotype the presence of five cusps on some of the upper postcanines (Fig. 4B). This elevated number of cusps distinguishes it from *Thrinaxodon*, *Galesaurus*, and every other known cynodont from the *Lystrosaurus declivis* AZ (Abdala et al., 2013; Pusch et al., 2019, 2022; Norton et al., 2020). Some *Thrinaxodon* specimens may have four cusps on the upper postcanines, but the extra cusp is in a labial position (Abdala et al., 2013). The presence of only sectorial teeth in this specimen excludes most cynognathians, as well as the probainognathian *Aleodon*, and it differs from *Cynognathus*, *Lumkuia*, and the specimen described by Abdala et al. (2005) by the absence of hooked cusps on the upper teeth (Abdala et al., 2020; Abdala, 2021).

4. Discussion

4.1. Fossil tetrapod fauna and age of Commissie Drift 303

As presented above, the lithology and stratigraphy at Commissie Drift 303 are referrable to the lower Burgersdorp Formation in the proximal part of the Main Karoo Basin (Neveling, 2004; Neveling et al., 2005). The same horizons are identified, including the thick mudrocks of Horizon 1, which departs quite sharply from the mostly arenaceous Katberg Formation. Our week of field work led to the discovery of only 14 tetrapod remains, most of them unidentifiable. Such scarcity of fossil tetrapods at Commissie Drift 303 is uncommon for a Triassic aged Main Karoo Basin locality, and more specifically is inconsistent with a *Lystrosaurus declivis* AZ age as this biozone is well-known for its abundance of fossil material (Kitching, 1977; Botha and Smith, 2020; Smith et al., 2022). Moreover, the *Lystrosaurus declivis* AZ does not extend into the lower Burgersdorp Formation (Botha and Smith, 2020).

Kitching (1977) reportedly found some *Lystrosaurus murrayi* to the “East of Commissie Drift”, but despite our best efforts to relocate this

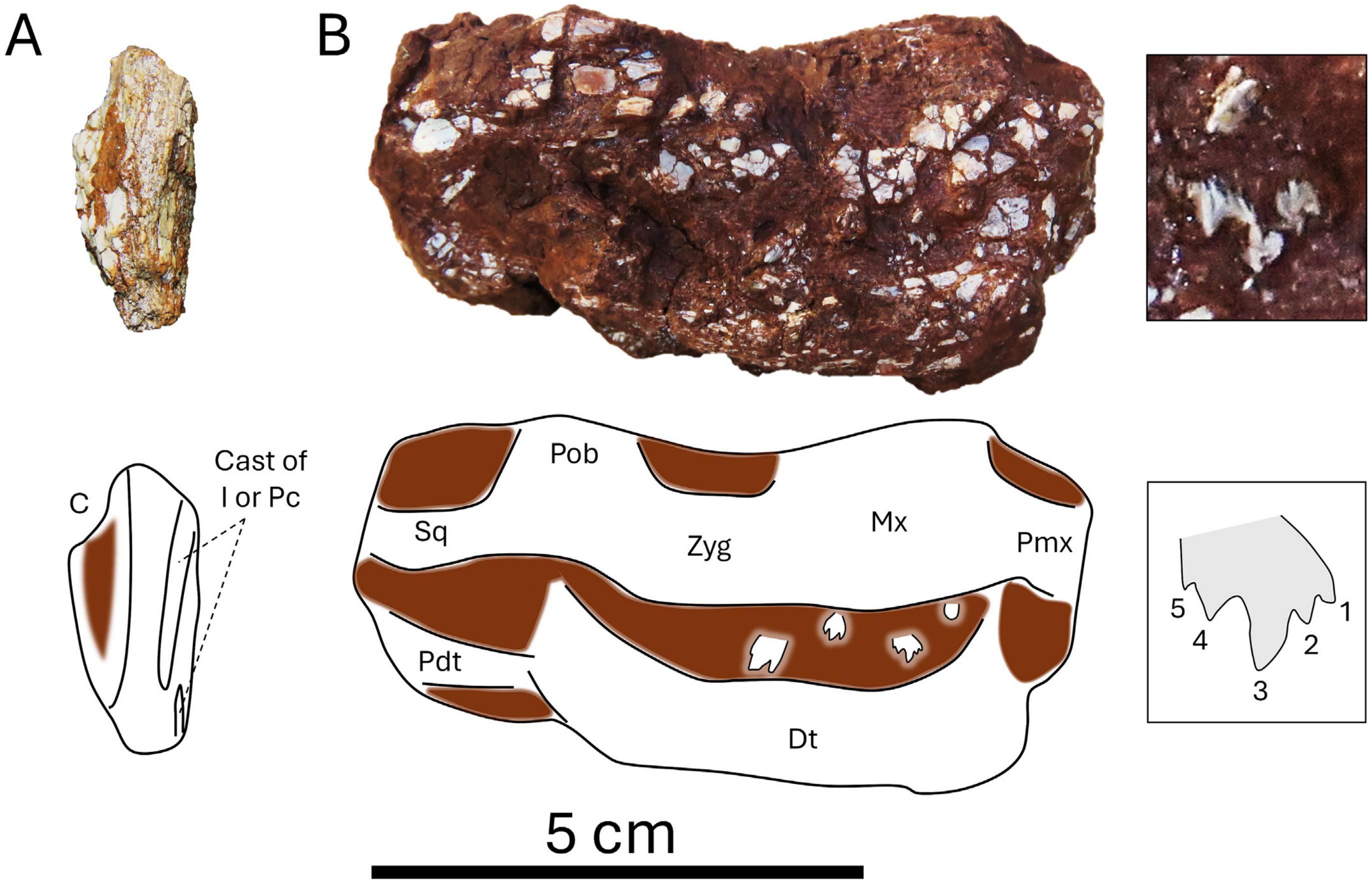


Fig. 4. Pictures (top) and interpretative drawings (bottom) of the two possible cynodonts discovered at Commissie Drift 303. A, Jaw fragment of ?*Cynognathus* (BP/1/9369). B, Skull of cf. *Nythosaurus* in lateral view (BP/1/9366), with a magnification of the second postcanine. Abbreviations: C, canine; Dt, dentary; I, incisor; Mx, maxilla; Pc, postcanine; Pdt, postdentary bones; Pmx, premaxilla; Pob, postorbital bar; Sq, squamosal; Zyg, zygomatic arch.

material at the Evolutionary Studies Institute, Iziko South African Museum of Natural History, and National Museum Bloemfontein, no specimen could be found. To our knowledge, the closest dicynodont fragment is an isolated tusk from Groenfontein, next to Smithfield, which was found some 15 km to the north-west of Commissie Drift. Moreover, no *Lystrosaurus* remains from the upper Katberg Formation can be firmly identified as *Lystrosaurus murrayi* (Neveling, 2004; Botha and Smith, 2020), which makes this reported occurrence quite suspicious. With *Nythosaurus larvatus* no longer considered synonymous with *Thrinaxodon liorhinus*, and no specimen of *Lystrosaurus* from Commissie Drift 303 located in any collections, there is simply no definite index fossil supporting a *Lystrosaurus declivis* AZ assignation for the rocks of this locality.

The fossil fauna we recovered includes mostly unidentifiable temnospondyl remains, tetrapod burrows, a partial cf. *Nythosaurus* skull, a large theriodont canine (possibly *Cynognathus*), and a small archosauromorph in a burrow (Figs. 3, 4). As detailed above, this archosauromorph differs from *Prolacerta* by its enlarged neural spine. This vertebra and the rest of the postcrania from this burrow cast may belong to one of the other small early archosauromorph taxa also known from the lower Burgersdorp Formation (Hancox et al., 2023). Similarly, *Nythosaurus* has been classically considered a *Lystrosaurus declivis* AZ cynodont, but a tooth from Driefontein 11 (Hancox et al., 2023; fig. 1), found in the *Langbergia*–*Garjainia* Subzone of the *Cynognathus* Assemblage Zone (LGCAZ), also matches the morphology of the lower postcanines of *Nythosaurus larvatus* (Pusch et al., 2022). More decisively, we found no plant, dicynodont, nor any procolophonid fossils, and the identifiable fauna is dominated by temnospondyl amphibians. In the Main Karoo Basin, this fauna is classically recovered in the LGCAZ and found in the lower Burgersdorp Formation (Hancox et al., 1995, 2020, 2023; Neveling, 2004; Neveling et al., 2005). Altogether, this supports that the rocks at Commissie Drift 303 belong to the LGCAZ, which suggests they would have been likely deposited during the late Olenekian (~247 Ma; Hancox et al., 2020), rather than during the Induan as previously assumed.

4.2. The validity of Nythosaurus and implications for cynodont evolution

The holotype of *Nythosaurus larvatus* is a rather poorly preserved skull that barely differs from *Thrinaxodon liorhinus*, and for these reasons has long been synonymised with the later or considered a nomen dubium (Pusch et al., 2022). Thanks to CT scanning, Pusch et al. (2022) demonstrated that the specimen preserves a complete palate and basicranium, and provided a more complete study of the holotypic skull. They resurrected the taxon based on the presence of a complete secondary palate, and differences in the dentition (*e.g.*, ten lower postcanines, whereas *Thrinaxodon* typically has nine or less, and the presence of five cusps on some upper postcanines, instead of three as in *Thrinaxodon*) and bony inner ear (enlarged posterior semicircular canal). Although the diagnostic value of these characters could be debated, the late Olenekian age of *Nythosaurus larvatus* now supports its distinctiveness as it no longer shares the same age as *Thrinaxodon liorhinus*.

Compared to other Triassic biozones, cynodonts are rare in the LGCAZ because of the paucity and bad state of preservation of fossils, and many remain undescribed (Abdala et al., 2005). Cynodonts are represented by some isolated teeth, including lower postcanines resembling those of *Nythosaurus* (Hancox et al., 2023, fig. 1r), but the more diagnostic material supports that *Langbergia* and *Cynognathus* are the only valid cynodont taxa from this subzone (Abdala et al., 2020; Hancox

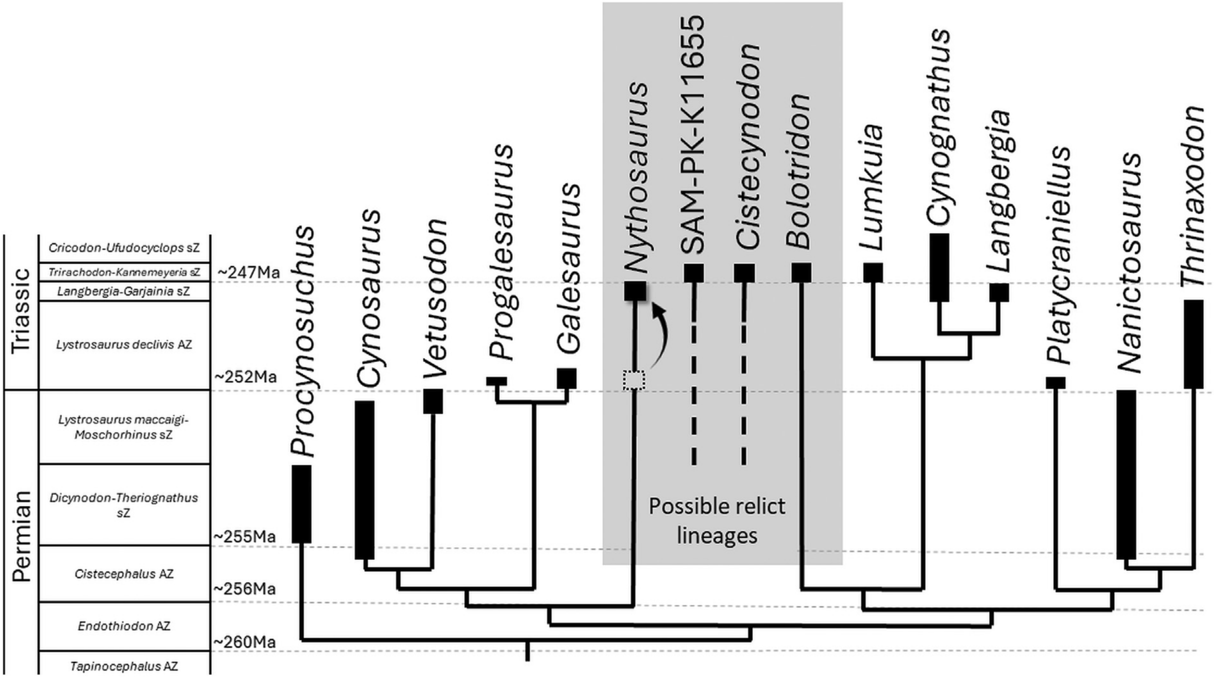


Fig. 5. Phylogeny of cynodont (after Pusch et al., 2024) illustrating the new stratigraphical position of *Nythosaurus larvatus*, and how it closely allies with other non-eucynodont relict taxa from the *Cynognathus* AZ. Phylogenetic placement of SAM-PK-K11655 and *Cistecynodon* hypothesised from Wolvaardt et al. (2023) and Benoit et al. (2024a), respectively.

et al., 2020; Abdala, 2021). Abdala et al. (2005) also briefly described an unnamed species of cynognathian cynodont from the LGCAZ. The validity and hereby recognised late Olenekian age of *Nythosaurus larvatus* increase the number of documented cynodont taxa in the LGCAZ to four (Fig. 5). Note that Abdala et al. (2020) and Abdala (2021) consider that *Lumkuia fuzzi* is from the LGCAZ, whereas a provenance from the *Trirachodon–Kannemeyeria* Subzone of the *Cynognathus* AZ is more generally accepted (Hancox et al., 2020; Benoit et al., 2022).

5. Conclusion

The geological and palaeontological re-assessment of the type locality of the cynodont *Nythosaurus larvatus* support a late Olenekian age and its validity as a distinct taxon. The “galesaurid-grade” morphology of *Nythosaurus larvatus* makes it a relict non-eucynodont taxon compared to the more derived cynognathians and probainognathians that began their evolutionary radiation in the late Olenekian (Abdala et al., 2020; Abdala, 2021; Pusch et al., 2022). Other non-eucynodont taxa from the *Cynognathus* AZ include *Cistecynodon*, *Bolotridon*, and a possible new taxon from Lemoenfontein 44 (Fig. 5; Abdala and Giannini, 2002; Pusch et al., 2021; Wolvaardt et al., 2023; Benoit et al., 2024b). So far, Africa is the only continent where non-eucynodont cynodonts are known to have survived into the *Cynognathus* AZ and even, perhaps, into the Cretaceous (Lasseron, 2019). Instead of being the result of an evolutionary radiation, these taxa suggest that Africa may have been a refugium for non-eucynodont species. Many cynodont specimens from the *Cynognathus* AZ are still unidentified (Abdala et al., 2005) and their description will be crucial to address this hypothesis in the future.

CRediT authorship contribution statement

J. Benoit: Writing – review & editing, Writing – original draft, Validation, Supervision, Funding acquisition, Formal analysis, Conceptualization. **S. Jirah:** Writing – review & editing, Validation, Methodology, Data curation. **E.S. Lund:** Writing – review & editing, Visualization, Methodology. **T. Lafferty:** Writing – review & editing, Methodology. **V. Buffa:** Writing – review & editing, Writing – original draft. **L.A. Norton:** Writing – review & editing, Methodology.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Abdala, F., 2021. Permo–Jurassic cynodonts: the early road to mammalness. In: Alderton, D., Elias, S.A. (Eds.), Encyclopedia of Geology, 2nd edition vol. 3. Academic Press, United Kingdom, pp. 206–226.

Abdala, F., Giannini, N.P., 2002. Chiniquodontid cynodonts: systematic and morphometric considerations. Palaeontology 45, 1151–1170. https://doi.org/10.1111/1475-4983.00280.

Abdala, F., Neveling, J., Rubidge, B.S., 2005. A new cynodont from the base of the *Cynognathus* Assemblage Zone (Lower Triassic) of the Karoo Basin: wrong teeth or wrong skull? In: Pankhurst, R.J., Veiga, G.D. (Eds.), Gondwana 12: Geological and Biological Heritage of Gondwana. Academia Nacional de Ciencias, Cordoba, Argentina, p. 31

Abdala, F., Jasinoski, S.C., Fernandez, V., 2013. Ontogeny of the Early Triassic cynodont *Thrinaxodon liorhinus* (Therapsida): dental morphology and replacement. Journal of Vertebrate Paleontology 33, 1408–1431. https://doi.org/10.1080/02724634.2013.775140.

Abdala, F., Gaetano, L.C., Martinelli, A.G., Soares, M.B., Hancox, P.J., Rubidge, B.S., 2020. Non-mammaliaform cynodonts from western Gondwana and the significance of Argentinean forms in enhancing understanding of the group. Journal of South American Earth Sciences 104, 102884. https://doi.org/10.1016/j.jsames.2020.102884.

Abdala, F., Hendrickx, C., Jasinoski, S.C., Gaetano, L.C., Liu, J., 2023. The pre-eminence of the Karoo Basin in the knowledge of the Permo–Jurassic cynodonts: a historical synthesis and taxonomical quantification. Palaeontologia Africana 56, 213–227.

Benoit, J., 2023. Synchrotron scanning reveals the deep evolutionary root of the mammalian brain: the surprisingly advanced endocast morphology of *Lumkuia fuzzi* (Cynodontia: Probainognathia). Palaeontologia Africana 56, 103–110.

Benoit, J., Nxumalo, M., Norton, L.A., Gaetano, L.C., Rubidge, B., Abdala, F., 2022. Synchrotron scanning sheds new light on *Lumkuia fuzzi* (Therapsida, Cynodontia) from the Middle Triassic of South Africa and its phylogenetic placement. Journal of African Earth Sciences 196, 104689. https://doi.org/10.1016/j.jafrearsci.2022.104689.

Benoit, J., Kammerer, C.F., Dollman, K., Groenewald, D.P., Smith, R.M.H., 2024a. Did gorgonopsians survive the end-Permian "Great Dying"? A re-appraisal of three gorgonopsian specimens (Therapsida, Theriodontia) reported from the Triassic *Lystrosaurus declivis* Assemblage Zone, Karoo Basin, South Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 638, 112044. https://doi.org/10.1016/j.palaeo.2024.112044.

Benoit, J., Araujo, R., Lund, E.S., Bolton, A., Lafferty, T., Macungo, Z., Fernandez, V., 2024b. Early synapsids neurosensory diversity revealed by CT and synchrotron scanning. Anatomical Record 2024, 1–18. https://doi.org/10.1002/ar.25445.

Bordy, E.M., Sztanó, O., Rampersadh, A., Almond, J., Choiniere, J.N., 2019. Vertebrate scratch traces from the Middle Triassic Burgersdorp Formation of the main Karoo Basin, South Africa: sedimentological and ichnological assessment. Journal of African Earth Science 160, 103594. https://doi.org/10.1016/j.jafrearsci.2019.103594.

Botha, J., Smith, R.M.H., 2020. Biostratigraphy of the *Lystrosaurus declivis* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa. South African Journal of Geology 123, 207–216.

Brink, A.S., 1988. Illustrated Bibliographical Catalogue of the Synapsida. Handbook 10, Part II. Geological Survey, Department of Mineral and Energy Affairs, South Africa.

Broom, R., 1905. Notes on the localities of some type specimens of the Karoo fossil reptiles. Records of the Albany Museum 1 (4), 275–278.

Broom, R., 1906. On the Permian and Triassic faunas of South Africa. Geological Magazine 3, 29–30. https://doi.org/10.1017/S001675680012271X.

Broom, R., 1910. Observations on some specimens of South African fossil reptiles preserved in the British Museum. Transactions of the Royal Society of South Africa 2, 19–25. https://doi.org/10.1080/00359191009519357.

Broom, R., 1911. On the structure of the skull in cynodont reptiles. Proceedings of the Zoological Society of London 81, 893–925. https://doi.org/10.1111/j.1096-3642.1911.tb01962.x.

Broom, R., 1912. On some new fossil reptiles from the Permian and Triassic Beds of South Africa. Proceedings of the Zoological Society of London 82, 1073–1082. https://doi.org/10.1111/j.1469-7998.1912.tb07564.x.

Broom, R., 1915. Croonian lecture: on the origin of mammals. Philosophical Transactions of the Royal Society of London B 206, 1–48. https://doi.org/10.1098/rstb.1915.0001.

Broom, R., 1932. The Mammal-like Reptiles of South Africa and the Origin of Mammals. H. F. & G, Witherby, London.

Edinger, T., 1975. Paleoneurology 1804–1966: an annotated bibliography. Advances in Anatomy, Embryology and Cell Biology 49, 3–258.

Ezcurra, M.D., 2016. The phylogenetic relationships of basal archosauromorphs, with an emphasis on the systematics of proterosuchian archosauriforms. PeerJ 4, e1778.

Ezcurra, M.D., Scheyer, T.M., Butler, R.J., 2014. The origin and early evolution of Sauria: reassessing the Permian saurian fossil record and the timing of the crocodile–lizard divergence. PLoS One 9, e89165.

Gower, D.J., Hancox, P.J., Botha-Brink, J., Sennikov, A.G., Butler, R.J., 2014. A new species of *Garjainia* Ochev, 1958 (Diapsida: Archosauriformes: Erythrosuchidae) from the Early Triassic of South Africa. PLoS One 9, e111154.

Groenewald, G.H., Welman, J., Maceachern, J.A., 2001. Vertebrate burrow complexes from the Early Triassic *Cynognathus* Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa. Palaios 16, 148–160. https://doi.org/10.1669/0883-1351(2001)016<0148:VBCFTE>2.0.CO;2.

Hancox, P.J., Shishkin, M.A., Rubidge, B.S., Kitching, J.W., 1995. A threefold subdivision of the *Cynognathus* Assemblage Zone (Beaufort Group, South Africa) and its palaeogeographic implications. South African Journal of Science 91, 143–144.

Hancox, P.J., Neveling, J., Rubidge, B.S., 2020. Biostratigraphy of the *Cynognathus* assemblage zone (Beaufort group, Karoo supergroup), South Africa. South African Journal of Geology 123, 217–238. https://doi.org/10.25131/sajg.123.0016.

Hancox, P.J., Montgomery, C., Heckert, A., Duffin, C., Hoffman, D., Schneiderhan, E., 2023. The fauna of the Lower Burgersdorp Formation (*Cynognathus* Assemblage Zone–*Langbergia* Subzone) of South Africa. The Anatomical Record 306, 121–124.

Hopson, J.A., 1979. Paleoneurology. In: Gans, C., Northcutt, R.G., Ulinski, P. (Eds.), Biology of the Reptilia. Academic Press, New York, pp. 39–146.

Hopson, J.A., Kitching, J.W., 1972. A revised classification of the cynodonts (Reptilia, Therapsida). Palaeontologia Africana 14, 71–85.

Kitching, J.W., 1977. The Distribution of the Karroo Vertebrate Fauna: With Special Reference to Certain Genera and the Bearing of this Distribution on the Zoning of the Beaufort Beds. Bernard Price Institute for Palaeontological Research, University of the Witwatersrand.

Krapovickas, V., Mancuso, A.C., Marsicano, C.A., Domnanovich, N.S., Schultz, C.L., 2013. Large tetrapod burrows from the Middle Triassic of Argentina: a behavioural adaptation to seasonal semi-arid climate? Triassic tetrapod burrows from Argentina. Lethaia 46, 154–169. https://doi.org/10.1111/j.1502-3931.2012.00329.x.

Lasseron, M., 2019. Enigmatic teeth from the Jurassic–Cretaceous transition of Morocco: the latest known non-mammaliaform cynodonts (Synapsida, Cynodontia) from Africa? Comptes Rendus Palevol 18, 897–907. https://doi.org/10.1016/j.crpv.2019.05.002.

Lucas, S.G., Hancox, P.J., 2022. Definition, correlation and age of the *Cynognathus* Assemblage Zone, Lower–Middle Triassic of Pangea. Paleontological Journal 56, 1518–1537. https://doi.org/10.1134/S0031030122110089.

MacLean, P.D., 1990. The Triune Brain in Evolution: Role in Paleocerebral Functions. Plenum Press, New York.

Neveling, J., 2004. Stratigraphic and sedimentological investigation of the contact between the *Lystrosaurus* and *Cynognathus* Assemblage Zones (Beaufort Group: Karoo Supergroup). Council for Geoscience Bulletin 137, 1–165.

Neveling, J., Hancox, P.J., Rubidge, B.S., 2005. Biostratigraphy of the lower Burgersdorp Formation (Beaufort Group; Karoo Supergroup) of South Africa — implications for the stratigraphic ranges of early Triassic tetrapods. Palaeontologia Africana 41, 81–87.

Norton, L.A., Abdala, F., Rubidge, B.S., Botha, J., 2020. Tooth replacement patterns in the Early Triassic epicynodont *Galesaurus planiceps* (Therapsida, Cynodontia). PLoS One 15 (12), e0243985. https://doi.org/10.1371/journal.pone.0243985.

Norton, L.A., Abdala, F., Benoit, J., 2023. Craniodental anatomy in Permian–Jurassic Cynodontia and Mammaliaformes (Synapsida, Therapsida) as a gateway to defining mammalian soft tissue and behavioural traits. Philosophical Transactions of the Royal Society B 378 (1880), 20220084. https://doi.org/10.1098/rstb.2022.0084.

Owen, R., 1876. Descriptive and Illustrated Catalogue of the Fossil Reptilia of South Africa in the Collection of the British Museum. British Museum of Natural History, London.

Owen, R., 1887. On the skull and dentition of a Triassic saurian (*Galesaurus planiceps*, Ow.). The Quarterly Journal of the Geological Society of London 43, 1–6. https://doi.org/10.1144/GSL.JGS.1887.043.01-04.03.

Parrington, F.R., 1936. On the tooth-replacement in theriodont reptiles. Philosophical Transactions of the Royal Society of London B 226 (532), 121–142. https://doi.org/10.1098/rstb.1936.0005.

Pusch, L.C., Kammerer, C.F., Fröbisch, J., 2019. Cranial anatomy of the early cynodont *Galesaurus planiceps* and the origin of the mammalian endocranial characters. Journal of Anatomy 234, 592–621. https://doi.org/10.1111/joa.12958.

Pusch, L.C., Kammerer, C.F., Fröbisch, J., 2021. Cranial anatomy of *Bolotridon frerensis*, an enigmatic cynodont from the Middle Triassic of South Africa, and its phylogenetic significance. PeerJ 9, e11542. https://doi.org/10.7717/peerj.11542.

Pusch, L.C., Kammerer, C.F., Fernandez, V., Fröbisch, J., 2022. Cranial anatomy of *Nythosaurus larvatus* Owen, 1876, an Early Triassic cynodont preserving a natural endocast. Journal of Vertebrate Paleontology 42 (3), e2174441. https://doi.org/10.1080/02724634.2023.2174441.

Pusch, L.C., Kammerer, C.F., Fröbisch, J., 2024. The origin and evolution of Cynodontia (Synapsida, Therapsida): reassessment of the phylogeny and systematics of the earliest members of this clade using 3D-imaging technologies. The Anatomical Record 307, 1634–1730. https://doi.org/10.1002/ar.25394.

Rinehart, L.F., Lucas, S.G., 2013. The functional morphology of dermal bone ornamentation in temnospondyl amphibians. New Mexico Museum of Natural History & Science Bulletin 61, 524–532.

Seeley, H.G., 1889. Researches on the structure, organization, and classification of the fossil Reptilia. Part VI. On the anomodont Reptilia and their allies. Philosophical Transactions of the Royal Society of London B 180, 215–296.

Seeley, H.G., 1894. Researches on the structure, organisation, and classification of the fossil Reptilia. Part IX. Section 1. On the Therosuchia. Philosophical Transactions of the Royal Society of London B 185, 987–1018.

Smith, R.M.H., Rubidge, B.S., Day, M.O., Botha, J., 2020. Introduction to the tetrapod biozonation of the Karoo Supergroup. South African Journal of Geology 123, 131–140.

Smith, R.M.H., Botha, J., Viglietti, P.A., 2022. Taphonomy of drought-afflicted tetrapods in the Early Triassic Karoo Basin, South Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 604, 1–19. https://doi.org/10.1016/j.palaeo.2022.111207.

Van Heerden, J., 1972. Intraspecific variation and growth changes in the cynodont reptile *Thrinaxodon liorhinus* Seeley, 1894. Navorsinge van die Nasionale Museum 2, 307–347.

Van Heerden, J., 1974. Intraspecific variations and growth changes in the Cynodont reptile *Thrinaxodon liorhinus*: junior synonyms of *Thrinaxodon liorhinus* and *Galesaurus planiceps*. Navorsinge van die Nasionale Museum 2, 318–336.

Van Heerden, J., 1988. Distribution and synonymy of the cynodont reptile, *Thrinaxodon liorhinus*. South African Journal of Science 84, 130–131.

Watson, D.M.S., 1913. Further notes on the skull, brain, and organs of special sense of *Diademodon*. Annals and Magazine of Natural History 12, 217–228.

Wolvaardt, F.P., Hancox, P.J., Browning, C., Strong, M., 2023. Biostratigraphic and palaeoenvironmental significance of a rich tetrapod fossil accumulation in the Lower to Middle Burgersdorp Formation of the Karoo Basin. Journal of African Earth Sciences 198, 104776. https://doi.org/10.1016/j.jafrearsci.2022.104776.