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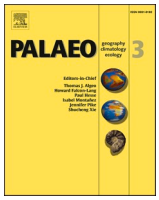
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Did gorgonopsians survive the end-Permian "Great Dying"? A re-appraisal of three gorgonopsian specimens (Therapsida, Theriodontia) reported from the Triassic *Lystrosaurus declivis* Assemblage Zone, Karoo Basin, South Africa

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ABSTRACT

Gorgonopsians were the dominant carnivores of the late Permian (Lopingian) and it is widely accepted that the clade became extinct at the Permian-Triassic boundary, almost 252 million years ago. However, South African collections house three historically-collected gorgonopsian specimens listed as Early Triassic in age, based on their discovery at localities producing the index fossil *Lystrosaurus*. Initial reports suggested that these specimens had been reworked from underlying Permian strata, but this possibility was never thoroughly addressed. The possible survival of gorgonopsians into the Triassic would significantly alter our understanding of the end-Permian mass extinction and post-extinction ecosystem dynamics. Here we use Synchrotron X-ray micro-computed microtomography to confirm the identifications and investigate the taphonomic histories of these three specimens. We also relocated the original localities to determine their stratigraphic position. We confirm that all three specimens are indeed gorgonopsians, belonging to the small-bodied genus *Cyonosaurus*, and that taphonomic assessments do not support reworking. Two of them can be confidently assigned to the latest Permian *Lystrosaurus maccaigi-Moschorhinus* Subzone of the *Daptocephalus* Assemblage Zone. In contrast, at the locality listed for the third specimen, NMQR 389, the lowermost outcropping strata belong to the upper Palingkloof Member of the Balfour Formation, which is Early Triassic in age. Despite the evident absence of Permian-aged rocks, other Permian fossils were reported from the same locality, thus casting doubts about the age of NMQR 389. Additionally, differences in preservation style between this skull and the newly collected material at the site cast doubt on its provenance. Although not supporting gorgonopsian survival into the Triassic, these new occurrences expand the range of the genus *Cyonosaurus* higher up in the extinction zone, increasing the complexity of the ecological turmoil that carnivores endured during "The Great Dying".

1. Introduction

Gorgonopsians were sabre-toothed therapsids that include the top predators of the late Permian Period (~260–252 million years ago). Their striking craniodental adaptations for carnivory, large maximum body size, and relative abundance have made them among the most iconic terrestrial taxa of the late Palaeozoic (Kammerer, 2016; Angielczyk and Kammerer, 2018). They became extinct around 252 million years ago during the end-Permian mass extinction (EPME), also known as "The Great Dying", which wiped out up to 90% of species globally (Benton and Newell, 2014; Smith et al., 2020). Historically, gorgonopsian extinction was an uncontroversial topic—due to a lack of

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resolution in gorgonopsian alpha taxonomy, reviews of the EPME usually only addressed extirpation of the clade as a whole (e.g. Colbert, 1973; Viglietti, 2016; Viglietti et al., 2016). In analyses of genus-level turnover, the ranges of characteristic macropredatory taxa of the late Permian were usually reconstructed as extending to the mass extinction interval (see, e.g., *Inostrancevia* in the Russian South Urals Basin [Benton et al., 2004] and *Aelurognathus* and *Rubidgea* in the South African Karoo Basin [Smith and Botha, 2005]). However, recent work has revealed greater complexity in gorgonopsian turnover during the terminal Permian than previously thought. Sennikov and Golubev (2006) argued that gorgonopsians went extinct in European terrestrial communities well in advance of the Permian-Triassic boundary (PTB), with therocephalians and the earliest archosauriform reptiles taking over macropredatory niches in the terminal Permian. Kammerer et al. (2023) presented updated stratigraphic ranges for Karoo gorgonopsians at the species level, demonstrating that the majority of taxa, including all members of the extremely large-bodied group Rubidgeinae (e.g. *Aelurognathus*, *Rubidgea*), not only did not reach the PTB but did not extend into the upper subzone of the latest Permian *Daptocephalus* Assemblage Zone (AZ). The only large-bodied gorgonopsian they recognised in the upper *Daptocephalus* AZ (*Lystrosaurus maccaigi-Moschorhinus* Subzone) was *Inostrancevia*, representing the first African records of a genus historically considered a Russian endemic (e.g. Ivakhnenko, 2003) and suggesting replacement of Gondwanan top predators by Laurasian immigrants during ecosystem destabilisation. These unexpected results show the complicated relationships between the major ecological disturbances preceding the PTB and terrestrial vertebrate assemblages, and reinforce the need for high-resolution stratigraphic data of taxa known mostly from historical records.

Despite these issues concerning gorgonopsian extinction dynamics in the late Permian, one aspect of their extinction has remained almost universally agreed-upon: that by the Triassic, this group had completely died out. There are a few specimens that are problematic for this statement, however. It has been noted repeatedly in the literature that in the 1960s and 1970s, the South African palaeontologist James Kitching found three gorgonopsian skulls in what he recognised as the "*Lystrosaurus* zone" (Kitching, 1977; Nicolas and Rubidge, 2010; Benoit et al., 2022) which is now mostly equivalent to the *Lystrosaurus declivis* Assemblage Zone of Botha and Smith (2020). Although the absolute age of its lowermost strata is disputed (e.g. Botha et al., 2020; Gastaldo et al., 2020; Viglietti et al., 2021; Rochín-Bañaga et al., 2023), palaeontological, stratigraphic, and geochemical evidence support that the *Lystrosaurus declivis* Assemblage Zone is entirely of early Triassic age (Botha and Smith, 2020; Shen et al., 2023). Some recent studies indicate that the upper Palingkloof Member is not older than 252.24 +/-0.1 Mya (Gastaldo et al., 2020) and the lower Palingkloof beds may be as young as 251.7+/-0.3 Mya (Botha et al., 2020). Thus, it should be kept in mind that until we have more reliable radiometric dates for samples through the *Daptocephalus* to *Lystrosaurus declivis* AZs transition, the precise placement of the currently recognised PTB-aged beds (i.e. 251.902 +/-0.024 Mya of Cohen et al., 2013) in any of the Karoo study sections remains debatable.

Accepting that Kitching's specimens are from *L. declivis* AZ strata would mean that the clade Gorgonopsia survived into the Triassic, which would impact our current understanding of the terrestrial EPME. Smith and Botha-Brink (2014) presented biostratigraphic evidence for a three-phased extinction event over the estimated 170,000 years that spanned the transition from the *Daptocephalus* to *L. declivis* faunal assemblages. Botha et al. (2020) refined the biostratigraphic ranges and added detrital zircon dates supporting synchroneity with the marine mass extinction. Subsequently, Viglietti et al. (2021) applied a time-bin analysis to standardise these stratigraphic data. This extended the extinction higher in the succession, resulting in an interval lasting approximately one million years, thus giving support to the protracted model of extinction of Karoo faunas, as initially proposed by King (1991). Regardless of the absolute age of the *Lystrosaurus declivis* Assemblage Zone, and whether its base coincides with the PTB, the possible survival of gorgonopsians from the *Daptocephalus* into the *L. declivis* faunal assemblage is worthy of investigation, as it would substantially alter our understanding of patterns and processes during the terrestrial EPME, and provide additional evidence for the survival of typically 'Permian' taxa into the earliest Triassic (as argued for '*Dicynodon*'-grade dicynodonts by Olivier et al., 2019; see also Angielczyk et al., 2022).

The anomaly of three gorgonopsian specimens from strata younger than their currently accepted range has been largely overlooked in the literature likely because, firstly, three specimens represent a small sample size among the tens of thousands of known Karoo tetrapod fossils. Secondly, their stratigraphic positions are not well-resolved, as Kitching's original "*Lystrosaurus* zone" now overlaps the currently accepted Permian-aged *Daptocephalus* Assemblage Zone (with the species *Lystrosaurus maccaigi* being abundant in the upper subzone of the *Daptocephalus* Assemblage Zone). And thirdly, immediately after their discovery, two of these specimens were deemed to be reworked –i.e. specimens eroded from older strata and redeposited in younger beds– and therefore not biostratigraphically acceptable, while the third was identified as a therocephalian (Kitching, 1964, 1977; Sigogneau, 1970; Nicolas and Rubidge, 2010; Benoit et al., 2022). Consequently, the evidence was considered too weak to go against the generally well-established vertebrate-based Karoo biostratigraphy that terminates the gorgonopsian lineage at the PTB (Kitching, 1977; Smith et al., 2020). Though conveniently compliant with the former and current vertebrate-based Karoo biostratigraphic schemes, the "reworked hypothesis" was only anecdotally proposed, and the lack of supporting evidence was never fully addressed.

Currently these three specimens are regarded as anomalous data points and as such they have been removed from every large-scale analysis of Karoo faunal turnover, biostratigraphy, and PTB dataset since the 1970s (e.g. Rubidge, 1995; Nicolas and Rubidge, 2010; Smith et al., 2020; Viglietti et al., 2021; Kammerer et al., 2023). Here, we address the long overdue need for a thorough investigation of these anomalies by i) confirming the identifications of all three specimens, ii) revisiting the reported localities where the specimens were discovered, and iii) analysing their taphonomic modifications using Synchrotron X-Ray tomography to test the reworking hypothesis.

2. Material and methods

2.1. Specimens

Specimen BP/1/4593 (Fig. 1A) is a calcareous nodule that has been precipitated around a partial gorgonopsian skull preserving the snout and skull roof. The basicranium and posterior portion of the palate are not preserved. This specimen is mostly unprepared, highly fractured, and held together by a thick coating of Plaster of Paris that covers the ventral aspect of the skull. Its existence has only been briefly mentioned by Kitching (1977) and Nicolas and Rubidge (2010). It was reportedly discovered in 1974 in the "*Lystrosaurus* zone" on the farm Fairydale (plot Fairydale 193, Free State Province, South Africa) "from a mud-pebble conglomerate in a channel-lag deposit" (Kitching, 1977: p.26) alongside fragments of *Daptocephalus* and *Lystrosaurus* skulls. Kitching (1977) and Nicolas and Rubidge (2010) hypothesised that these fossils were reworked from strata of the underlying *Daptocephalus* AZ.

Specimen BP/1/3895 (Fig. 1B) is an almost complete skull without lower jaw, missing the dental margin of the maxilla and premaxilla. The palate and basicranium are broken into small pieces that lie scattered on the ventral side of the specimen. It was found in 1965 by Albert Hotton (son of Nicholas Hotton III) and James Kitching on the farm New Castle of the Admiralty Estate on Oliviershoek Pass (plot Newcastle 2378, KwaZulu-Natal Province, South Africa) (Kitching, 1964, 1977). Kitching (1964, 1977) noted that the skull appeared to be water-worn and deduced that the damage was due to the skull having been reworked

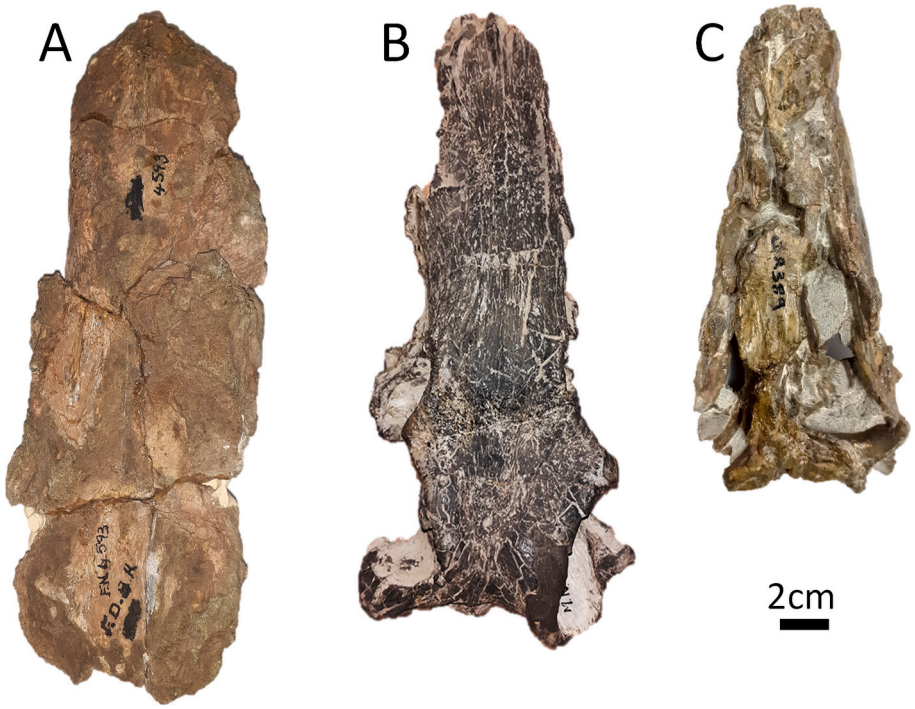


Fig. 1. Skulls of all three anomalous "*Lystrosaurus* zone" gorgonopsians in dorsal view. A, BP/1/4593; B, BP/1/3895; C, NMQR 389.

from the underlying layers of the "*Daptocephalus* zone". This conclusion was subsequently accepted by Sigogneau (1970) and Nicolas and Rubidge (2010) without further examination of the taphonomic modifications of the material.

Specimen NMQR 389 (Fig. 1C) is a largely complete, but dorsoventrally crushed and laterally sheared gorgonopsian skull with occluded lower jaw. Large portions of the skull roof are broken off, making it appear to have a narrow intertemporal bar. It was found by James Kitching at a locality he reported as Oranje (plot Tweefontein 508, Free State, South Africa). The spelling "Oranje" is rare in the literature (Hoffman and Esterhuyse, 1965; Schoch and Rubidge, 2004), and the farm name is more commonly spelled "Orangia" (Reisz and Scott, 2002) as it now appears on the 1:50000 and 1:250000 topocadastral and geological maps. Here, the spelling "Orangia" is preferred to avoid confusion with farm Oranje 254 in the nearby Springfontein District (see the Results section below). Specimen NMQR 389 was not originally identified as a gorgonopsian, presumably because its damaged intertemporal region makes the skull look like it has a sagittal crest (Fig. 1C), as is typical of therocephalians. The skull was recently re-identified by one of the authors as a gorgonopsian (C.K. in Benoit et al., 2022). As Kitching (1977) referred this specimen to an Early Triassic therocephalian species, *Scaloposaurus constrictus*, which he discovered in an otherwise *Lystrosaurus*-rich fauna, he did not provide further geological background to his discovery, nor did he consider this to be a biostratigraphic anomaly.

2.2. Scanning parameters

BP/1/3895, BP/1/4593, and NMQR 389 were scanned at the European Synchrotron and Radiation Facility, Grenoble, France on beamline BM18 (http://paleo.esrf.eu/; CT data DOI: 10.15151/ESRF-ES-781826130 and 10.15151/ESRF-ES-735689005) with propagation phase-contrast synchrotron X-ray micro-computed tomography. For BP/1/4593, the beamline setup was for a filtered white beam of 155 keV, with molybdenum (3.75 mm) and tungsten (0.3 mm) attenuator filters, a 2000 nm thick luAg scintillator, a sample-detector distance of 20 m, and an isotropic voxel size of 20 μm. For BP/1/3895 and NMQR 389, the beamline setup was for a filtered white beam of 178 keV, with molybdenum (1.3 mm) and tungsten (0.3 mm) attenuator filters, a 2000 nm thick luAg scintillator, a sample-detector distance of 18.4 m, and an isotropic voxel size of 14.42 μm.

Acquisition was done with a PCO edge 4,2 sCMOS (PCO, Kelheim Germany), recording 10,000 projections for BP/1/4593 and 11,000 projections for BP/1/3895 and NMQR 389, with a total exposure time of 30 ms, with three accumulated images of 10 ms (Cau et al., 2017). The specimens were scanned with a 'tetra-acquisition' setup, with the centre of rotation shifted twice to create four radiographs that were stitched together in post processing to create a larger slice to encompass the complete specimen. The final tomographic volume was reconstructed using PyHST2 (Mirone et al., 2014) and using the single distance Paganin phase retrieval approach (Paganin et al., 2002).

2.3. Fieldwork

Farm plots Newcastle 2378 (Bergville District, KwaZulu-Natal), Oranje 254 (Springfontein District, Free State), Fairydale 193, Donald 207, and Tweefontein 508 (Bethulie District, Free State) were visited to determine the provenance of the three gorgonopsian skulls. Field trips were conducted under South African Heritage Resources Agency collection permits n°3621, 18640, SAH19/13092. All in situ tetrapod fossils discovered were taphonomically logged, photographed, and positioned using a handheld GPS. All collected fossils are catalogued and curated at the Evolutionary Studies Institute of the University of the Witwatersrand. Mechanical preparation was conducted by Charlton Dube and Thilivhali Nemavhundi using tungsten-carbide tipped air-scribes under binocular microscopes.

James Kitching unfortunately left no fieldnotes, but the relocation of the provenance of the three gorgonopsians was greatly helped by the wall-sized compilation of 1:250000 topocadastral maps he made in 1972. On this map, he placed colour-coded pins corresponding to the biozones encountered at each locality (green for the "*Lystrosaurus* zone" and purple for the "*Daptocephalus* zone"). The original map was damaged and had to be recreated, but the current version of the map nevertheless provides a reasonably accurate snapshot of Kitching's

knowledge of Karoo biostratigraphy and the area he had explored. This map is referred to as Kitching's wall-map (or Kitching, 1972) throughout the current work.

2.4. Institutional abbreviations

BP: Evolutionary Studies Institute (former Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg; NMQR: National Museum, Bloemfontein.

3. Results

3.1. Specimen BP/1/4593

3.1.1. Description and identification

Crushed, incomplete, and never prepared, this specimen was previously identified as Gorgonopsia indet. by Kitching (1977) and Nicolas and Rubidge (2010). Although identification is stymied somewhat by loss of most of the ventral portion of the skull and its high degree of dorsoventral compression, CT data have revealed a suite of features permitting identification as *Cyonosaurus* sp. (Benoit et al., 2022).

Ongoing alpha taxonomic revision of Gorgonopsia has yet to address the majority of small-bodied taxa, with the only exceptions being basal gorgonopsians of mostly middle Permian age (Kammerer, 2014; Kammerer et al., 2015; Kammerer and Masyutin, 2018). Sigogneau-Russell (1989) recognised three valid species of *Cyonosaurus* (*C. longiceps* [the type], *C. kitchingi*, and *C. rubidgei*), as well as three morphotypes of taxonomically uncertain attribution (referred to as *Cyonosaurus* cf. *longiceps*, *Cyonosaurus* cf. *rubidgei*, and *Cyonosaurus* sp.). These species were diagnosed based primarily on size and snout proportions, both made problematic by ontogenetic variation, especially since Sigogneau-Russell (1989: p. 84) noted that several of these specimens were "certainly" juvenile. Additional research is needed to determine whether there is any consistent variation between the species of *Cyonosaurus* or whether they should all be considered synonymous with *C. longiceps*. With this said, at the genus level, *Cyonosaurus* presents a consistent and readily-identified morphotype.

Sigogneau-Russell (1989: p. 83) diagnosed *Cyonosaurus* on the basis of the following characters: "Skull narrow posteriorly. Snout long, and as high as wide. Temporal fossa elongated. Orbit small. Intertemporal space much wider than interorbital, itself narrow. Skull arches very slender. Large supraorbital frontal. Preparietal rhomboidal. Squamosal long on zygomatic arch. Long lachrymal. Interparietal wide. Pterygoid transverse apophyses posteriorly situated. Ossified prootic, short anteriorly. Dentary slender, with sloping symphysis. Numerous and small postcanines."

Some of these characters are problematic; an ossified prootic, for example, is present in all gorgonopsians, with taxa where Sigogneau-Russell considered it absent being based on damage (e.g. *Arctops*, which in well-preserved specimens clearly shows a well-ossified prootic; Laurin, 1998; Kammerer, 2017). Other characters, such as orbital and temporal dimensions, vary with growth (and although few ontogenetic series are known for gorgonopsians, those that exist show similar typical allometric trends for therapsids, see e.g. Kammerer, 2015, 2016). With that noted, several of the proportional characters in Sigogneau-Russell's diagnosis cannot be explained by potential juvenility.

The extremely long snout of *Cyonosaurus*, for example, both differentiates it from the other abundant small-bodied gorgonopsian taxon in the late Permian Karoo Basin, *Aelurosaurus*, and provides evidence against *Cyonosaurus* representing an early growth stage of one of the larger gorgonopsian taxa (as juveniles tend to have proportionally shorter snouts than adults, not vice versa). The postparietal (=interparietal) of *Cyonosaurus* is widely exposed in dorsal view in all specimens that have not suffered lateral crushing. Furthermore, the rhomboidal or diamond-shaped preparietal is consistently present in *Cyonosaurus* specimens and differentiates it from many other gorgonopsians (see e.g. Kammerer, 2016, 2017), albeit not *Aelurosaurus*.

The most diagnostic character of *Cyonosaurus* was noted by Bendel et al. (2018) concerning its upper dentition, in which there are always 6–7 extremely small, close-packed postcanine teeth occupying the mid-length of the ventral margin of the maxilla. Other characters diagnosing *Cyonosaurus* include a 'strap-like' postfrontal, of roughly uniform width throughout its length (i.e. not strongly tapering posteriorly), which terminates posteriorly in a straight suture with the parietal, and a narrow, elongate interchoanal body of the vomer, unlike the proportionally shorter, more transversely expanded structures seen in *Arctops*, *Gorgonops*, and even longirostrine members of Rubidgeinae (Kammerer, 2015, 2016, 2017).

Although the snout of BP/1/4593 appears relatively wide, it is proportionally similar to definite *Cyonosaurus* specimens that have suffered intense dorsoventral compression (e.g. BP/1/8849). While the occiput of BP/1/4593 is not preserved, based on the position of the pineal foramen and orbits, this specimen definitely had an extremely long snout for a gorgonopsian (Fig. 2A), comparable to other *Cyonosaurus* specimens. Combined with the well-preserved, diamond-shaped preparietal and postfrontal morphology matching that seen in BP/1/3895 and better-preserved *Cyonosaurus* specimens (e.g. BP/1/137), this generic referral becomes fairly robust. The anterior portion of the vomer and vomerine process of the premaxilla are the only palatal portions of this specimen preserved, but they show the narrow interchoanal body of the vomer typical of *Cyonosaurus* (Fig. 2C).

3.1.2. Litho- and biostratigraphy of locality

Specimen BP/1/4593 was found in 1974 by James Kitching on a farm he called Fairydale. He interpreted the deposit as a channel-lag conglomerate, which he used to support that the specimen was locally reworked (Kitching, 1977). This interpretation was later relayed by Nicolas and Rubidge (2010). Kitching also reported finding other damaged specimens of *Lystrosaurus* and juvenile *Daptocephalus* in the same channel lag, that he presumed to have been reworked as well. Unfortunately, we could not relocate these other dicynodont specimens in the collections of the Evolutionary Studies Institute.

The Fairydale locality, as referred to by Kitching and subsequent authors, actually encompasses two farm plots: Fairydale 193 (north of the R701 road) and the adjoining Donald 207 (south of the R701) (Fig. 3A). This was clarified by Smith et al. (2022) and accounts for why Donald 207 is not mentioned in Kitching's (1977) faunal list, even though he collected dozens of tetrapod fossils there. Kitching likely lumped the two portions together under the farm name "Fairydale" because they both used to (and still do) belong to the same landowner. According to Kitching's wall-map (Fig. 3B), he referred both plots to the "*Lystrosaurus* zone" (now the *Lystrosaurus declivis* Assemblage Zone of Botha and Smith, 2020).

Despite the expansive surface area of outcrops at Fairydale 193 and Donald 207, relocating the provenance of BP/1/4593 was possible thanks to a note made by James Kitching in his 1977 volume. There he describes the location where he found the gorgonopsian (p. 26): "The nearest *Daptocephalus* zone beds are at present exposed approximately two miles [about 3km] to the north and also six miles [about 10km] to the south-east of this locality". No place on Kitching's (1977) map or his 1972 wall-map matches this description, but it best fits the Fairydale 193 plot (Fig. 3B). To Kitching's knowledge at the time (as reflected by the wall map), Fairydale 193 was located between "*Daptocephalus* zone" outcrops situated about 2 km to the north and 5 km to the south, whereas Donald 207 was farther removed from any "*Daptocephalus* zone" outcrops (Fig. 3B). As such, although the description of the locality of BP/1/4593 only loosely matches Fairydale 193, it definitely excludes Donald 207 as its possible locality of origin.

James Kitching placed a pin into a gully on the Fairydale 193 farm, about a kilometre east of the farmhouse, near a dam (Fig. 3B; GPS coordinates: S30°23.569′ E26°13.764′). Upon further exploration by our team, the small outcrops here proved highly fossiliferous (Figs. 3C, D,

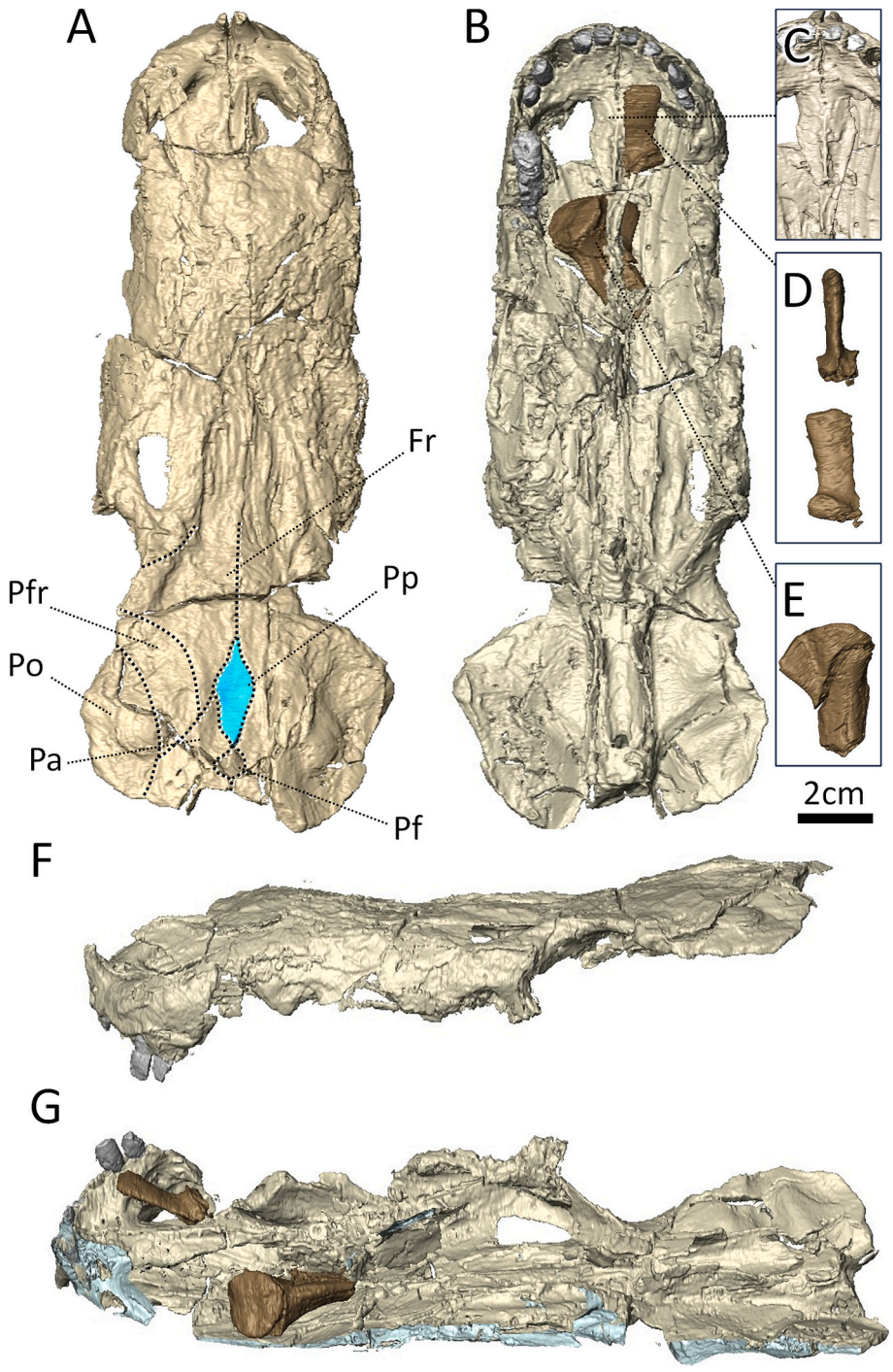


Fig. 2. Synchrotron scan-based 3D digital reconstructions of skull BP/1/4593.
A, dorsal view; B, ventral view; C, ventral view of the vomer with the vertebra fragment removed digitally; D, vertebra fragment located on the ventral surface of the vomer in anterior (top) and lateral (bottom) views; E, humerus fragment located within the nasal cavity in anterior view; F, left lateral view of the skull; G, skull in lateral view in its original ventral up position and right side removed in order to illustrate how the vertebra and humerus fragments are lying on the ventral surfaces of the vomer and nasal cavity, respectively. Abbreviations: Fr, frontal; Pa, parietal; Pf, parietal foramen; Pfr, postfrontal; Po, Postorbital; Pp, preparietal.

4A, B), and delivered a fragment of the symphysis of a large *Lystrosaurus* (BP/1/9240, possibly L. *maccaigi*), the complete skull of a definite *Daptocephalus leoniceps* preserved lateral up (BP/1/9221), as well as some other fragments of very large, but unidentifiable, dicynodonts. The identification of the large skull as *Daptocephalus* is supported by the rounded curvature of the snout (readily differentiating it from the steep, elongate snout of *Lystrosaurus*, but also from the more weakly-sloping snout of *Dicynodon*; see Kammerer et al., 2011 and Kammerer, 2019), the presence of a well-developed circumorbital ridge, and shape of the zygomatic arch (Fig. 4A). The lack of a septomaxillary-lacrimal contact in this specimen also clearly excludes it from identification as *Lystrosaurus*. The identification of the fragmentary lower jaw is supported by the morphology of its symphysis, which is broad and quadrangular in dorsal view, and almost vertical in lateral view (Fig. 4B), as in the genus *Lystrosaurus*. This identification is also supported by the sharp angulation between the anterior and lateral faces of the symphysis, forming a ridge. Its large size and the co-occurrence with *Daptocephalus* suggest that it belongs to the species *L. maccaigi*. These specimens closely match

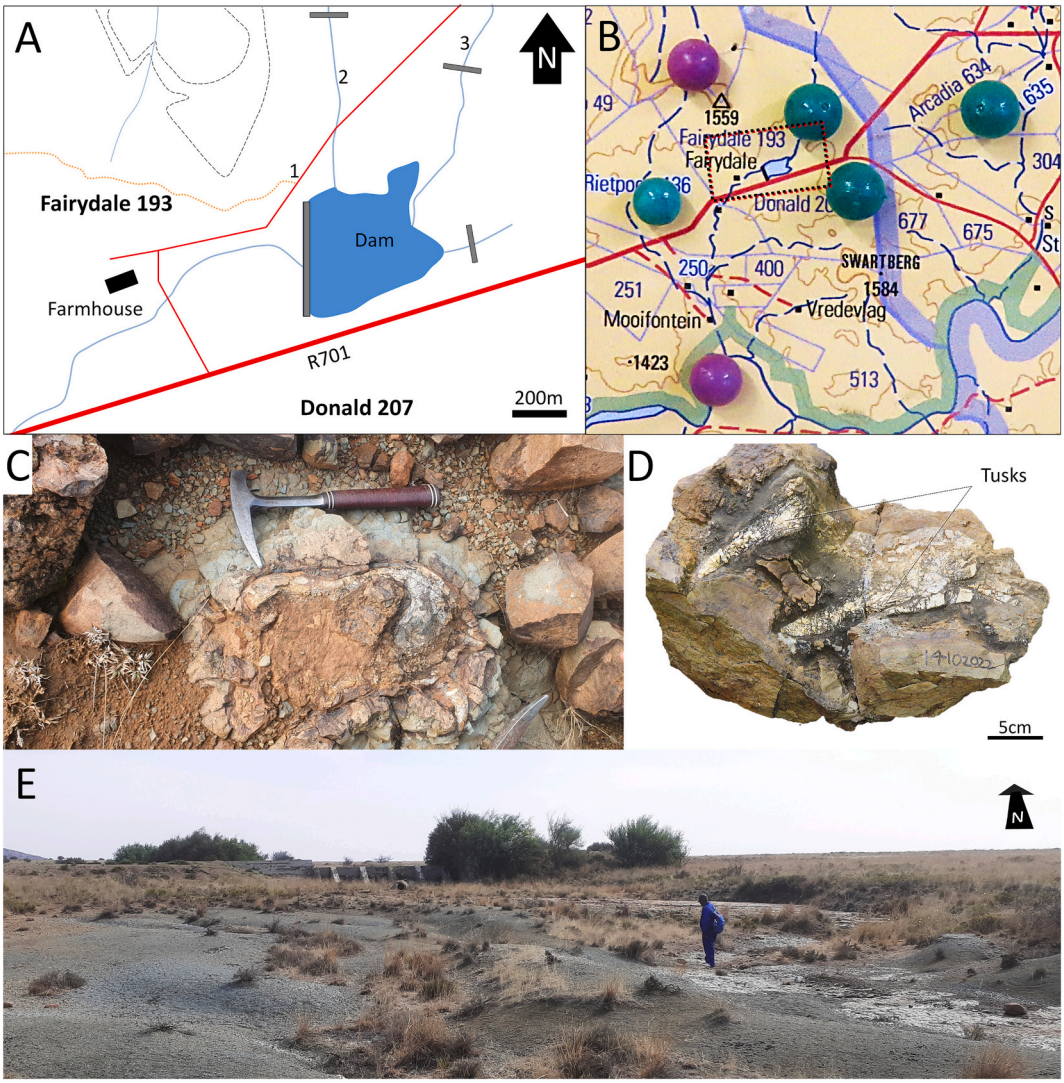


Fig. 3. Late Permian locality at Fairydale 193.
A, simplified map of the site. Roads are in solid red lines, dolerite dykes are in dotted orange lines, rivers are in solid blue lines, outline of hills are marked by dotted black lines. 1, locality where *Daptocephalus* BP/1/9221 was found; 2, locality where *Lystrosaurus maccaigi* (BP/1/9240; see Fig. 4B) was found; 3, locality where Kitching's pin is planted; B, excerpt of Kitching's wall-map (1972) showing the position of A in dotted lines. Green pins, *Lystrosaurus* zone; purple pins, *Daptocephalus* zone; C, field photo of the excavation of the *Daptocephalus* skull (BP/1/9221) discovered at the locality marked 1 on the map; D, picture of a large unidentified dicynodont (BP/1/9215) from the same locality showing the metamorphic halo; E, picture of the locality marked 2 on the map where *Lystrosaurus maccaigi* was found (upper Palingkloof Member of the Balfour Formation). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the assemblage that James Kitching found alongside BP/1/4593 (i.e., "fragmentary juvenile *Daptocephalus* skull together with damaged *Lystrosaurus* remains" Kitching, 1977: p. 26), strongly supporting that this (rather than a Triassic exposure) is the original locality where this gorgonopsian specimen was found.

3.1.3. *Taphonomic observations of BP/1/4593*

Kitching (1977) mentions finding BP/1/4593 in "a mud-pebble conglomerate in a channel lag deposit", but we did not find any channel lag or intraformational conglomerate with intraclasts large enough to match the size of BP/1/4593 (let alone a *Daptocephalus* skull) during our repeated fieldwork at Fairydale 193 and Donald 207. In fact, the volume and mass of the specimen far outweighs the maximum clast size of any intraformational conglomerate beds in the entire Karoo Permo-Triassic succession. Intraformational mud-pebble conglomerate lenses are commonplace on Donald 207, but despite almost 30 years of uninterrupted field work by R.S. and more than 760 fossils logged from this site (Smith, 1995; Smith and Ward, 2001; Ward et al., 2005; Smith and Botha-Brink, 2014; Botha et al., 2020; Viglietti et al., 2021; Smith et al., 2022), not a single specimen that could have been reworked from the underlying Permian strata has ever been discovered. Fairydale 193 lacks any exposures of what can be convincingly described as a conglomerate. The gully where L. *maccaigi* BP/1/9240 was discovered exposes blue-grey siltstone only (Fig. 3E). Noteworthily, the specimens found near a dolerite dyke (such as BP/1/9215 and BP/1/9221) were encased in very hard, highly metamorphosed nodular haloes (Fig. 3C, D), whereas those far away from the contact metamorphism (such as BP/1/9240) were not. It is possible that Kitching interpreted these metamorphic alteration haloes as large pebbles, and their local concentration around the dolerite dyke as representing a channel lag. The yellow-orange colour of the nodule containing BP/1/4593 (Fig. 1A) matches that of these haloes (Fig. 3C, D), which supports that it is preserved in such a nodule rather than in a channel-lag. It is possible that Kitching (1977), in the absence of a better explanation to account for the presence of a "*Daptocephalus*

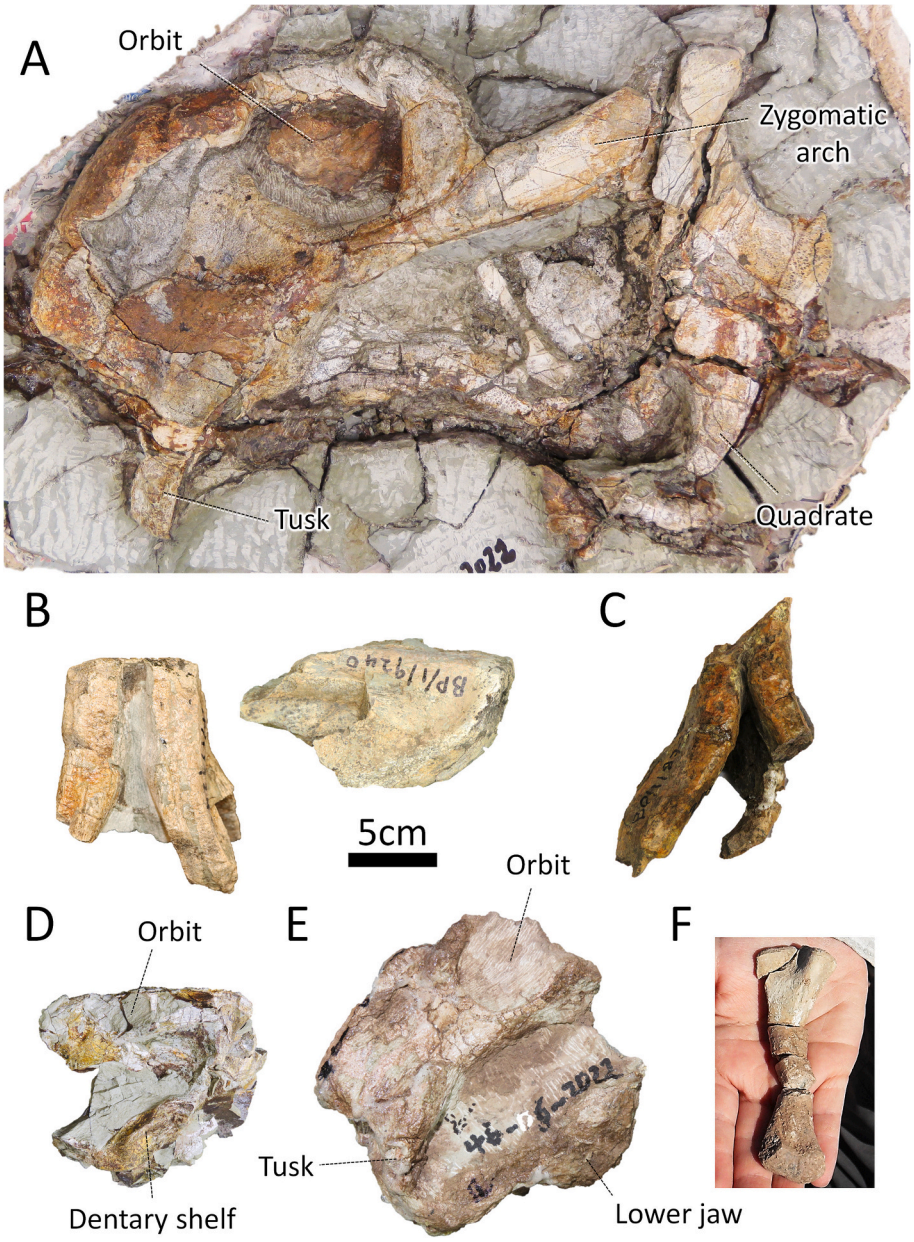


Fig. 4. A selection of specimens found in the course of this project.
A, *Daptocephalus leoniceps* skull from Fairydale 193 in lateral view (BP/1/9221), snout pointing to the left; B, *Lystrosaurus maccaigi* jaw symphysis fragment from Fairydale 193 (BP/1/9240) in dorsal view (left, symphysis pointing up) and lateral view (right, symphysis pointing to the right); C, *Dicynodon* or *Daptocephalus* lower jaw fragment from Newcastle 2378 (BP/1/8737) in dorsal view, symphysis pointing up; D, *Dicynodontoides* sp. skull and lower jaw from Oranje 254 (field n°11-08-2022) in lateral view, snout pointing to the left; E, *Lystrosaurus* sp. skull and lower jaw from Tweefontein 508 (field n°46-06-2022) in lateral view, snout pointing to the left; F, field picture of the femur of cf. *Proterosuchus* from Tweefontein 508 (field n°23-09-2023).

zone" fauna in rocks that he attributed to the "*Lystrosaurus* zone", interpreted these metamorphic nodules as large pebbles reworked in a channel lag system.

The skull of specimen BP/1/4593 was buried in a ventral-up attitude, as is evidenced by the presence of a vertebral arch lying on the ventral surface of the vomer, and another large bone (the proximal end of a humerus) lying on the ventral surface of the nasal cavity (Fig. 2C-G). Regardless of whether these bones belong to the same individual as BP/1/4593, these large bones must have entered the nasal cavity before it was infilled with sediment, but after the palate was damaged (Fig. 5). This supports the interpretation that sun cracking and damage were done before complete burial and fossilisation. Had the damage occurred during a reworking event, the nasal cavity would have already been filled with sediment, thus preventing these bones from penetrating the nasal cavity. The skull might have been already partly buried ventral-up at that point (Fig. 5B), accounting for the preservation of its roof while most of the ventral aspect was destroyed. As such, the extensive damage described by Kitching (1977) was likely present before complete fossilisation, which negates the reworking interpretation.

Additionally, BP/1/4593 shows no evidence of post-burial exhumation, transportation, or reburial, which usually manifest as rounding and abrasion of edges. We therefore conclude that Kitching discovered some exposures assignable to the *Daptocephalus* AZ on Fairydale 193, which have been overlooked by subsequent researchers who focused their attention on the more productive *Lystrosaurus declivis* AZ outcrops on Donald 207. Because the fossils recently recovered by the research team from Fairydale 193 comprise *Daptocephalus leoniceps* and *Lystrosaurus* (including one probable L. *maccaigi*) and do not show evidence of

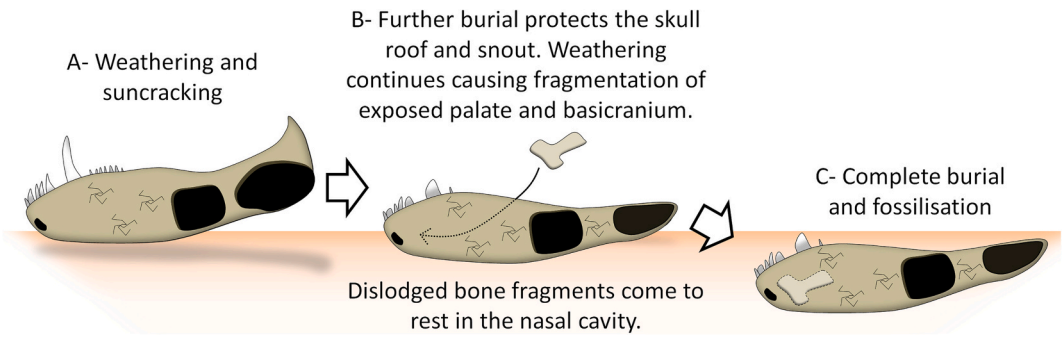


Fig. 5. Simplified taphonomic history of skull BP/1/4593.

reworking, these are best interpreted as an in situ paleofauna of the latest Permian *L. maccaigi - Moschorhinus* Subzone of the *Daptocephalus* Assemblage Zone. This subzone encompasses the Elandsberg and lowermost part of the Palingkloof members of the Balfour Formation, making BP/1/4593 the first confirmed occurrence of the genus *Cyonosaurus* above the arenaceous Ripplemead member (Viglietti et al., 2017).

3.2. Specimen BP/1/3895

3.2.1. Description and identification

Of the three specimens under discussion, BP/1/3895 has received the most attention in the published literature. It was identified as *Cyonosaurus* cf. *longiceps* by Sigogneau (1970) based on the elongate, narrow snout and intertemporal calvarial morphology. Due to erosion of the ventral portion of the skull, unfortunately the most diagnostic features of *Cyonosaurus* are missing in BP/1/3895. However, based on the combination of a proportionally elongate, narrow snout, diamond-shaped preparietal, broad postparietal, and postfrontal morphology (Fig. 6A), this specimen can be confidently identified as *Cyonosaurus*. Although Sigogneau-Russell's (1989) tentative association of this specimen with *C. longiceps* is likely, we regard it as *Cyonosaurus* sp. pending comprehensive revision of this genus.

3.2.2. Litho- and biostratigraphy of locality

Specimen BP/1/3895 was found in 1964 by US palaeontologist Nicholas Hotton III and his son Albert during a research trip with James Kitching on plot Newcastle 2378 (also known as Admiralty, Admiralty Estates, or New Castle of the Admiralty) on Oliviershoek Pass in the Bergville district of KwaZulu-Natal. While this locality is best known for its rich and diverse fossil fauna typical of the *Lystrosaurus declivis* AZ (Brink, 1956; Kitching, 1964, 1977; Fernandez et al., 2013), outcrops yielding fossil plant and tetrapod specimens typical of the *Daptocephalus* AZ are present on Newcastle 2378 and the neighbouring farm, Kilburn 14639 (Page, 1983; Groenewald, 1990; Groenewald et al., 2022). This makes relocating the exact place where the gorgonopsian was found crucial to determining its litho- and biostratigraphic position.

Fortunately, Hotton recorded where he found the specimen in his field notes. By retracing the route recorded in his notebook and using his written description of the locality, we could locate the most likely outcrop at Oliviershoek Pass where BP/1/3895 was collected (Fig. 7A; GPS coordinates: S28° 36.282′ E29°03.642′). Hotton's notes record the locality as "Oliviershoek pass – Newcastle Estates. Donga off road at mileage 3745 [from the Harrismith Hotel]. Elevation of road at mileage 3745 is 4600 (ft) (recorded twice) at 78 degrees(F) at 9h55" and he went on to describe the only fossil that was found there as "crushed *Lystrosaurus* from near top of donga". Tracking the mileage from Harrismith Hotel (and accounting for the fact that the new road diverges from the old one in places), we were able to drop down into a gully almost immediately downslope from the old road at the mileage and elevation indicated by Hotton. The outcrop consists of a deep, narrow erosion gully, which conforms to Kitching's description of the locality as "small but very productive exposures, mainly on the slope of the mountain below the road embankment in the pass" (Kitching, 1977: p. 95). A pin on Kitching's 1972 wall-map indicates that he indeed visited this spot (Fig. 7B), which adds credence to this locality being the discovery site of the gorgonopsian.

Near the head of the erosion gully is a three-metre-high sandstone cliff (Fig. 7C). An intraformational conglomerate outcropping in the gully at the base of this horizontally laminated channel sandstone contains isolated bones with similar black colour and brittle texture as BP/1/3895. The only identifiable in situ fossil from this outcrop that we found came from the grey mudrocks in the floor of the gully below the channel sandstone (Fig. 7D). This is a dicynodont lower jaw with a narrow, gently sloping symphysis that clearly distinguishes it from that of *Lystrosaurus* (Fig. 4C; BP/1/8737). Given its size, it likely belongs to *Daptocephalus* or *Dicynodon,* either of which would support an age consistent with the *Daptocephalus* AZ. Thus, if the locality of BP/1/3895 is correct, the associated fauna indicates that it came from Permian-aged strata. In an adjoining gully to the north of this site, an in situ *Thrinaxodon* skull (BP/1/8738) was discovered nine meters above the stratigraphic level of the channel sandstone in variegated mudstones of the Palingkloof Member (Groenewald, 1990; Neveling, 2004); previously known as the Harrismith Member of the now defunct Normandien Formation in this part of the basin (Groenewald et al., 2022). This confirms that *Lystrosaurus declivis* AZ fossils can be found nearby but in distinctly higher strata, which likely accounts for Kitching reporting "*Lystrosaurus*, *Thrinaxodon* and *Lydekkerina*" skeletons associated with the gorgonopsian (Kitching, 1977: p. 26).

Given the above, we interpret this locality as an erosion gully that cuts through the lower *Lystrosaurus declivis* AZ strata down into the underlying upper *Daptocephalus* AZ succession. The prominent channel sandstone near where BP/1/3895 was likely discovered is the Schoondraai member of the Balfour Formation, which coincides with the latest Permian L. *maccaigi - Moschorhinus* Subzone of the *Daptocephalus* AZ in the north-eastern Free State (Groenewald, 1990; Groenewald et al., 2022). Work on the PTB in this part of the basin is ongoing, but it is generally accepted that the condensed succession is less complete in the north of the main Karoo Basin than in the south (Botha et al., 2020). *Daptocephalus leoniceps* has not yet been recovered from above the Schoondraai member (Groenewald, 1990). As such, in this section, the top of the channel sandstone likely marks the EPME, which in the rest of the Karoo basin is temporally linked to the PTB (Smith and Botha-Brink, 2014; Botha et al., 2020; Viglietti et al., 2021). This supports a latest Permian age for the gorgonopsian specimen BP/1/3895.

3.2.3. Taphonomic observations of BP/1/3895

Kitching (1964, 1977) noted that the bone surface of BP/1/3895 appeared to be water-worn and concluded that the skull had been reworked from the underlying *Daptocephalus*-containing strata. This assumption was accepted by Sigogneau (1970, 1989) and Nicolas and Rubidge (2010); however, our current assessment of the state of preservation of the specimen is not consistent with reworking based on the

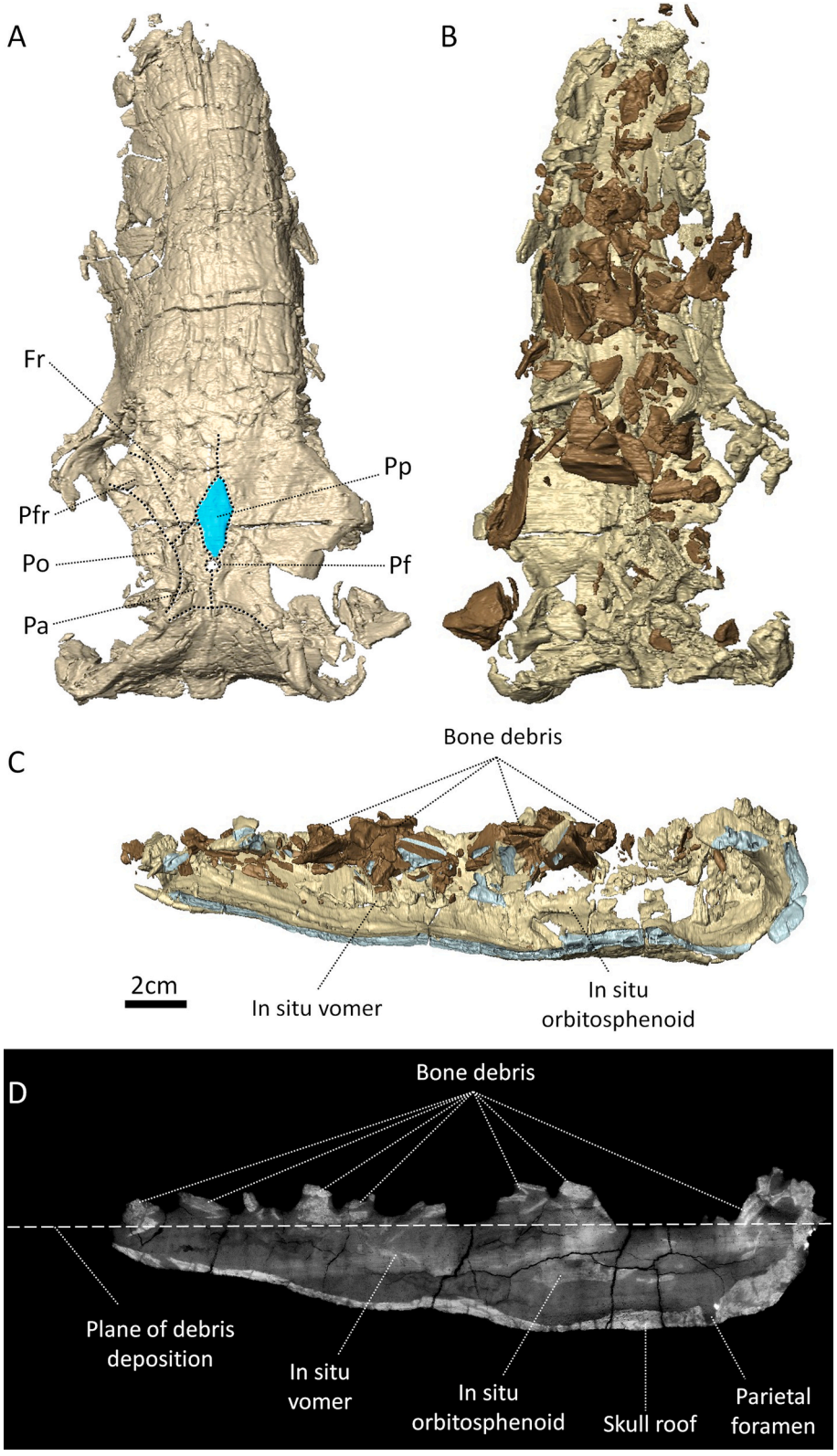


Fig. 6. Synchrotron scan-based 3D digital reconstructions and slides of skull BP/1/3895.
A, dorsal view; B, ventral view; C, skull in lateral view in its original ventral up position and right side removed in order to show the position of the bone debris, vomer and orbitosphenoid inside the skull; D, sagittal CT section of the skull showing the position of the bone debris, and in situ vomer and orbitosphenoid inside the skull. Abbreviation: Fr, frontal; Pa, parietal; Pf, parietal foramen; Pfr, postfrontal; Po, Postorbital; Pp, preparietal.

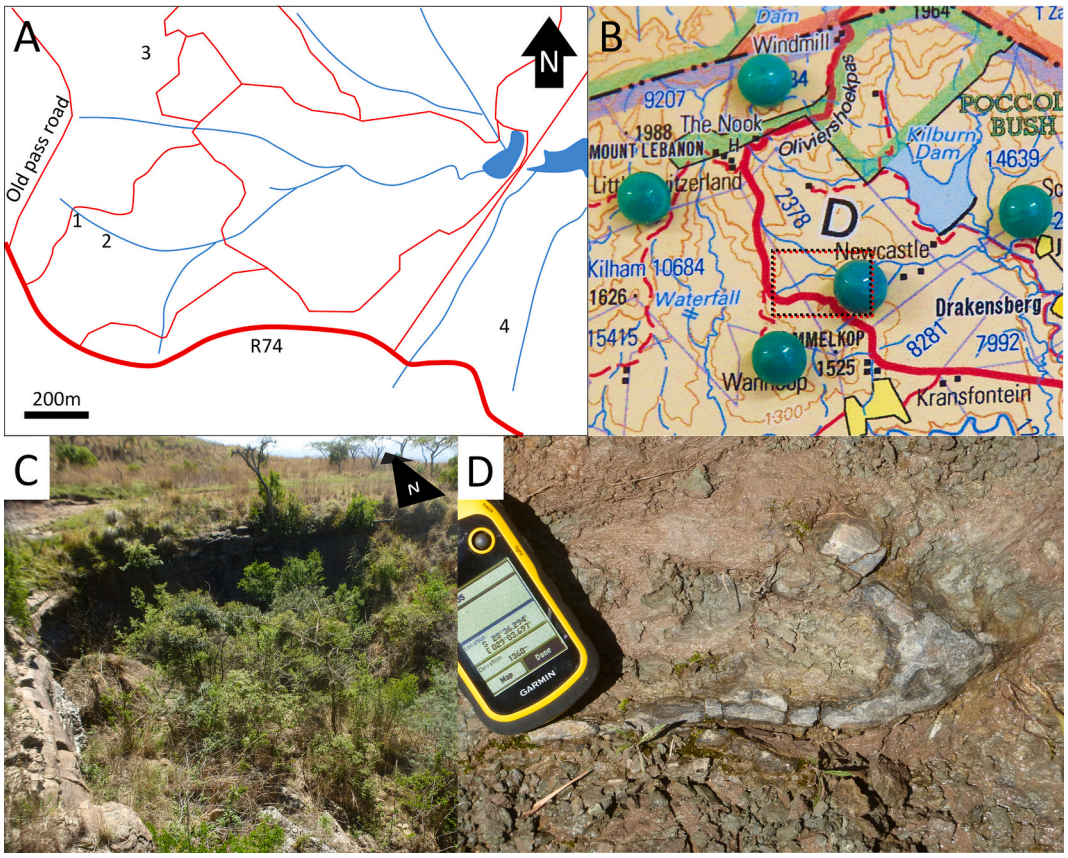


Fig. 7. Late Permian locality at Newcastle 2378.
A, simplified map of the site. Roads are in solid red lines, rivers are in solid blue lines. 1, locality indicated in Hotton's notebook; 2, locality where indet. dicynodont lower jaw (BP/1/8737) was found; 3, locality where *Thrinaxodon* skull (BP/1/8738) was found; 4, locality where Kitching's pin is planted; B, excerpt of Kitching's wall-map (1972) showing the position of A in dotted lines. Green pins, "*Lystrosaurus* zone"; C, field photo of the locality indicated in Hotton's notebook and marked 1 on the map (Schoondraai member of the Balfour Formation); D, field photo of indet. dicynodont lower jaw (BP/1/8737) at the locality marked 2 on the map. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

following observations.

Firstly, the edges of the margin of the maxilla are sharp and angular and have not been rounded as would be expected if they had been water-worn (Fig. 6). Secondly, the dorsal surface of the skull has lost much of its smooth periosteal bone and is rough and sun-cracked, which is indicative of substantial sub-aerial weathering for up to 5 years before burial (i.e. weathering stage 4 of Behrensmeyer, 1978; Fig. 1B). Finally, synchrotron X-ray micro-scanning revealed that the weathered fragments of the palate, basicranium and maxillae are mostly concentrated in a single horizontal plane on the ventral side of the skull (Fig. 6B-D). This plane is located at the same level as the margin of the broken-off maxillae and squamosals. The vomer and orbitosphenoid, however, are still "floating" in situ (Fig. 6C-D), which indicates that the event that damaged the palate, maxillae and basicranium did not affect the whole skull, as the vomer and orbitosphenoid were maintained in place by sediments (Fig. 8).

These taphonomic clues suggest that, after remaining exposed for considerable time, the dorsal side of the skull became embedded in the floodplain alluvium while the ventral-most aspect of the skull was subjected to further weathering (Fig. 8). The broken-off fragments are preserved in very close proximity to their original position in the skull and in a single horizon, which suggests quick burial after they fell away. Rather than water-borne sediment, windblown dust is more likely to have covered these fragments without scattering them. Our taphonomic analysis indicates that the damage on BP/1/3895 was caused by prolonged in situ subaerial weathering during the burial process. Thus, there is no need to invoke reworking (i.e. exhumation, transportation and re-burial) either before final burial, or after fossilisation, to account

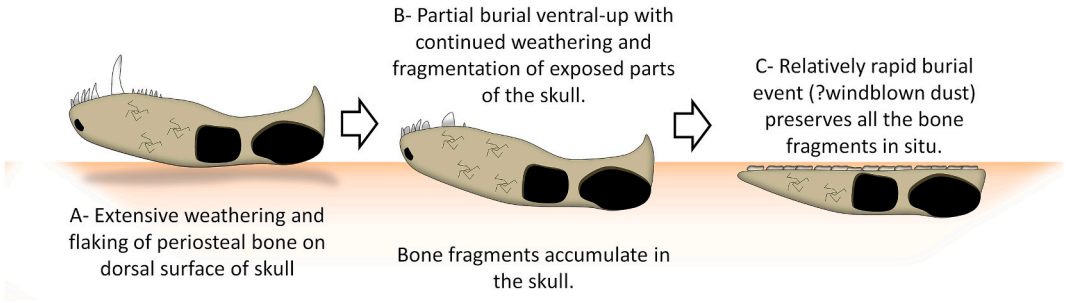


Fig. 8. Simplified taphonomic history of skull BP/1/3895.

for the damage visible on BP/1/3895. We conclude that specimen BP/1/3895 is not reworked and originates from latest Permian strata immediately below the PTB.

3.3. Specimen NMQR 389

3.3.1. Identification and description

Kitching (1977) assigned this specimen to the relatively abundant Early Triassic baurioid therocephalian taxon *Scaloposaurus constrictus*. Largely ignored by subsequent workers, it was recognised as a gorgonopsian by C.K. during a research trip to the National Museum in 2010 (see Benoit et al., 2022). Damage to the skull roof of this specimen has made it look like a narrow intertemporal bar is present (Fig. 9A), similar to the undamaged condition in therocephalians. However, the palatal morphology of NMQR 389 is clearly gorgonopsian-like: no suborbital fenestra is present, both the palatine and pterygoid are dentigerous, with a delta-shaped palatine boss followed by a ridge-like pterygoid boss extending to the anteromedial margin of the pterygoid transverse process, and the palatines have a midline suture excluding the vomer from contacting the pterygoid ventrally (Fig. 9B). Referral to the genus *Cyonosaurus* is based on the mediolaterally-narrow, triangular morphology of the palatine bosses, elongate, narrow snout, and postcanine tooth row consisting of small, closely-packed teeth restricted to the maxillary midlength (Fig. 9C).

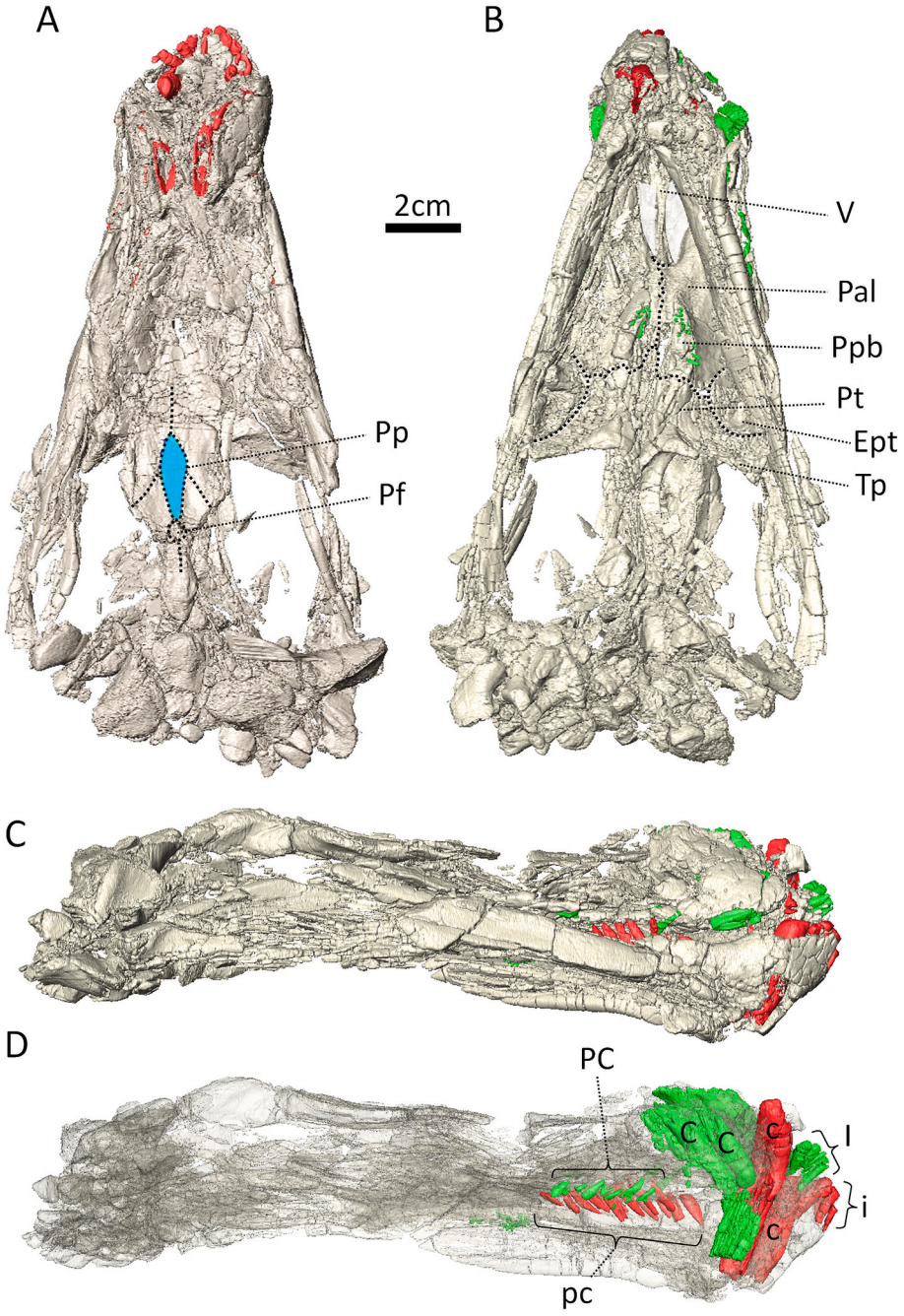


Fig. 9. Synchrotron scan-based 3D digital reconstructions and slides of skull NMQR389.
A, dorsal view; B, ventral view; C, right lateral view; D, left lateral view, skull in transparent to show the teeth (mirrored for comparison). Abbreviations: C, upper canine; c, lower canine; Ept, ectopterygoid; I, upper incisors; i, lower incisors; Pal, palatine; PC, upper postcanines; pc, lower postcanines; Pf, parietal foramen; Pp, prepariental; Ppb, pterygo-palatine boss; Pt, pterygoid; Tp, transverse process of the pterygoid; V, vomer.

3.3.2. Litho- and biostratigraphy of locality

Specimen NMQR 389 was found in 1948 by James Kitching on a farm that he recorded as "Oranje, in the Bethulie District". Confusingly, no farm in the Bethulie District is named "Oranje", whereas on 1:50000 topocastral and 1:250000 geological maps, the farm name is spelled "Orangia" (Fig. 10B). Orangia is a sub-division of the larger farm Tweefontein 508 located near Donovan's Kop on the northern bank of the Caledon River, east of Bethulie. The same locality has, in fact, also been referred to as "Tweefontein" or "Donovan's Kop, Tweefontein" in the literature (Reisz and Laurin, 1991; Hamley et al., 2021). To add to the confusion, Kitching provided separate entries for "Oranje" and "Tweefontein" in his faunal lists (Kitching, 1977: p. 96 and 98), which shed doubt on whether "Oranje" and Orangia are one and the same. We are however confident that Orangia (on Tweefontein 508) and Kitching's "Oranje" in the Bethulie District designate the same place because the other closest place to Bethulie called "Oranje" (with that spelling) is plot Oranje 254, in the Springfontein District (GPS coordinates: S30°20.3034 E25°29.601), where the exposures belong to the Ripplemead member of the Balfour Formation, in the *L. maccaigi-Moschorhinus* subzone of the *Daptocephalus* Assemblage Zone (Viglietti, 2016; Viglietti et al., 2017; Groenewald et al., 2019). Fieldwork at Oranje 254 confirmed that the fossil fauna there includes the genus *Dicynodontoides* (Fig. 4D) but excludes *Lystrosaurus*. This is inconsistent with the abundant *Lystrosaurus* fossils that Kitching (1964, 1977) reportedly

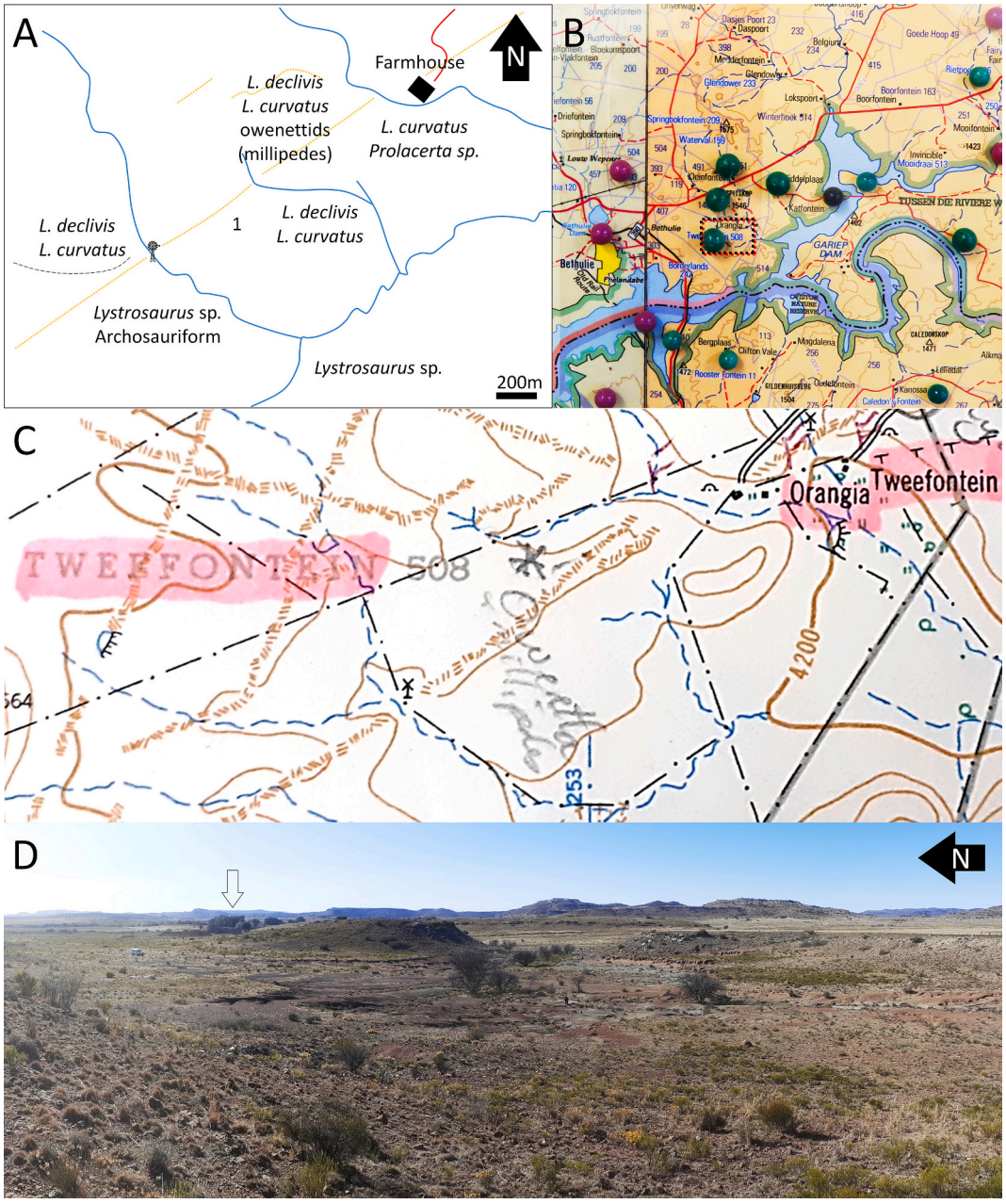


Fig. 10. All localities around the Orangia farmhouse at Tweefontein 508.
A, simplified map of the site. Roads are in solid red lines, dolerite dykes are in dotted orange lines, rivers are in solid blue lines. 1, locality where Kitching's pin is planted; taxa names indicate where faunal elements of the *Lystrosaurus declivis* Assemblage Zone have been found; B, excerpt of Kitching's wall-map (1972) showing the position of A in dotted lines. Green pins, "*Lystrosaurus* zone"; purple pins, "*Daptocephalus* zone"; C, excerpt of the topocadastral map of Bethulie used by Kitching on which the position of the millipedes he found is indicated; D, field photo of the locality where the millipedes were found (upper Palingkloof Member of the Balfour Formation, the location of the Orangia farmhouse corresponds to a group of trees north of the flat top hill indicated by an hollow arrow). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

discovered at "Oranje" and indicates that it is not where he found NMQR 389. Furthermore, Kitching's 1972 wall-map has no pin on Oranje 254, whereas Tweefontein 508 does (Fig. 10B). Linking Kitching's "Oranje" to Orangia is further supported by the fact that he found millipedes there (Kitching, 1977), which is indicated in pencil on Tweefontein 508 on a 1:50000 topocadastral map kept at the Evolutionary Studies Institute (Fig. 10C). These millipedes have recently been described and their provenance marked as Orangia (Groenewald et al., 2023). Finally, Orangia on Tweefontein 508 is a well-known *Lystrosaurus declivis* AZ locality, which is consistent with the fauna reported by Kitching (1977: p. 96) and there is, therefore, little doubt that "Oranje" is in fact Orangia, a portion of the farm Tweefontein 508 in the Bethulie district (GPS coordinates: S30°29.314 E26°03.001).

Our fieldwork at Tweefontein 508 around the Orangia farmhouse confirmed the presence of extensive low-lying exposures of the *Lystrosaurus declivis* Assemblage Zone strata (Fig. 10A). The fossil fauna includes the skulls of abundant small to medium-sized *Lystrosaurus* specimens, including *Lystrosaurus declivis* and *L. curvatus* (e.g. field n°46-06-2022; Fig. 4E), owenettids (e.g. Kitching, 1977; Reisz and Scott, 2002), *Prolacerta* sp. (field n°42-08-2022) and postcrania of a large archosauriform (possibly *Proterosuchus*, field n°23-09-2023, as indicated by the concave articular head of the femur, absence of 4th trochanter and relatively large size, which is a combination of characters unique to *Proterosuchus* among South African archosauriforms; Fig. 4F). The absence of large-bodied animals, and the individual ranges of the faunal elements listed above, support that Orangia exposes rocks of the uppermost part of the Palingkloof Member of the Balfour Formation (Viglietti, 2020). Despite thorough exploration of all the exposures on Tweefontein 508, no *Lystrosaurus maccaigi*, *Daptocephalus*, *Dicynodon*, or fragments thereof were recovered. Because the exact provenance of NMQR 389 is unknown, it is not completely excluded that it was found by Kitching on a *Daptocephalus* AZ-aged outcrop that no longer exists on Tweefontein 508, but this is highly unlikely given that we visited all the localities pinned on his 1972 wall map (and many other outcrops on Tweefontein 508) and confirmed that the fossil fauna is devoid of any *Daptocephalus* AZ elements (Fig. 10A). This makes the possible existence of a *Daptocephalus* AZ-aged outcrop at the site very unlikely. Additionally, although the largely flat landscape prevented us from drawing a proper stratigraphic log, it must be noted that the topographically lowest available outcrops on Tweefontein 508 are ten to twelve metres below the base of the lowest Katberg Formation. This is not enough to get down to the level of the *Daptocephalus* AZ, given the thickness of the deposits in the area and the near absence of dip (Viglietti, 2016; Smith and Botha-Brink, 2014; Smith et al., 2022). Overall, the new data presented here support that Kitching (1977) locality "Oranje" encompasses strata of the upper Palingkloof Member and is of *Lystrosaurus declivis* AZ age.

Unfortunately, several factors make confident attribution of NMQR 389 to an Orangia/Tweefontein 508 provenance questionable. First is the preservation of this specimen, which differs strongly in colouration from fossils found at this locality in our recent fieldwork (see NMQR 389 on Fig. 1C compared to Orangia specimens in Fig. 4E and F). Second is the presence of another fossil of distinctly Permian aspect among Kitching's collections from this site. This is NMQR 378, a small (~6 cm dorsal length), badly damaged skull identified in the collections as an indeterminate therocephalian. However, examination by C.K. (pers. obs., 2010) indicates that this specimen instead represents the Permian dicynodont *Dicynodontoides*. The dicynodont nature of the specimen is clearly indicated by the beak-like lower jaw with lateral dentary shelf and pterygoids forming an 'X'-shaped structure without a distinct transverse process, and referral to *Dicynodontoides* is supported by the extremely anterior position of the caniniform process, apparent absence of a mandibular fenestra, and bulging exposure of the pineal foramen at around mid-length of an otherwise narrow intertemporal bar. At present, it is uncertain how to explain these seemingly Permian specimens from a site that we are confident exposes Triassic strata only. Possibly, given the history of confusion surrounding the locality name, some specimens were mislabeled, and may in fact be from one or more different sites in the Bethulie area that include upper *Daptocephalus* AZ exposures. This casts doubt on whether NMQR 389 was found at Orangia at all, and thus, we cannot confidently identify NMQR 389 as representing a *Lystrosaurus declivis* AZ record of *Cyonosaurus*.

3.3.3. Taphonomic observations of NMQR389

Reworking was never proposed for NMQR 389, and given that the skull is highly fragmented and fragile (Fig. 9), it would not have eroded into a single coherent block, but in small fragments instead. Reworking can be safely excluded.

4. Discussion and conclusions

We review the location, geology, taphonomy, and identification of three gorgonopsians from the South African Main Karoo Basin that were reportedly discovered in the *Lystrosaurus declivis* AZ (i.e. in the Early Triassic following a placement of the PTB between the *Daptocephalus* and *Lystrosaurus declivis* AZs). All three specimens are confidently referred to *Cyonosaurus*, the most abundant genus of long-snouted, small-bodied gorgonopsian in the late Permian of southern Africa. Previously, *Cyonosaurus* was known to have ranged from the base of the *Cistecephalus* Assemblage Zone to the top of the *Dicynodon - Theriognathus* Subzone of the *Daptocephalus* Assemblage Zone (in the Ripplemead member of the Balfour Formation [Viglietti, 2020; Kammerer et al., 2023]). By re-investigating the localities and stratigraphic positioning of BP/1/3895, BP/1/4593, and NMQR 389, we have been able to confidently expand the range of *Cyonosaurus longiceps* well up into the extinction interval of the EPME (Fig. 11).

The geology and palaeontology of the provenance of BP/1/4593 and BP/1/3895 are consistent with *Cyonosaurus longiceps* occurring in the latest Permian. Accepting that the PTB coincides with the faunal turnover that happened between the *Daptocephalus* and *Lystrosaurus declivis* Assemblage Zones, as supported by most workers (Lucas et al., 1994; Benton and Newell, 2014; Smith and Botha-Brink, 2014; Botha and Smith, 2020; Shen et al., 2023), both specimens would be from layers just below the PTB (the Schoondraai and lowermost Palingkloof members of the Balfour Formation) (Fig. 11).

Specimen NMQR 389 poses a greater challenge, as no outcrop that James Kitching visited at Tweefontein 508 and around the Orangia farmhouse exposes rocks of the *Daptocephalus* AZ (Fig. 10A). This supports the idea that NMQR 389 comes from rocks of the *Lystrosaurus declivis* AZ, but a specimen of a late Permian dicynodont (NMQR 378) is also recorded from the same locality. This suggests that some fossils from nearby *Daptocephalus* AZ outcrops may have been mixed with those collected at Orangia, or later mislabelled. If Orangia is the correct locality, it would push the range of *Cyonosaurus* to the upper Palingkloof Member of the Balfour Formation, making this genus the only gorgonopsian surviving past the PTB marker (following the zircon dating by Botha et al., 2020). Gastaldo et al. (2020, 2021) alternatively proposed that the 252 million years PTB marker should be much higher up in the *Lystrosaurus declivis* AZ, which would place BP/1/4593, BP/1/3895, and NMQR 389 all well within the Permian even if the latter was part of the *Lystrosaurus declivis* AZ. Regardless of where the PTB is placed, *Cyonosaurus* can be shown to co-occur with the genus *Lystrosaurus* in the *L. maccaiggi – Moschorhinus* subzone of the *Daptocephalus* AZ. Occurrence in the *Lystrosaurus declivis* AZ, although not rejected outright, is substantially more questionable, given the problematic aspects of Kitching's "Oranje" fossils noted above. Given the lack of reliable evidence, the most conservative approach remains to consider that gorgonopsians became extinct at the end of the *Daptocephalus* AZ (and Permian) until proven otherwise.

The genus *Lystrosaurus* was historically regarded as an exclusively Triassic taxon (e.g., Du Toit, 1937; Groenewald and Kitching, 1995), and the co-occurrence of *Cyonosaurus* with *Lystrosaurus*, confirmed by our field work, accounts for the reason all three specimens were originally

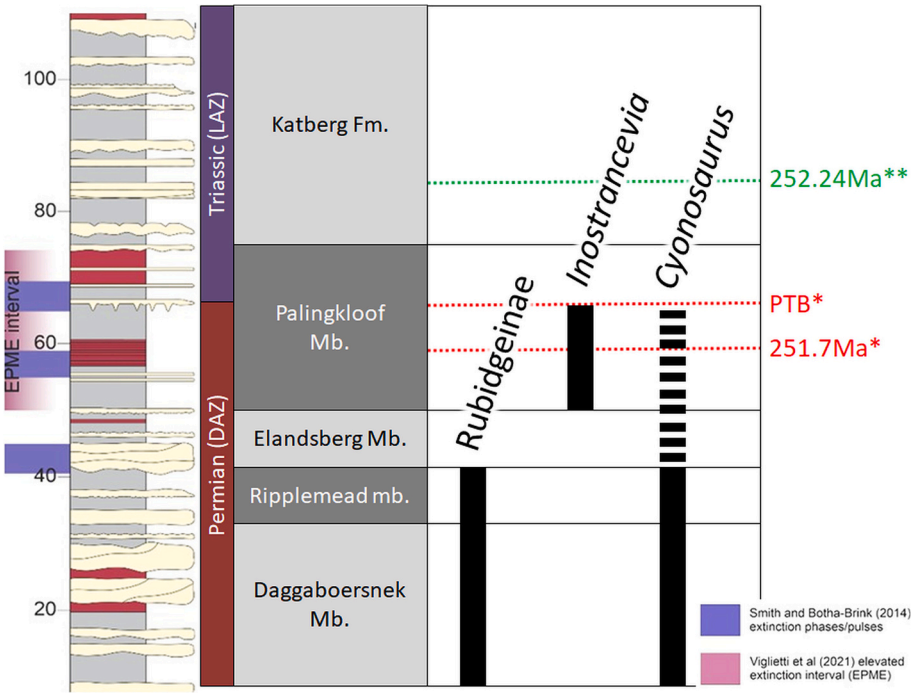


Fig. 11. Stratigraphic distribution of latest Permian South African gorgonopsians.
Ranges of the Rubigeinae and *Inostrancevia* after Kammerer et al. (2023). Range of *Cyonosaurus*, present study. Abbreviation: DAZ: *Daptocephalus* Assemblage Zone; EPME, end-Permian mass extinction; Fm, Formation; LAZ, *Lystrosaurus declivis* Assemblage Zone; Mb, member. *Position of the PTB and date after Botha et al. (2020); **Date after Gastaldo et al. (2020).

assigned to the "*Lystrosaurus* zone" by Kitching (1977). Furthermore, the boundary between the *Daptocephalus* and *Lystrosaurus* Assemblage Zones was historically placed at the base of the Palingkloof Member (Groenewald and Kitching, 1995), although in reality it is within the Palingkloof Member (Smith, 1995; Botha and Smith, 2007). As the taxonomy of *Lystrosaurus* species has been sorted (Grine et al., 2006) and Karoo biostratigraphy more refined, it became evident that *L. maccaigi* overlapped with *Daptocephalus*, and that both were stratigraphically older than the species *L. murrayi* and L. *declivis* (Smith, 1995; Lucas et al., 1994). The overlap in the ranges of *Lystrosaurus* and *Daptocephalus* in the upper Balfour Formation was later documented in detail and shown to encompass some 45 m of strata in the southern Karoo Basin that immediately preceded the EPME (Smith, 1995; Botha and Smith, 2007; Smith and Botha-Brink, 2014; Botha and Smith, 2020). Most recently, this overlap zone was hypothesised to be an early extinction phase of a more prolonged extinction event (Viglietti, 2020; Viglietti et al., 2021).

Kitching's "*Lystrosaurus* zone" was accordingly divided into the *Lystrosaurus declivis* Assemblage Zone and older L. *maccaigi* - *Moschorhinus* Subzone of the *Daptocephalus* Assemblage Zone (Botha and Smith, 2020). In the latter part of his career, Kitching (1995) acknowledged this overlap, but the "*Lystrosaurus* zone" label attached to specimens BP/1/4593, BP/1/3895, and NMQR 389 was not revised. We here provide an updated stratigraphic assessment of all three specimens demonstrating that at least two of them can be safely included in future research on Karoo faunal changes as coming from the upper *Daptocephalus* Assemblage Zone (lower Palingkloof Formation). The third is more problematic, but even if not part of the *Lystrosaurus declivis* Assemblage Zone (upper Palingkloof Formation), adds further support for survival of *Cyonosaurus* to at least the end of the Permian.

King (1991) and more recently Viglietti et al. (2021) proposed a protracted model of the Permian-Triassic mass extinction in the Karoo. Kammerer et al. (2023) further explored this possibility, proposing that invasive carnivores from the northern hemisphere, the inostranceviine gorgonopsians, ecologically replaced the local rubidgeines as the large-bodied carnivores as early as the beginning of the *L. maccaigi* - *Moschorhinus* Subzone of the *Daptocephalus* Assemblage Zone. In this respect, the survival of *Cyonosaurus longiceps* in this subzone is significant, as it becomes the only endemic gorgonopsian that survived this invasion (Fig. 11). Although James Kitching did not realise it, given the biostratigraphic knowledge available at this time, he had discovered the youngest occurrences of *Cyonosaurus longiceps*, and in fact the youngest occurrence of an endemic Karoo Basin gorgonopsian. This confirms that the ecological replacement of carnivores by immigrant taxa in the Karoo at the onset of the mass extinction was limited to large-bodied taxa and supports the idea that smaller bodied animals were more resilient to the early phases of the EPME, perhaps because they were more ecologically flexible, as hypothesised by Kammerer et al. (2023).

Declaration of Generative AI and AI-assisted technologies in the writing process

No AI was used during the preparation of this work.

CRediT authorship contribution statement

Julien Benoit: Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Christian F. Kammerer:** Writing – review & editing, Writing – original draft, Validation, Investigation. **Kathleen Dollman:** Writing – review & editing, Methodology. **David P. Groenewald:** Writing – review & editing, Investigation. **Roger M.H. Smith:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology.

Declaration of competing interest

The authors declare no competing interest.

Data availability

Data will be made available on request.

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References

Angielczyk, K.D., Kammerer, C.F., 2018. 5. Non-Mammalian synapsids: The deep roots of the mammalian family tree. In: Zachos, F., Asher, R. (Eds.), Mammalian Evolution, Diversity and Systematics. De Gruyter, Berlin, Boston, pp. 117–198.

Angielczyk, K.D., Liu, J., Sidor, C.A., Yang, W., 2022. The stratigraphic and geographic occurrences of Permo-Triassic tetrapods in the Bogda Mountains, NW China — Implications of a new cyclostratigraphic framework and Bayesian age model. J. Afr. Earth Sci. 195, 104655.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiol. 4, 150–162.

Bendel, E.-M., Kammerer, C.F., Kardjilov, N., Fernandez, V., Fröbisch, J., 2018. Cranial anatomy of the gorgonopsian *Cynariops robustus* based on CT-reconstruction. PLoS One 13 (11), e0207367.

Benoit, J., Kammerer, C., Smith, R.M.H., 2022. Like a Tyrannosaur in the Paleocene: Did a Gorgonopsian Survive the End-Permian Extinction? Book of Abstract of the 82nd Annual Meeting of the Society of Vertebrate Paleontology, 2–5 November, Toronto, Canada, pp. 80–81.

Benton, M.J., Newell, A.J., 2014. Impacts of global warming on Permo-Triassic terrestrial ecosystems. Gondwana Res. 25, 1308–1337.

Benton, M.J., Tverdokhlebov, V.P., Surkov, M.V., 2004. Ecosystem remodeling among vertebrates at the Permian-Triassic boundary in Russia. Nature 432, 97–100.

Botha, J., Smith, R.M.H., 2007. *Lystrosaurus* species composition across the Permian/Triassic boundary of South Africa. Lethaia 40, 125–137.

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

Botha, J., Huttenlocker, A.K., Smith, R.M.H., Prevec, R., Viglietti, P., Modesto, S., 2020. New geochemical and palaeontological data from the Permo-Triassic boundary in the South African Karoo Basin test the synchrony of terrestrial and marine extinctions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 540, 109467.

Brink, A.S., 1956. Note on a new skeleton of *Thrinaxodon liorhinus*. Palaeontol. Afr. 6, 15–22.

Cau, A., Beyrand, V., Voeten, D.F., Fernandez, V., Tafforeau, P., Stein, K., Barsbold, R., Tsogtbaatar, K., Currie, P.J., Godefroit, P., 2017. Synchrotron scanning reveals amphibious ecomorphology in a new clade of bird-like dinosaurs. Nature 552, 395.

Cohen, K.M., Finney, S.C., Gibbard, P.L., Fan, J.-X., 2013. The ICS international chronostratigraphic chart. Episodes 36, 199–204.

Colbert, E.D., 1973. Tetrapods and the Permian-Triassic transition. In: Logan, A., Hill, L. V. (Eds.), Memoir 2. Permian Systems and Their Mutual Boundary. Canadian Society of Petroleum Geologists, Calgary, pp. 481–492.

Du Toit, A.L., 1937. Our Wandering Continents: An Hypothesis of Continental Drifting. Oliver and Boyd, Edinburgh and London (366 pp).

Fernandez, V., Abdala, F., Carlson, K.J., Cook, D.C., Rubidge, B.S., Yates, A., Tafforeau, P., 2013. Synchrotron reveals early Triassic Odd couple: Injured Amphibian and Aestivating Therapsid Share Burrow. PLoS One 8, e64978.

Gastaldo, R.A., Kamo, S.L., Neveling, J., Geissman, J.W., Looy, C.V., Martini, A.M., 2020. The base of the *Lystrosaurus* Assemblage Zone, Karoo Basin, predates the end-Permian marine extinction. Nat. Commun. 11, 1428.

Gastaldo, R.A., Neveling, J., Geissman, J.W., Kamo, S.L., Looy, C.V., 2021. A tale of two Tweefonteins: what physical correlation, geochronology, magnetic polarity stratigraphy, and palynology reveal about the end-Permian terrestrial extinction paradigm in South Africa. GSA Bull. 134, 691–721.

Grine, F.E., Forster, C.A., Cluver, M.A., Georgi, J.A., 2006. Cranial variability, ontogeny and taxonomy of *Lystrosaurus* from the Karoo Basin of South Africa. In: Carrano, M. T., Gaudin, T., Blob, R., Wible, J. (Eds.), Amniote Paleobiology: Perspectives on the Evolution of Mammals, Birds, and Reptiles. University of Chicago Press, Chicago, pp. 432–503.

Groenewald, G.H., 1990. The use of palaeontology in the correlation of lithostratographic units in the Beaufort Group, Karoo Sequence of South Africa. Palaeontol. Afr. 27, 21–30.

Groenewald, G.H., Kitching, J.W., 1995. Biostratigraphy of the *Lystrosaurus* assemblage zone. In: Rubidge, B.S. (Ed.), South African Committee for Stratigraphy. Biostratigraphic Series, Biostratigraphy of the Beaufort Group (Karoo Supergroup). Council for Geoscience, Pretoria, pp. 35–39.

Groenewald, D.P., Day, M.O., Rubidge, B.S., 2019. Vertebrate assemblages from the north-Central Main Karoo Basin, South Africa, and their implications for mid-Permian biogeography. Lethaia 52, 486–501.

Groenewald, D.P., Day, M.O., Penn-Clarke, C.R., Rubidge, B.S., 2022. Stepping out across the Karoo retro-foreland basin: improved constraints on the Ecca-Beaufort shoreline along the northern margin. J. Afr. Earth Sci. 185, 104389.

Groenewald, D.P., Botha, J., Smith, R.M.H., 2023. Fossil millipedes associated with articulated tetrapod skeletons in the early Triassic Karoo Basin, South Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 617, 111508.

Hamley, T., Cisneros, J.C., Damiani, R., 2021. A procolophonid reptile from the lower Triassic of Australia. Zool. J. Linnean Soc. 192, 554–609.

Hoffman, A.C., Esterhuyse, D.J., 1965. Preliminary report on archaeological, palaeontological and anthropological field expeditions in the Orange River area. Navorsinge van die Nasionale Museum 2, 23–27.

Ivakhnenko, M.F., 2003. Eotherapsids from the east European placket. Paleontol. J. 37, S339–S465.

Kammerer, C.F., 2014. A redescription of *Eriphostoma microdon* Broom, 1911 (Therapsida, Gorgonopsia) from the *Tapinocephalus* assemblage zone of South Africa and a review of Middle Permian gorgonopsians. In: Kammerer, C.F., Angielczyk, K. D., Fröbisch, J. (Eds.), Early Evolutionary History of the Synapsida. Springer, Dordrecht, pp. 171–184.

Kammerer, C.F., 2015. Cranial osteology of *Arctognathus curvimola*, a short-snouted gorgonopsian from the late Permian of South Africa. Pap. Palaeontol. 1, 41–58.

Kammerer, C.F., 2016. Systematics of the Rubidgeinae (Therapsida: Gorgonopsia). PeerJ 4, e1608.

Kammerer, C.F., 2017. Anatomy and relationships of the south African gorgonopsian *Arctops* (Therapsida, Theriodontia). Pap. Palaeontol. 3, 583–611.

Kammerer, C.F., 2019. Revision of the Tanzanian dicynodont *Dicynodon huenei* (Therapsida: Anomodontia) from the Permian Usili Formation. PeerJ 7, e7420.

Kammerer, C.F., Masyutin, V., 2018. Gorgonopsian therapsids (*Nochnitsa* gen. nov. and *Viatkogorgon*) from the Permian Kotelnich locality of Russia. PeerJ 6, e4954.

Kammerer, C.F., Angielczyk, K.D., Fröbisch, J., 2011. A comprehensive taxonomic revision of *Dicynodon* (Therapsida: Anomodontia) and its implications for dicynodont phylogeny, biogeography, and biostratigraphy. Soc. Vert. Paleontol. Mem. 11, 1–158.

Kammerer, C.F., Smith, R.M.H., Day, M.O., Rubidge, B.S., 2015. New information on the morphology and stratigraphic range of the Middle Permian gorgonopsian *Eriphostoma microdon* Broom, 1911. Pap. Palaeontol. 2, 201–221.

Kammerer, C.F., Viglietti, P.A., Butler, E., Botha, J., 2023. Rapid turnover of top predators in African terrestrial faunas around the Permian-Triassic mass extinction. Curr. Biol. 33, 1–8.

King, G.M., 1991. Terrestrial tetrapods and the end Permian event: A comparison of analyses. Hist. Biol. 5, 239–255.

Kitching, J.W., 1964. On the *Lystrosaurus* zone and its fauna with special reference to some immature Lystrosauridae. Palaeontol. Afr. 11, 61–76.

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 (131 pp).

Kitching, J.W., 1995. Biostratigraphy of the *Dicynodon* Assemblage Zone. In: Rubidge, B. S., Johnson, M.R., Kitching, J.W., Smith, R.M.H., Keyser, A.W., Groenewald, G.H. (Eds.), Biostratigraphy of the Beaufort Group (Karoo Supergroup). South African Committee for Stratigraphy, Pretoria, pp. 29–34.

Laurin, M., 1998. New data on the cranial anatomy of *Lycaenops* (Synapsida, Gorgonopsidae) and reflections on the possible presence of streptostyly in gorgonopsians. J. Vertebr. Paleontol. 18, 765–776.

Lucas, S.P., Cheng, Z., Smith, R.M.H., 1994. The *Dicynodon-Lystrosaurus* overlap zone and the Permian-Triassic boundary in nonmarine strata. J. Vertebr. Palaeontol. 14 (suppl, to 3), 34A.

Mirone, A., Brun, E., Gouillart, E., Tafforeau, P., Kieffer, J., 2014. The PyHST2 hybrid distributed code for high speed tomographic reconstruction with iterative reconstruction and a priori knowledge capabilities. Nucl. Inst. Methods Phys. Res. B 324, 41–48.

Neveling, J., 2004. Stratigraphic and sedimentological investigation of the contact between the *Lystrosaurus* and the *Cynognathus* assemblage zones (Beaufort Group: Karoo Supergroup). Bull. Geol. Surv. S. Afr. 137, 164.

Nicolas, M., Rubidge, B.S., 2010. Changes in Permo-Triassic terrestrial tetrapod ecological representation in the Beaufort Group (Karoo Supergroup) of South Africa. Lethaia 43, 45–59.

Olivier, C., Battail, B., Bourquin, S., Rossignol, C., Steyer, J.-S., Jalil, N.-E., 2019. New dicynodonts (Therapsida, Anomodontia) from near the Permo-Triassic boundary of Laos: Implications for dicynodont survivorship across the Permo-Triassic mass extinction and the paleobiogeography of southeast Asian blocks. J. Vertebr. Paleontol. 39, e1584745.

Paganin, D., Mayo, S., Gureyev, T.E., Miller, P.R., Wilkins, S.W., 2002. Simultaneous phase and amplitude extraction from a single defocused image of a homogeneous object. J. Microsc. 206, 33–40.
Page, T.C., 1983. Pure and Applied Sedimentology of the Ecca-Beaufort Rocks of the Drakensberg Pumped Storage Scheme. Unpublished MSc thesis. University of Natal, Pietermaritzburg, South Africa (204 pp).
Reisz, R., Laurin, M., 1991. *Owenetta* and the origin of turtles. Nature 349, 324–326.
Reisz, R.R., Scott, D., 2002. *Owenetta kitchingorum* sp. nov., a small parareptile (Procolophonia: Owenettidae) from the lower Triassic of South Africa. J. Vertebr. Paleontol. 22, 244–256.
Rochín-Bañaga, H., Gastaldo, R.A., Davis, D.W., Neveling, J., Kamo, S.L., Looy, C.V., Geissman, J.W., 2023. U-Pb dating of pedogenic calcite near the Permian–Triassic Boundary, Karoo Basin, South Africa. GSA Bull. https://doi.org/10.1130/B36968.1.
Rubidge, B.S., 1995. Biostratigraphy of the Beaufort Group (Karoo Supergroup). Department of Mineral and Energy Affairs, Geological Survey, p. 46.
Schoch, R.R., Rubidge, B.S., 2004. The amphibamid *Micropholis* from the *Lystrosaurus* Assemblage Zone of South Africa. J. Vertebr. Paleontol. 25, 502–522.
Sennikov, A.G., Golubev, V.K., 2006. Vyazniki Biotic Assemblage of the terminal Permian. Paleontol. J. 40, S475–S481.
Shen, J., Chen, J., Yu, J., Algeo, T.J., Smith, R.M.H., Botha, J., Frank, T.D., Fieldging, C. R., Ward, P.D., Mather, T.A., 2023. Mercury evidence from southern Pangea terrestrial sections for end-Permian global volcanic effects. Nat. Commun. 14, 6.
Sigogneau, D., 1970. Révision Systématique des Gorgonopsiens Sud-africains. Editions du Centre national de la recherche scientifique, Paris, p. 407.
Sigogneau-Russell, D., 1989. Theriodontia I. Handbuch der Paläoherpetologie. 17 B/I. Gustav Fischer Verlag, Stuttgart, p. 127.
Smith, R.M.H., 1995. Changing fluvial environments across the Permian-Triassic boundary in the Karoo Basin, South Africa and possible causes of tetrapod extinctions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 117, 81–104.
Smith, R., Botha, J., 2005. The recovery of terrestrial vertebrate diversity in the South African Karoo Basin after the end-Permian extinction. C. R. Palevol. 4, 623–636.
Smith, R.M.H., Botha-Brink, J., 2014. Anatomy of a mass extinction: sedimentological and taphonomic evidence for drought-induced die-offs at the Permo-Triassic boundary in the main Karoo Basin, South Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 316, 99–118.
Smith, R.M.H., Ward, P.D., 2001. Pattern of vertebrate extinctions across an event bed at the Permian/Triassic boundary in the Main Karoo Basin of South Africa. Geol. 29, 1147–1150.
Smith, R.M.H., Rubidge, B.S., Day, M.O., Botha, J., 2020. Introduction to the tetrapod biozonation of the Karoo Supergroup. S. Afr. J. Geol. 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. Palaeogeogr. Palaeoclimatol. Palaeoecol. 604, 1–19.
Viglietti, P.A., 2016. Stratigraphy and Sedimentary Environments of the Late Permian *Dicynodon* Assemblage Zone (Karoo Supergroup, South Africa) and Implications for Basin Development. Unpublished PhD Thesis. University of the Witwatersrand, Johannesburg, South Africa (266 pp).
Viglietti, P.A., 2020. Biostratigraphy of the *Daptocephalus* assemblage zone (Beaufort Group, Karoo Supergroup) South Africa. S. Afr. J. Geol. 123, 191–206.
Viglietti, P.A., Smith, R.M.H., Angielczyk, K.D., Kammerer, C.F., Fröbisch, F., Rubidge, B. S., 2016. The *Daptocephalus* Assemblage Zone (Lopingian), South Africa: A proposed biostratigraphy based on a new compilation of stratigraphic ranges. J. Afr. Earth Sci. 113, 153–164.
Viglietti, P.A., Rubidge, B.S., Smith, R.M.H., 2017. Revised lithostratigraphy of the Upper Permian Balfour and Teekloof formations of the main Karoo Basin, South Africa. S. Afr. J. Geol. 120, 45–60.
Viglietti, P.A., Benson, R.B.J., Smith, R.M.H., Botha, J., Kammerer, C.F., Skosan, Z., et al., 2021. Evidence from South Africa for a protracted end-Permian extinction on land. PNAS 118 (17), e2017045118.
Ward, P.D., Botha, J., Buick, R., De Kock, M.O., Erwin, D.H., Garrison, G.H., Kirschvink, J.L., Smith, R.M.H., 2005. Abrupt and gradual extinction among late permian land vertebrates in the Karoo Basin, South Africa. Science 307, 709–714.